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 late Devonian (latest Famennian, 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) in 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.

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 Repository¹). 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 genus

GSA Data Repository item 2015350, 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.

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 873334; 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.

¹GSA Data Repository item 2015350, palynology, stratigraphy, additional images, taphonomy, and climate data, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.
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 spor 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 lemura (Fig. 4E), Contagiosporites optivus (Fig. 4F), Nikitinsporites spitzbergensis (Fig. 4D), and Triangulatisporites rootii (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), Enigmaphyton axes, and Protelepidoendropsis 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.
Correct, showing dominant east-west compression. Localities AF2, AF3: Outlines of casts trees at three forest localities. Locality AF1: Figure 6. Comparison of spacing of upright short relative to the long axis of the stem ellipses affected the sediments. Average shortening of the have been distorted into ellipses with the long axis john and Dallmann, 2014). Upright stem sections was east to west, infilling the fault trough (Piep- west of the Munindalen thrust (Fig. 1B), where (Figs. 1 and 6; Item DR4). Eight further upright stems were mapped demonstrate monospecific stands of Proteolepi- dendropity 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 m2 (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 ba- sis into which the Plantekløfta Formation was deposited. Palynological samples in the up- per parts of the locality AF2 paleosol contain amorphous organic matter indicating a strati- fied 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 lysocpd 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 cladoxyloids (height ~8–12 m, density 900–2100 per hectare) and rhizomatous aneurophytales. At Gilboa, with a considerable exposure of the forest floor, only one, perhaps drifted, arborescent lysocpd specimen was found (Stein et al., 2012). While the Gilboa Forest demonstrates ecological complexity, the Munindalen lysocpd forests demonstrate that monospecific stands formed parts of the ecological landscape. Although the in-situ Plantenklofta Formation forests are of early Frasnian age, the first occurrence of drifted *Protolepidodendropsis* trunks is in the late Givetian lower part of the Fiskeklofta 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 archaeoportidalean trunks in separate discrete but superficially similar dark paleosols horizons within the Plantenklofta 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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