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 pseudosporochlaenales (small to medium trees showing some morphological similarity to living tree ferns and palms) and archaeopteridales (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, ca. 380 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 Hoeg. 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: archaeopteridales, pseudosporochlaenales, and lycopsids (Meyer-Berthaud et al., 2010). Records of arborescent pseudosporochlaenalean 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., 2010). Archaeopteridales 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 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 late Givetian–early Frasnian Mimerdalen Subgroup and a critique of the previous Famennian age attribution is provided in Item DR3. The prominent mudstone at the base of the Plantekløfta 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 Geneso
Taghanic transgressive flooding. The prominent mudstone at the top of the Fiskeklofta 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.

### Planteklofta 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 sporopollens. 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 Canfield, 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 Planteklofta 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 lemurator (Fig. 4E), Contagisporites optivus (Fig. 4F), Nikitinsporites spitsbergensis (Fig. 4D), and Triangulatisporites rootii (Items DR2 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), Estigmaphyton axes, and Protolepidodendron typical of the “Upper Svalbardia Sandstone” (e.g., Vogt, 1941; Høeg, 1942) from locality PK3 (Fig. 1B) in beds mapped as Planteklofta Formation by Dallmann et al. (2004). Ibyka in particular suggests an age no younger than early Frasnian.
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 tree casts 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* Höeg 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 Höeg (1942, as *Bergeria mimerensis* from Höeg’s “Planteiøfta” and “Plantergygen” 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 33% 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 lycopodisp 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 aneurophytales. At Gilboa, with a considerable exposure of the forest floor, only one, perhaps drifted, arborescent lycopodisp specimen was found (Stein et al., 2012). While the Gilboa Forest demonstrates ecological complexity, the Munindalen lycopodisp 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 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 Mimerdal Subgroup.

We have also recognized the presence of in-situ vertical archaeopteridalean trunks in separate discrete but superficially similar dark paleosol horizons within the Planteklofta 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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