



Ordovician-Devonian lichen canopies before evolution of woody trees

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ABSTRACT

Devonian evolution of woodlands has been envisaged as a protracted increase in size of vascular plants, which can be reconstructed from fossil stumps and trunks. However, Late Silurian and Early Devonian nematophytes such as *Prototaxites* would have towered over land plants, including vascular plant trees, in the same fossil plant assemblage, until finally overtaken by vascular land plants during the Early Carboniferous. Nematophytes lack tissues of vascular plants, and some have spherical photobionts encircled and indented by hyphae, as in lichens. Nematophytes were not monolithic poles, but branched, and trunk spacing in paleosols is evidence that they formed closed canopies. Depths of root and hyphal bioturbation and pedogenic calcite precipitation in paleosols though time increase with greater height of trees. In addition to large non-vascular trunks and early land plants in Ordovician to Devonian paleosols, there also were extensive, nutrient-gathering, networks of glomeromycotan mycorrhizae. An Ordovician-Silurian “age of lichens”, when nematophytes were the tallest elements of terrestrial vegetation and soils were riddled with mycorrhizae, may have nurtured and sheltered Ordovician-Silurian land plants and then Devonian woody plants. Fungi preceded and facilitated the evolution of early land plants.

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1. Introduction

Ecological tiering is most inspiring in tropical rain forests. On Barro Colorado Island, Panama, for example, a canopy of almindro (*Dipteris panamensis*) about 30 m tall, with emergents to 40 m, rises above a tier of palms (*Astrocaryum standleyanum*, *Scheelea zonensis*) 10–20 m tall, and shrubs of *Psychotria* spp. up to 2 m tall, but ground cover is limited by activity of leaf-cutter ants and termites (Leigh, 1999). Comparable reconstructions of fossil forests can be made from known allometric relationships between tree height and trunk diameter at breast height (Niklas, 1994), checked against complete fossil trees (Stein et al., 2007, 2012; Retallack and Huang, 2011; Retallack and Landing, 2014). Tiering also is known below ground in soils, with buttress roots in surface layers, tap roots deeper (Leigh, 1999), and fungal rhizines reaching down to the water table and limits of soil oxygenation (Graham et al., 2010a, 2010b). Depth of bioturbation and the declining acidity of soil water toward calcic horizons in soils reflect both productivity (Breecker and Retallack, 2014), and stature of vegetation (Retallack and Huang, 2011). Thus, paleosols provide an additional line of evidence for vegetation height and productivity in deep time.

Comparable marine tiering in deep time has been reconstructed using similar methods. Stalked crinoids and tall sponges

exploit the water column a meter or so above bottom, with bryozoans, corals, brachiopods and clams below them. The height above the sea floor exploited by filter feeders increased from Cambrian to Ordovician (Bottjer and Ausich, 1986). Below the sea floor, Early Cambrian bioturbation was shallow (Jensen et al., 2007), but deep burrows evolved by Ordovician time (Sheehan and Schiefelbein, 1984). Just as Cambrian-Carboniferous marine communities evolved both higher and deeper tiers and corresponding rise in productivity (Bottjer and Ausich, 1986), so too did life on land.

In contrast with early Paleozoic fossil plants, which are rare and usually removed from growth position (Lang, 1937; Edwards and Axe, 2012; Edwards et al., 2013), paleosols provide evidence of Paleozoic vegetation in growth position on many stratigraphic horizons from root traces and depth to carbonate nodules (Edmunds, 1997; Driese et al., 1997; Driese and Mora, 2001; Hillier et al., 2008; Retallack, 2009a,b, Retallack, 2015a,b). Many fossil plant localities yield nematophytes much larger than associated vascular land plants (Hueber, 2001; Hillier et al., 2008, Retallack, 2015a,b, 2020). This study reviews such evidence, and provides new evidence of nematophyte traces within paleosols of Ordovician and Silurian age to reconstruct the long-term evolution of tiers below and above ground from Cambrian microbial earths to Carboniferous forest ecosystems.

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2. Material and methods

This study is a compilation of data on the size of fossil plants and soils. Paleosol data includes depth to carbonate (calcic or Bk horizon), corrected for burial compaction scaled to thickness of overburden (Sheldon and Retallack, 2001), from comprehensive accounts of Cambrian to Devonian paleosols in Australia (Retallack, 2009a,b), Ordovician paleosols of Pennsylvania and

Tennessee (Retallack, 2015a), Silurian paleosols of Pennsylvania (Retallack, 2015b), and Devonian–Carboniferous paleosols of Pennsylvania and New York (Retallack, 2011a). A visual survey of root traces and soil carbonate in paleosols from localities listed in Table 1, is presented in Figs. 1–5.

Fossil nematophyte data (Supplementary information Table S1) includes stem diameter at breast height (1.4 m) fossil trunks (Retallack and Landing, 2014; Retallack, 2020). Diameter at breast

Table 1

Geographic coordinates of fossil root traces and paleosols considered in this study.

Formation	Age	Soil pedotype	Locality	Reference	Fig.	Coordinates
John Day Form.	Eocene	Luca clay	Clarno, Oregon	Retallack et al., 2000	1C	44.935226°N 120.418859°W
Bald Hill Clayst.	Triassic	Long Reef clay	Long Reef, N,S,W	Retallack, 1997a	1A,B	33.742558°S 151.316718°E
Oneonta Format.	Devonian	Durso silt loam	Unadilla, New York	Retallack, 2011a	1D	42.311018°N 75.355649°W
Bloomsburg F.	Silurian	Brenda clay	Palmerton, Pennsylvania	Retallack, 2015b	2A,F	41.044748°N, 76.850463°W
Bloomsburg F.	Silurian	Barry silty clay loam	Palmerton, Pennsylvania	Retallack, 2015b	2B	41.044748°N, 76.850463°W
Bloomsburg F.	Silurian	Debbie silty clay loam	Palmerton, Pennsylvania	Retallack, 2015b	2C	41.044748°N, 76.850463°W
Bloomsburg F.	Silurian	Palmerton silty clay	Palmerton, Pennsylvania	Retallack, 2015b	2D-E	41.044748°N, 76.850463°W
Bloomsburg F.	Silurian	Lisette silty clay loam	Palmerton, Pennsylvania	Retallack, 2015b	5A-B	41.044748°N, 76.850463°W
Juniata Form.	Ordovician	Potters Mills clay	Potters Mills Pennsylvania	Retallack, 2015a	3A-D	40.760233°N, 77.614799°W
Juniata Form.	Ordovician	Bedford clay	Beans Gap, Tennessee	Retallack, 2015a	3F-G	36.351154°N, 83.397225°W
Juniata Form.	Ordovician	Bedford clay	Loysburg, Pennsylvania	Retallack, 2015a	3E	40.159054°N, 78.370507°W
Bays Form,	Ordovician	Morrison clay	Rogersville, Tennessee	Retallack, 2015a	3B	36.342949°N, 82.950278°W
Tmblagooda Ss.	Ordovician	Marla silt loam	Kalbarri, West. Australia	Retallack, 2009a	3C	27.818909°S 114.512616°E
Moodlatana F.	Cambrian	Irkili silty clay loam	Ten Mile Creek, S. Australia	Retallack, 2009b	4A	31.256773°S 138.942178°E
Moodlatana F.	Cambrian	Viparri silty clay loam	Ten Mile Creek, S. Australia	Retallack, 2009b	4B	31.256978°S 138.941532°E
Moodlatana F.	Cambrian	Mindi silty clay loam	Ten Mile Creek, S. Australia	Retallack, 2009b	4C-F	31.256978°S 138.941532°E

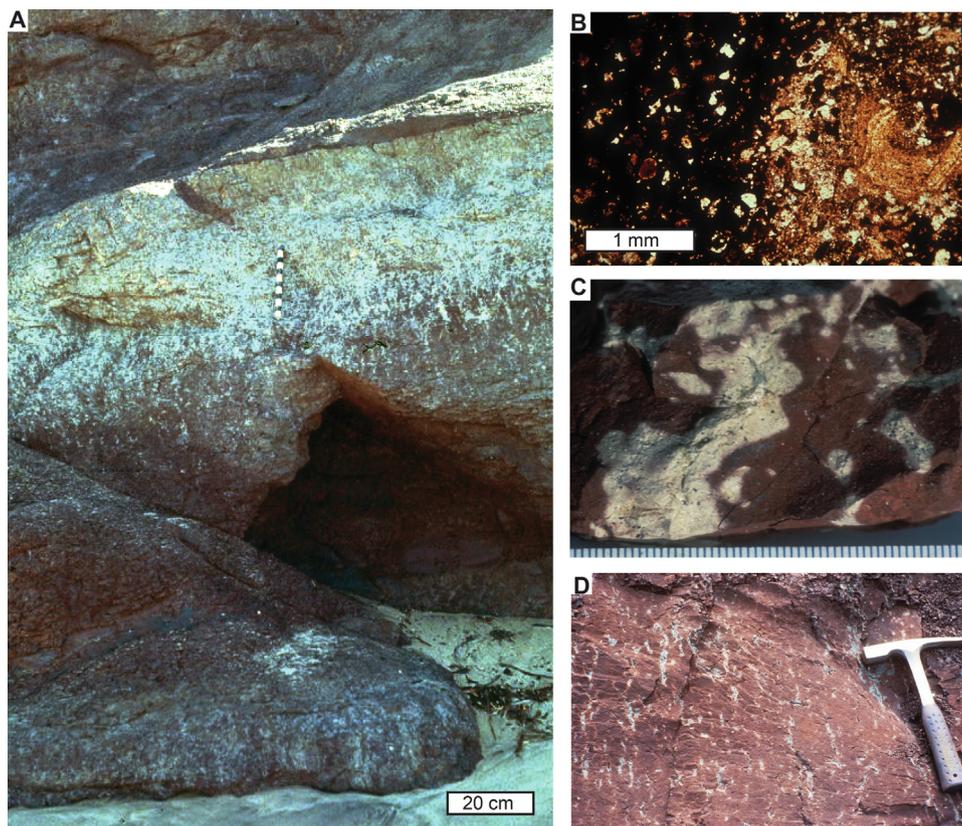


Fig. 1. Drab-haloed root traces of Devonian and younger geological age: (A) grey surface continuing below sharp top down into drab-haloed root traces of the type Long Reef clay paleosol, in the Bald Hill Claystone (Early Triassic) at Long Reef, New South Wales; (B) petrographic section through a root trace with concentric clayey fill and diffuse drab-halo outward into red matrix of the type Long Reef clay paleosol; (C) drab-haloed root trace, with root hole filled with white clay, from the type Luca clay paleosol, in the Big Basin Member of the John Day Formation (late Eocene) near Clarno, Oregon; (D) drab-haloed root traces, with birnessite-filled root holes, of Durso clay paleosol of Oneonta Formation (Late Devonian, Frasnian) near Unadilla, New York. Thin section R373 (B) and hand specimen R417 (C) in the Condon Collection of the Museum of Natural and Cultural History, University of Oregon. Scale in C is graduated in mm. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

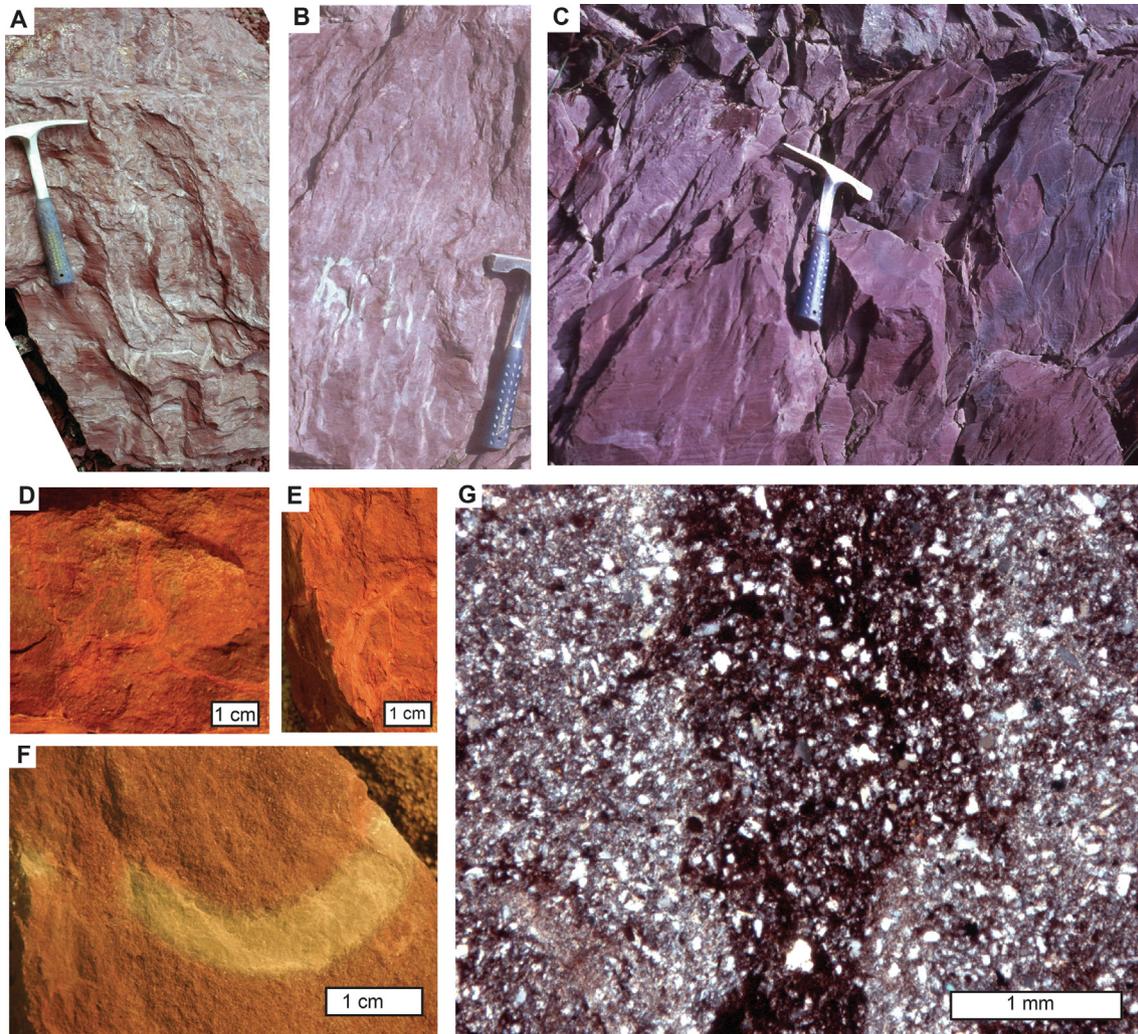


Fig. 2. Drab-haloed non-vascular mottles and vascular plant rhizome traces of Silurian (Ludlow) age, all from a measured section of the Bloomsburg Formation south of Palmerton, Pennsylvania; (A) Mn-rimmed drab mottle in Brenda clay paleosol at 18.4 m; (B) red pedotubules in upper part and Mn-rimmed drab mottles in lower part of Barry silty clay loam paleosol at 72.9 m; (C) red pedotubules in surface of Debbie paleosol at 59.1 m; (D-E) vascular plant rhizome traces from Palmerton silty clay paleosol at 142.7 m; (F) non-vascular tubular mottle from Brenda clay paleosol at 65 m; (G) thin section of non-vascular root-like structure with lateral branches from A horizon of Barry silty clay loam paleosol at 71.6 m. Specimens in Condon Collection of Museum of Natural and Cultural History, University of Oregon are F116316 (D), F116315 (E), F116308B (F), R2269 (G). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

height is used to calculate height by an allometric equation for vascular land plants (Niklas, 1994), and surprisingly, the same equation works for those few complete nematophyte trunks known (Retallack and Landing, 2014). This discovery of load-bearing taper in *Prototaxites*, can be added to anatomical observations negating the idea that *Prototaxites* grew horizontally, or was a rolled mat (Taylor et al., 2010). As was shown many years ago by Walton (1936), the diameter of fossil plants is unaffected by burial compaction, unlike thickness which is only a tenth of an original trunk diameter for many Paleozoic plants (Retallack, 1994). Diameters of land plants, both vascular and non-vascular, were compiled from a variety of sources (Supplementary Table S2). Only the largest trunks for each locality were measured for diameter (B in cm) at breast height (1.4 m), or proportional taper point of smaller plants (Retallack and Landing, 2014). Plant heights (H in m) were then estimated using allometric growth Eq. (1) of Niklas (1994, with $R^2 = 0.95$, standard error ± 0.9 m), based on 670 modern species of trees of all kinds.

$$H = 21.9B^{0.896} \quad (1)$$

This equation applied to the diameter of complete fossil nematophyte and cladoxyl tree trunks, correctly predicted their observed length (Stein et al., 2007, 2012; Retallack and Huang, 2011; Retallack and Landing, 2014).

3. Early Palaeozoic root traces and calcic horizons

Two especially important indices of vegetation height preserved in paleosols are drab-haloed root-traces and depth to carbonate nodules (calcic or Bk horizon). Pedogenic carbonate can be distinguished from marine carbonate nodules by the following criteria: nodules arranged in diffuse horizons below the upper surface of the bed at a distance that is similar within the same formation, micritic calciasepic and replacive fabric in thin section, growth both truncating and truncated by burrows and cracks in the same bed, and strong correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of different nodules within the same beds (Retallack, 2008, 2013, 2015a, 2015b).

Root traces and rhizomes are only known in middle Silurian (Ludlovian) and geologically younger soils (Retallack, 2015b), and thalli and rhizoids of non-vascular plants are as old as Middle

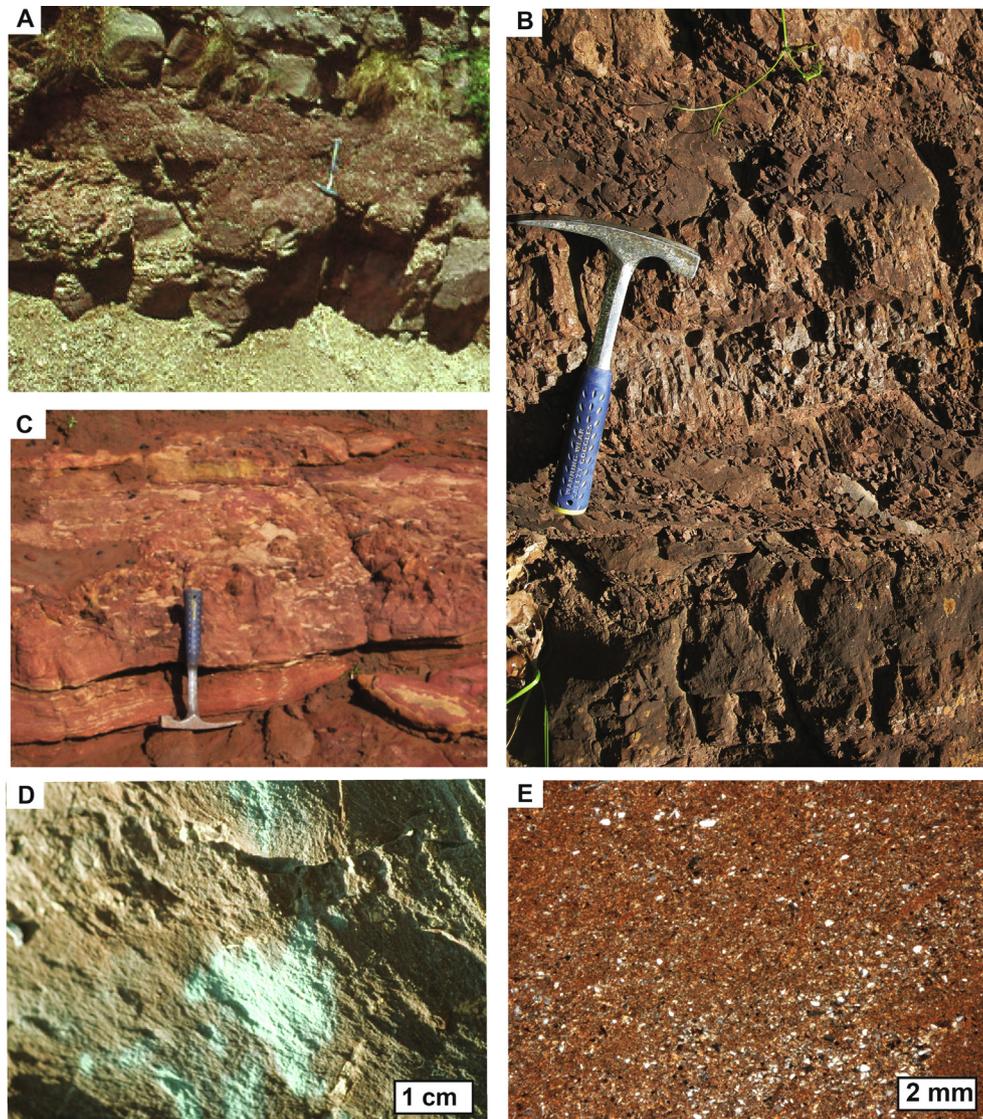


Fig. 3. Drab haloed nematophyte and filament traces of Ordovician age; (A) Potters Mills clay paleosol, with drab mottles in surface and calcareous nodules near hammer-head, at 617 m in the Late Ordovician (Hirnantian) Juniata Formation near Potters Mills, Pennsylvania; (B) Morrison clay paleosol above Faust Flat paleosols at 106 m of Late Ordovician (Sandbian) Bays Formation near Rogersville, Tennessee; (C) Marla silt loam paleosol, with drab mottles and calcareous nodules at hammer handle, in Early Ordovician (Floian), Tumblagooda Sandstone at 447.1 m near Ross Graham Lookout, Kalbarri National Park, Western Australia; (D) drab mottles in surface of Potters Mills clay paleosol (A, above); (E) drab mottles and clay skins in thin section of Bedford clay paleosol at 58 m in late Ordovician (Katian) Juniata Formation near Loysburg, Pennsylvania. Specimens in Condon Collection of Museum of Natural and Cultural History, University of Oregon are R2298 (E).

Ordovician (Darriwillian: Retallack, 2000, 2015a, 2020), but well drained, red paleosols as old as Ediacaran also have comparable filamentous disruption of bedding reaching deeply into paleosols (Fig. 4: Retallack, 2008, 2009b, 2011b, 2012b, 2013). Fossil stumps are a clear indication of tree size, and many of these rarities have been preserved in museums and fossil parks (Beckett, 1845; Cleal and Thomas, 1995; Calder et al., 2006; Stein et al., 2020). Drab-haloed root traces also reveal plant stature by their size and density, and are ubiquitous in paleosols (Fig. 1). The root trace itself is marked by a clearly defined tubular hole, often filled with clay, but extending beyond that into the red clayey paleosol matrix is a halo of green clayey matrix with identical petrographic texture and comparable analyzed values of total iron (Fig. 1B). Within the green-halo iron is in the ferrous oxidation state, but in the matrix it is in the oxidized or ferric oxidation state (Retallack et al., 2000; Retallack, 2011b). Such features are superficially similar to surface-water gley features in modern soils, but retention of iron is unlike such open system alteration, and deeply penetrating

root systems are also evidence against original waterlogging. Nor can these features be explained as holes filled with drab-colored material from above because of the gradational outer boundary. They are not rhizospheres either because they are on both large and small roots, and scale to volume, rather than surface area of the root (Retallack, 2011b). Drab-haloes were most likely formed by burial gleization, a process after burial in which anaerobic microbes oxidized remaining carbon of the root coupled with chemical reduction of iron oxides in the soil matrix (Retallack et al., 2000). Not only do the root traces reaching deep into well drained paleosol, but the humic surface of the paleosol is reduced to grey green color (Figs. 1A, 3C, 4A, 4C). This origin implies that the drab-haloed root traces represent the last crop of organic matter in the paleosol, as earlier dead and decayed root traces lacked microbial fuel for gleization.

Drab-haloed root traces are identical but larger than reduction haloes around fungal rhizines and cyanobacterial ropes in Cambrian to Silurian paleosols (Figs. 2–4), which been given the

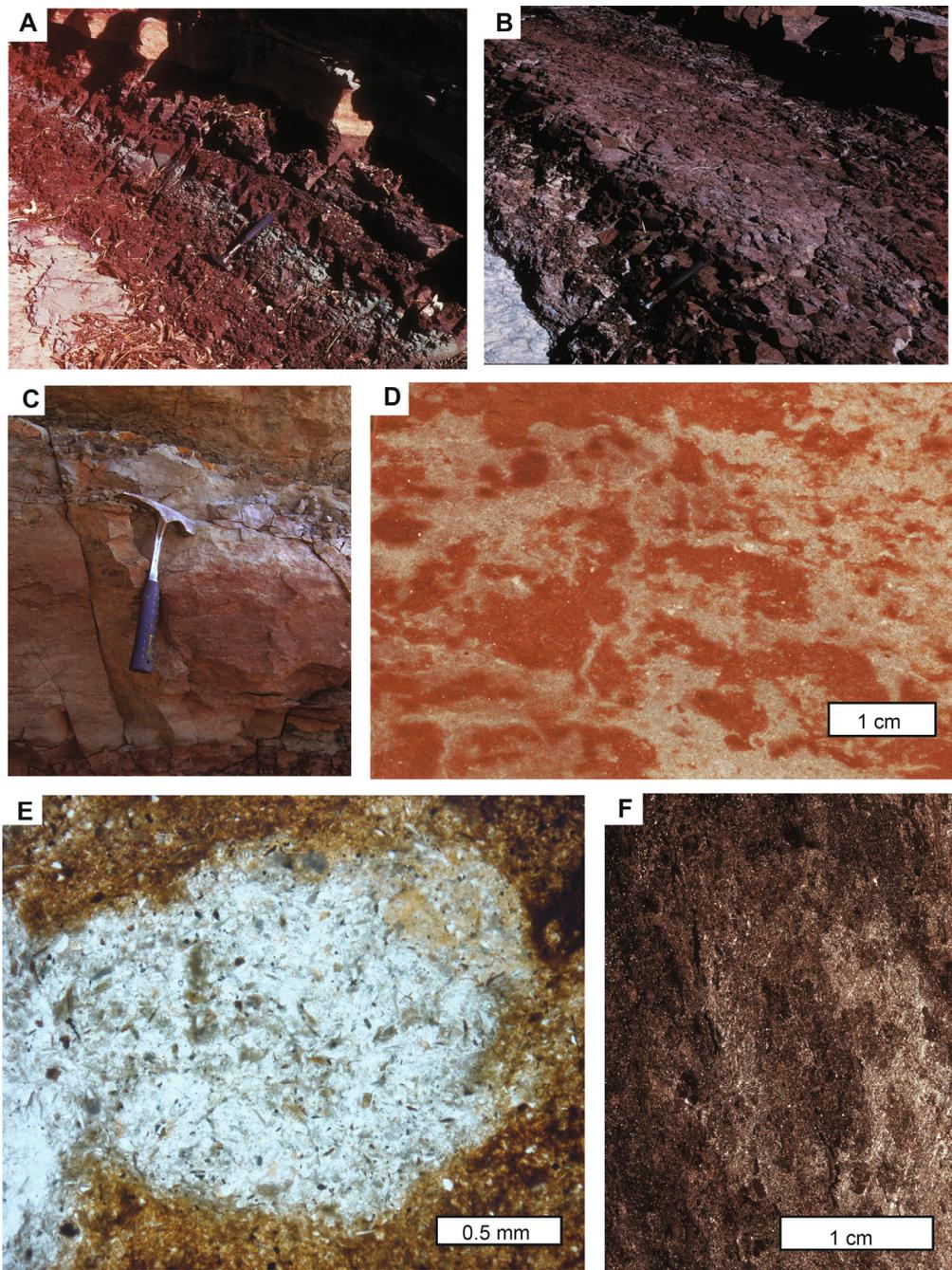


Fig. 4. Drab haloed filament traces of Middle Cambrian age, all from the Moodlatana Formation in Ten Mile Creek, Wirrealpa Station, South Australia; (A) drab top and filament traces down to horizon of calcareous nodules in type Irkili silty clay loam paleosol at 3610 m; (B) drab top and filament traces down to horizon of small calcareous nodules in Viparri silty clay loam paleosol at 3602 m; (C) drab top and filament traces in type Mindi silty clay loam paleosol at 3605 m; (D) cut slab and (E-F) thin sections of filament traces (*Prasinema gracile*) in A horizon of type Mindi silty clay loam paleosol at 3605 m. Specimens in Condon Collection of Museum of Natural and Cultural History, University of Oregon are F142257 (D-F).

ichnogeneric name *Prasinema* (Retallack, 2011b). Drab-haloed filament traces indicate the reach of hyphae and microbes much deeper within soils than early vascular and non-vascular plants with rhizoids. Drab-haloed traces with multiple filaments in the Late Silurian Bloomsburg Formation of Pennsylvania (Fig. 2A-C, F) can be attributed to *Prototaxites*, a nematophyte interpreted as a large lichenized fungus (Selosse, 2002; Retallack and Landing, 2014), and are much larger and more deeply reaching than known Late Silurian land plants in the same formation (Retallack, 2015b). Comparable disparity between land plant and nematophyte trunk bases

have been noted in other Siluro-Devonian paleosols (Hueber, 2001; Driese and Mora, 2001; Hillier et al., 2008).

Drab-haloed root and filament traces in paleosols are difficult to quantify, but there is a simpler measure of plant productivity in paleosols from the depth to pedogenic carbonate nodules (Figs. 2B, 3A-C; 4A-B). Drab-haloed root traces are found in both calcareous and non-calcareous soils and paleosols, but do not penetrate far beyond the level of carbonate nodules (calcic or Bk horizon). In modern soils the depth to nodules has been shown to correlate with mean annual precipitation (in mm), and also with

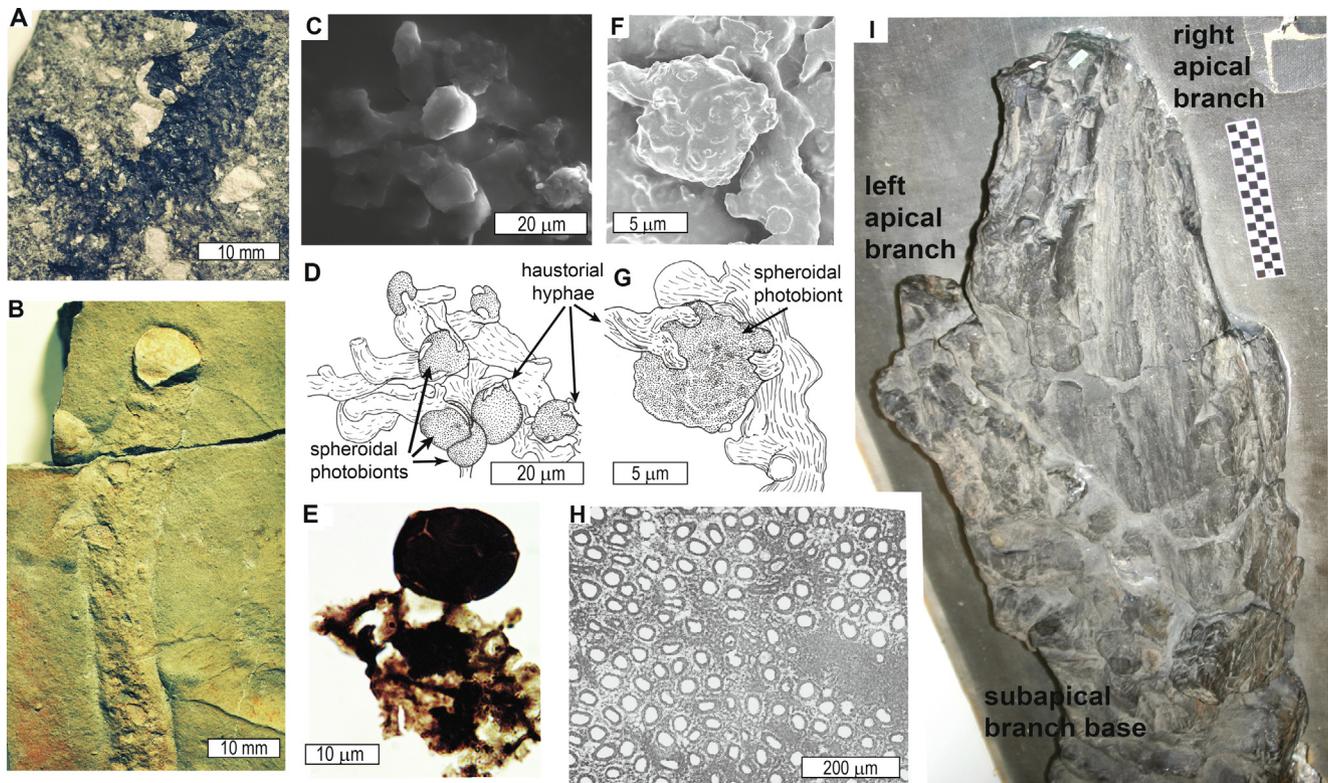


Fig. 5. Fossil fungi: A–D, *Prototaxites honeggeri* from the Middle Ordovician (Darrivilian), Douglas Lake Member, Lenoir Limestone at Douglas Dam, Tennessee; A, branching apical axes; B, cast of branching axis; C–D, coccoid chlorophyte photobiont with hyphal appressoria and haustoria; E, *Palaeoglomus strotheri*, mycorrhizal spore and arbuscule from the same Douglas Dam locality; E–H, *Prototaxites loganii* from middle Devonian (Givetian) Bellvale Sandstone, Schunemunk Mountain, New York; G, coccoid chlorophyte photobiont with hyphal appressoria and haustoria; H, skeletal hyphae in matrix of small binding hyphae from transverse section of trunk; I, detail of branching apex; . Illustrations A–E are from Retallack (2020) and F–I from Retallack & Landing (2014).

secondary soil productivity (ppm soil CO₂) near the end of the growing season (Retallack, 2005; Breecker and Retallack, 2014). The nodules are shallow in aridland low-productivity shrublands and deep in subhumid high-productivity forests. There is a clear relationship between height of trees and depth to carbonate in arid to humid Australia (Retallack, 2012a), but trees are now larger in drier regions than were pteridophytic cladoxyl and progymnosperm trees of the Devonian (Retallack and Huang, 2011). Long time series of terrestrial productivity from depth to carbonate of paleosols are a detailed paleoclimatic record that reveals global greenhouse spikes and carbon isotopic anomalies during the early Paleozoic (Retallack, 2009a). For paleosols, the depth to calcic horizon is reduced by burial compaction, and this can be calculated and subtracted to reconstruct the paleosol using standard burial compaction algorithms for particular sediment and soil types (Sheldon and Retallack, 2001). Again, the Late Silurian Bloomsburg Formation of Pennsylvania shows a large discrepancy between the depths to carbonate (Fig. 2B) typical for woodland soils (Retallack, 2012a) yet the only plants were shallow rhizomatous forms (Fig. 2–D–E), which would stimulate only limited and shallow soil respiration. This discrepancy may also be due to soil respiration of rhizines and hyphae of fungus (Fig. 2F–G).

4. Early Paleozoic fungi

The once puzzling Paleozoic nematophytes, such as *Prototaxites*, are now known from their cellular anatomy to have been fungi rather than tracheophytes, despite their great size (Hueber, 2001; Edwards and Axe, 2012; Edwards et al., 2013; Retallack, 2020). Hyphal anatomy of *Prototaxites* rules out previous interpretations

as yew trees or giant algae (Hueber, 2001), and continuity of tissues in massive trunks (Taylor et al., 2010) rules out interpretation as rolled up liverwort mats (Graham et al., 2010a, 2010b). Some nematophytes were lichens with spheroidal chlorophyte symbionts indented and encircled by fungal hyphae (Fig. 5C–D, F–G), regarded as the most convincing evidence for fossil lichens (Lücking and Nelsen, 2018). Hyphal connections with the spheroidal cells are both tangential and indenting, or appressorial and haustorial in the terminology of Honegger (1986). In the case of *Prototaxites loganii*, the spheroidal cells were 3–10 μm in diameter attached to curled generative hyphae within cortical nests. These observations together with their isotopic composition is evidence that the spheroidal cells were chlorophyte algae (Retallack and Landing, 2014). In the case of *Prototaxites honeggeri*, the spheroidal cells were similar, 7–9 μm in diameter and in cortical nests (Retallack, 2020). All nematophytes are united by large, constructional, aseptate hyphae (Fleming and Rigby, 1972; Strother, 1988; Hueber, 2001; Edwards and Axe, 2012).

Although nematophytes can be considered lichens, the kinds of fungus in *Prototaxites* are uncertain. The fungal component has been considered basidiomycotan, but the dominance of aseptate hyphae exclude that possibility, and possible basidiomycotan structures illustrated by Hueber (2001) may have been parasitic (Retallack and Landing, 2014). Variance in carbon isotopic composition of *Prototaxites* has been taken as an indication of basidiomycotan heterotrophy (Boyce et al., 2007), but could equally be due to observed overgrowth of other plants and fungi (Retallack and Landing, 2014). Alternatively, the hyphae of *Prototaxites* may have been ascomycotan, but again the dominance of aseptate hyphae exclude that possibility, and the ascomycotan hymenium reported

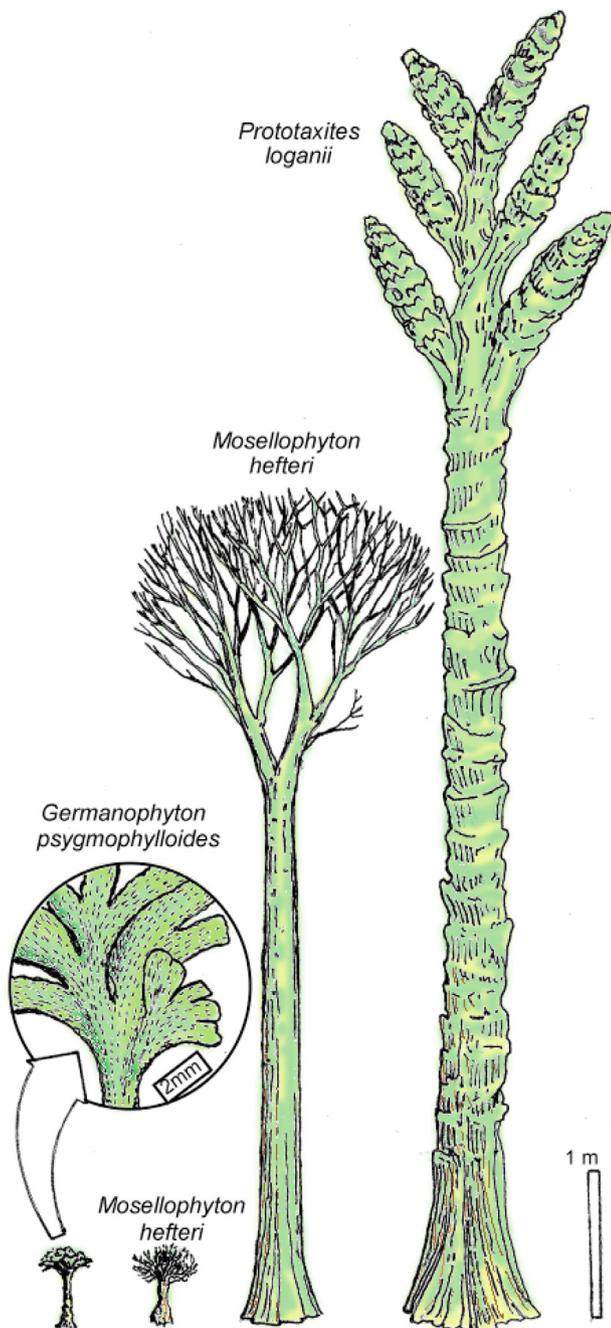


Fig. 6. Reconstructions of Silurian-Devonian nematophytes (Retallack, 2015d), now interpreted as glomeromycotan lichens (Retallack & Landing, 2014).

by Honegger et al. (2018) does not appear to be attached. The abundant aseptate hyphae in *Prototaxites* are more like those of Glomeromycota or Mucoromycotina (Retallack and Landing, 2014). Glomeromycota includes living Archaeosporales, such as *Geosiphon pyriforme* with its endosymbiotic cyanobacteria *Nostoc punctiforme* (Schüßler, 2012), perhaps represented by *Diskagma* as ancient as 2.1 Ga (Retallack et al., 2013). Molecular clocks place the origin of Glomeromycota at 1200–720 Ma (Hedges, 2003; Lutzoni et al., 2018). Glomeromycota are also in evidence from leiospheres and other large acritarchs of Mesoproterozoic to Devonian age with chitin walls that fracture in brittle fashion, multiple wall layers, chitin FTIR spectra, and attached hyphal filaments (Retallack, 2015d; Loron et al., 2019). *Geosiphon* and *Diskagma*

are excluded from lichens by Hawksworth (1988), because they enclose the photobiont in an intracellular vesicle (endolichen), rather than haustorial connections (ectolichen) seen in other lichens and *Prototaxites* (Fig. 5C–D,F–G). Lichens also have been regarded as a clade rather than grade of evolution by Nelsen et al. (2020) because the only currently known ectolichens are dikaryan fungi (Ascomycota and Basidiomycota). In that case, lichen ancestors of living taxa are unlikely to be geologically older than Silurian, because there is no evidence of ascospores, basidiospores or other dikaryan reproductive structures before then (Schmid, 1976; Honegger et al., 2013; Smith, 2016). However, Ordovician *Prototaxites honeggeri* (Retallack, 2020) with haustorial connection of photobionts but mainly aseptate hyphae (Fig. 5C–D) does not fit comfortably within either Dikarya (Lücking and Nelsen, 2018), nor Geosiphonaceae (Schüßler, 2012). A provisional solution is that nematophytes were ectolichens of Glomeromycota or Mucoromycotina, and thus an extinct clade with no living relatives. Despite there being no living ectolichen Glomeromycota, such an organism is plausible, given multiple origins and loss of lichenization in other fungal lineages (Nelsen et al., 2020).

Extinct Paleozoic nematophytes had squamulate branches and trunks (Fig. 5). Some nematophytes were sparsely branched, but others had numerous slender branches, and yet others had branches flattened into phylloids (Fig. 6). These three distinctive forms of branching are among the grounds for separating *Mosellophyton* and *Germanophyton* from *Prototaxites*, despite their very similar fungal histology (Høeg, 1942; Schaarschmidt, 1974; Schweitzer, 1999). A complete nematophyte plant, such as the branching Schunnemunk tree, was 8.88 m tall when excavated (Ries, 1897). The strengthening biopolymer of chitin can be as effective as lignin of tracheophytes in supporting a large plant, because nematophytes had the same allometric taper linking diameter to height as found in tracheophytes (Retallack and Landing, 2014).

5. In situ nematophytes of Ordovician Juniata Formation

A buried stand of nematophytes is preserved in the Late Ordovician (Hirnantian), upper Juniata Formation at Beans Gap Tennessee (Fig. 7A: Retallack, 2015a). The trunks are natural casts of stems in a 24-cm-thick bed of sandstone, and each trunk can be traced downward to drab mottled, rooting structures in the purple-red Bedford clay paleosol, which is a weakly developed Fluvent, immediately below (Fig. 7B–C). Poorly preserved parallel hyphae, arranged into concentric growth rings characteristic of nematophytes were found in thin sections of the trunks (Fig. 7D–H). These sandstone casts also included a central hollow, thick branches, and surface squamules, like those of *Prototaxites honeggeri* (Retallack, 2020). Comparable trunks have been reported from Algeria (Arbey and Koeniguer, 1979), also of Hirnantian age (Le Heron and Craig, 2008). Similar trunks from the Czech Republic were named *Lepidotruncus fortis* by Fritsch (1908), and are also Late Ordovician (Katian) in age (Kříž and Pojeta, 1974). The Czech and Algerian examples are like the Tennessee trunks in branching sparsely to create an open structure 10 times the diameter of the trunk bases (Fig. 7C), though in no case is the entire canopy preserved. The 10 Tennessee trunks of cf. *Lepidotruncus* at Beans Gap (Fig. 7B–C) average 18 ± 34 mm at the base and 14 ± 26 mm at height-diagnostic level 6 cm above the base, where the basal taper ends, and this gives plants 48 ± 8 cm tall from application of allometric scaling of other nematophytes (Retallack and Landing, 2014). The largest of these at 2.2 cm diameter at the base, and 1.65 cm diameter 6 cm above that, would have been 55 cm tall. The upper 31 cm of these organisms above the sandstone bed was thus not preserved, but there are at least 3 branches on each trunk in the

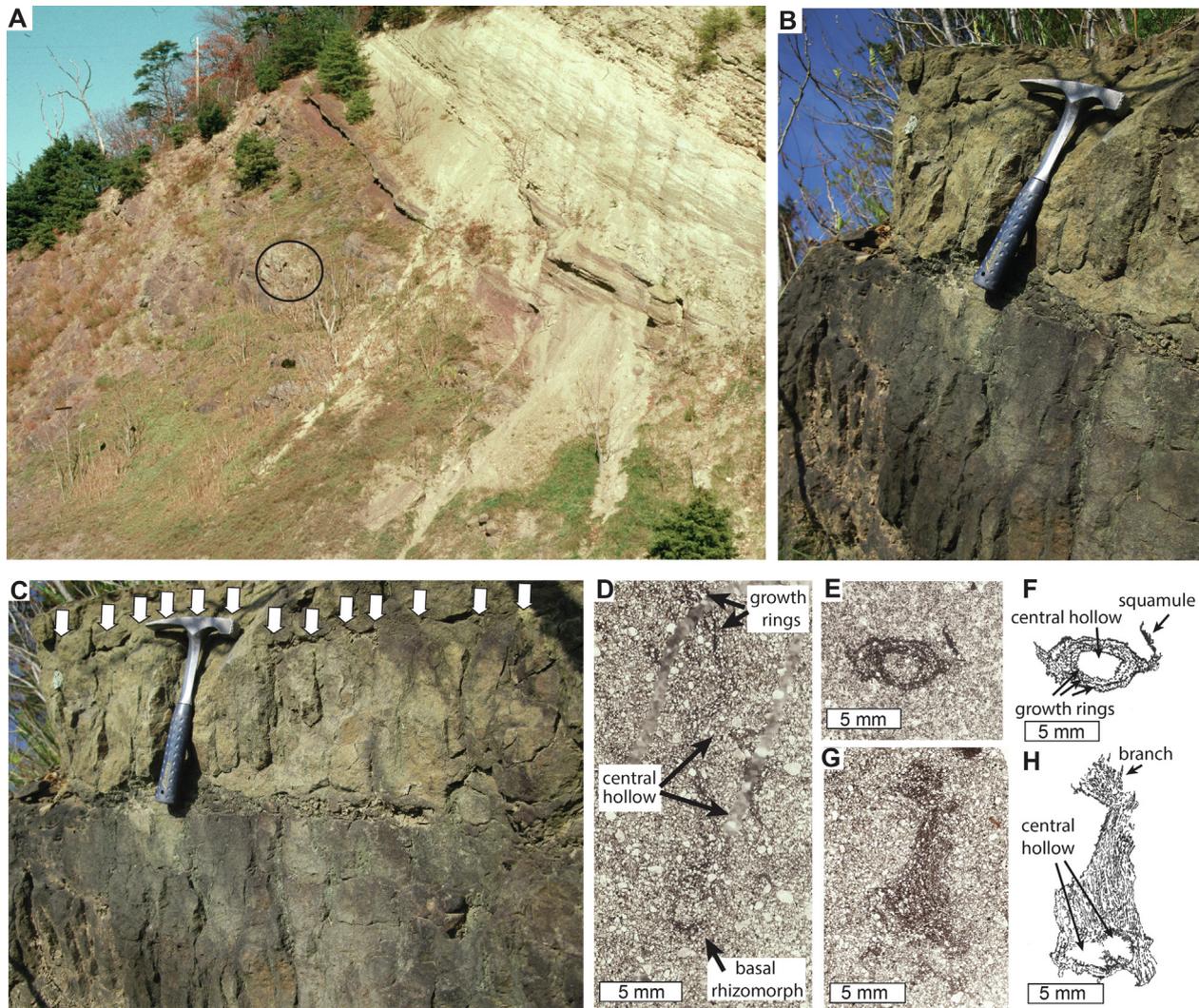


Fig. 7. Nematophyte paleosol in the Late Ordovician Juniata Formation in Beans Gap, Tennessee (A), with trunks entombed in sandstone above Bedford clay paleosol with greenish gray-haloed rhizine traces (B–C), and preservation of growth rings, central hollow, and parallel hyphae as dark organic matter within thin sections of siltstone (D–H). This is 716 m in measured section of Retallack (2015c), and thin sections in the Condon Collection of the University of Oregon Museum of Natural and Cultural History are F119070 (D–F).

preserved 24 cm, reaching out to the next trunk and forming a closed canopy. The midline spacing of these trunks is 6.5 ± 5.0 cm, and this gives an original density of 604 ± 787 plants/m² or $604,166 \pm 787,316$ plants/hectare. This stand of nematophytes would have been as dense and tall as a crop of corn (*Zea mays*: Tollenaar et al., 1994) or cotton (*Gossypium hirsutum*: Dong et al., 2010), and thus self-shading.

The nematophyte-bearing Bedford paleosol, like others in the Juniata Formation, has diffuse filaments (Fig. 7D,G) within large (2–4 cm diameter) drab-haloed mottles in the purple surface horizon of the paleosol below the preserved nematophyte trunks (Fig. 7B–C). Paleosols in the Juniata Formation also have threadlike (<2 mm diameter) drab tubules and calcite-filled tubes after plant rhizoids (Retallack, 2000, 2001, 2015a). This strongly bimodal distribution of plant rhizoids and nematophyte trunk bases in numerous paleosols in Tennessee and Pennsylvania also is evidence for a considerable size discrepancy between nematophytes and non-vascular land plants. Nematophyte paleosols in the Juniata Formation are weakly developed, and non-calcareous, with subdued colors indicative of seasonal waterlogging, unlike red, moderately developed, calcareous paleosols of non-vascular land plants (Retallack, 2015a).

Very few non-vascular land plants are known from the Juniata Formation, but they are either thalloid, so no more than 3 mm above the surface, or tubular, and no more than 1 mm diameter, so also ground-hugging (Retallack, 2015a). Ordovician spores also show affinities with ground-hugging bottle liverworts or thalloid liverworts, or slender leafy liverworts (Gray, 1985; Nøhr-Hansen and Koppelhus, 1988; Wellman et al., 2003). Megafossils of these non-vascular land plants are now known from the Middle Ordovician Douglas Lake Member of the Lenoir Limestone in Tennessee (Retallack, 2020). Modern relatives of these plants are also less than an order of magnitude tall than Ordovician nematophytes.

6. In situ nematophytes of Silurian Bloomsburg Formation

Nematophytes have been found in the Late Silurian (Ludlovian) Bloomsburg Formation as trunks (Fig. 8F; *Prototaxites*) and leaf-like structures (Fig. 8E; *Nematothallus*: Strother, 1988) in gray sandstone paleochannels (Retallack, 2015b). Paleosols of the Bloomsburg Formation also have drab mottles with numerous parallel filaments (Fig. 8C–D), like rooting structures of nematophytes (Driese and Mora, 2001; Hillier et al., 2008; Retallack, 2015a,b,c).

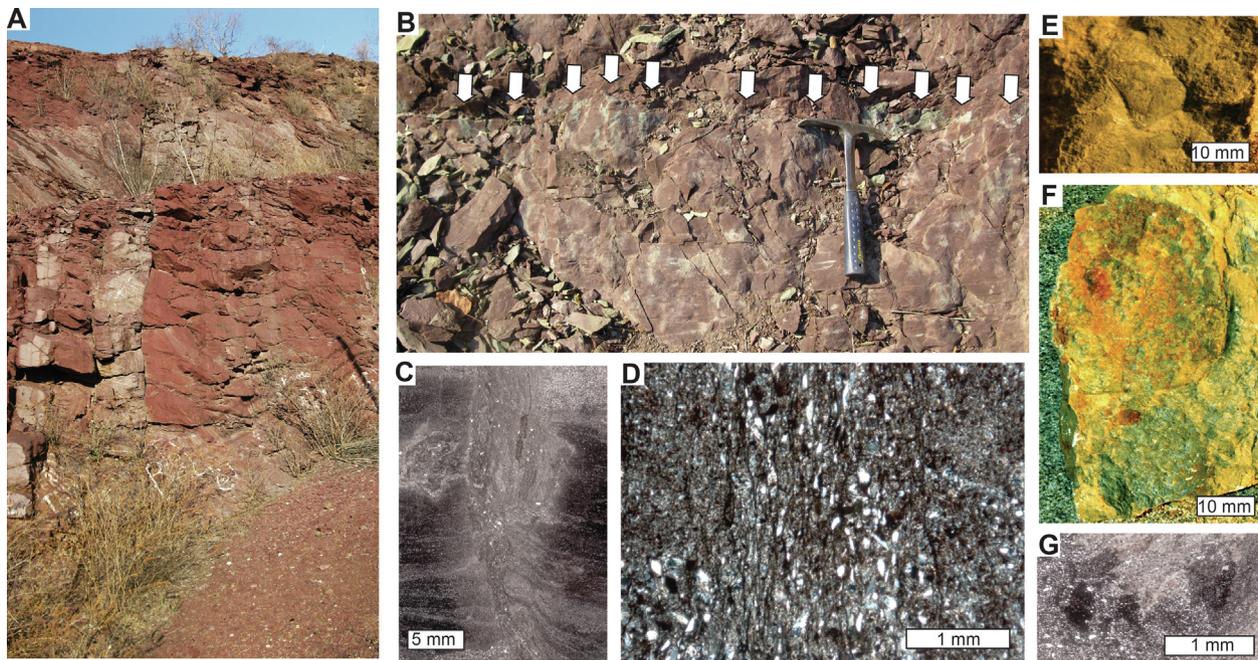


Fig. 8. Nematophyte drab haloes of the Late Silurian (Ludlovian) Bloomsburg Formation near Palmerton, Pennsylvania (A), in Lisette silty clay loam paleosol (B), and thin sections with diffuse rhizine like traces attributed to nematophytes (C–D). Also found in these outcrops are nematophyte fossils of Strother (1988): *Nematothallus lobata* (E), and *Prototaxites* sp. indet. (F116301), with hyphal structure in thin section (G). The paleosol (B) is at 29.8 m in measured section of Retallack (2015b). Thin sections and specimens in the Condon Collection of the University of Oregon Museum of Natural and Cultural History are R2275(C), R2275 (D), F1165305A (E), F116316 (F) and R2245 (G).

As in other cases of drab haloes in red paleosols, the drab areas represent burial reduction of iron oxides by bacterial decay of the last crop of organic structures before burial of the paleosol (Retallack et al., 2000; Retallack, 2011b). The Lisette paleosol, an Aquent (Fig. 8B at 29.8 m in section of Retallack, 2015b) had mottles 33 ± 17 mm in horizontal diameter. This can be converted to a basal trunk diameter (20 ± 5 mm) using the known relationship between mottle and root diameter ($2(D/\pi)^{-2}$; Retallack, 2008) and to diameter at characteristic height (7 ± 2 mm) from 0.75 taper factor in the reconstruction of Schaarschmidt (1974), and height calculated as 51 ± 10 cm tall using the algorithm of Retallack and Landing (2014). These plants were spaced at 20 ± 8 cm, for a density of 51 ± 70 m⁻² or $50,970 \pm 70,179$ ha⁻¹. Similar calculations can be done from drab-mottles in three paleosols of the Brenda pedotype, a Haplaquept (Retallack, 2015b). A Brenda paleosol at 18.5 m had mottles 37 ± 22 mm diameter, of plants 52 ± 16 cm tall, spaced at 17 ± 6 cm for a density of 61 ± 74 m⁻², or $61,265 \pm 74,579$ ha⁻¹. Two other Brenda paleosols (10.5 and 8.2 m in section) had trunks 58 ± 13 cm tall, spaced at 31 ± 11 cm for a density of 15 ± 10 m⁻², and 61 ± 10 cm tall, spaced at 30 ± 8 cm for a density of 13 ± 6 m⁻², respectively. Both Lisette and Brenda pedotypes had high ferrous iron at shallow depths (60 and 110 cm respectively), and so are interpreted as well drained soils with a shallow water table, a good combination for luxuriant growth. The known morphology of nematophytes (Fig. 6) and these spacings are indications of seasonally wet marshes with nearly continuous canopy. Silurian nematophytes of the Bloomsburg Formation were not scattered poles amid shrubby as envisaged for Devonian nematophytes (Hueber, 2001). These nematophytes like, those of the Juniata Formation, also would have been as dense and tall as a crop of corn or cotton (Tollenaar et al., 1994; Dong et al., 2010).

Paleosols of the Bloomsburg Formation also include rhizoids and rhizome traces of early vascular land plants, probably zosterophylls, no wider than 8 mm, and thus no taller than 30 cm

(Retallack, 2015b). Zosterophyll rhizomes and rhizoids are best known from other paleosols (Barry, Debbie, Lehigh Gap and Palmerton pedotypes) which lack nematophytes, but there are some land plant rhizomes with nematophytes in paleosols dominated by nematophytes (Lisette and Brenda pedotypes). Nematophytes were about twice the height of associated early vascular land plants, and even with the sparse short branches documented for *Prototaxites* (Retallack and Landing, 2014), would have formed a closed canopy. As for the Juniata Formation, nematophyte paleosols in the Bloomsburg Formation were weakly developed, non-calcareous, and seasonally waterlogging, unlike red, moderately developed, calcareous paleosols of non-vascular land plants (Retallack, 2015b).

7. Comparison with sedimentary record

This survey of early Paleozoic tiering above and below ground can be compared with the published record of tiering in early Paleozoic marine communities (Bottjer and Ausich, 1986), and the increase in nutritional quality and productivity of marine invertebrates through time (Bambach, 1993; Servais and Harper, 2018). The height of marine tiers above the seafloor increased with the height of fungal tiers on land, and the depth of marine burrowing below the seafloor increased with depth of roots and mycelia in soils (Fig. 9). These trends may both reflect increased exploitation of soil nutrients by increasingly effective systems of mycelia and roots (Servais et al., 2019; Mitchell et al., 2021). The unevenness of the paleosol and paleobotanical records is due to the particular sequences where these records were obtained in Australia and the northeastern United States, which were both calcareous red beds with a succession of Aridosol paleosols episodically interrupted by CO₂ greenhouse crises such as the Hirnantian mass extinction of the Ordovician (Retallack, 2009a, 2015a), and the Kačak extinction of the Devonian (Retallack and Huang, 2011). During these transient greenhouse pulses, plants of larger stature spread from previ-

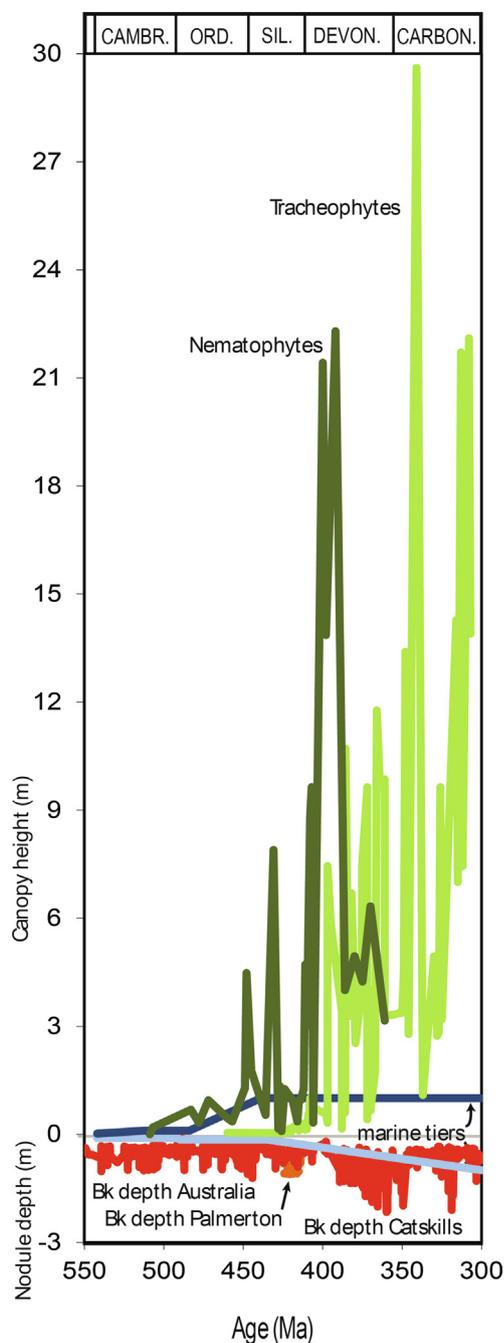


Fig. 9. Early Palaeozoic marine and non-marine tiering, highlighting Siluro-Devonian dominance of nematophytes (lichenized fungi) over tracheophytes (vascular land plants). Marine tiers are shown both above and below sediment-water interface (Bottjer & Ausich, 1986). Depth of bioturbation in paleosols (lower red line) extends to the compaction-corrected depth of the calcic horizon in paleosols in and near Flinders Ranges and Grampians National Parks (Retallack, 2009), the Bloomsburg Formation near Palmerton Pennsylvania (Retallack, 2015b), and the Catskill and Mauch Chunk Formation of New York and Pennsylvania (Retallack, 2011a). Non-vascular plants are not included, but all those known were thalloid ground-hugging or tiny leaved forms (Retallack, 2015a). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

ously wetter regions, where they had evolved. Later by promoting carbon sequestration and widespread deep weathering, global cooling and drying forced their retreat to humid refuges (Retallack and Huang, 2011). A plot of the tallest plants in the world at each stage could join the peaks, as in the simplified

marine curve (Bottjer and Ausich, 1986), but the spikes remain of interest as times of increased geographic spread of productive ecosystems (Retallack, 2009; Retallack and Huang, 2011).

The initial rise of nematophyte trees coincides with increased tier distance of crinoids and sponges above the seafloor, but not increased depth of marine burrowing, nor increased depth of calcic horizons on land (Fig. 10). These depths did not increase until the advent of vascular plant trees. Height of lichens may have been less significant to silicate weathering than their hyphal network, and the tallest lichens were not in calcareous, moderately developed paleosols, but in weakly developed, seasonally waterlogged soils (Figs. 7 and 8). The evolution of wide tapering tree roots greatly increased soil respiration, soil structure and silicate weathering, compared with hyphal weathering documented in Cambrian and Neoproterozoic paleosols (Retallack, 2013).

Changes in tiering of vegetation documented here (Fig. 10) also had profound effects for sedimentation on land. The binding effect of vegetation promoted meandering streams and heterolithic, lateral-accretion sets, over braided streams and planar cross-bedding (Davies and Gibling, 2010). Marked advances in vegetation stature and tiering encouraged biological diversity on land (Davies and Gibling, 2013). Deeper weathering in forested than earlier herbaceous communities also consumed atmospheric greenhouse CO₂ to an extent that Inceptisols and Aridisols under non-vascular plants induced the Late Ordovician (Hirnantian) ice age (Lenton et al., 2012; Retallack, 2015a), and forested Histosols and Alfisols induced the Late Devonian to Permian, Gondwanan ice age (Retallack, 1997b, Berner, 1998). These episodes of increased depth and intensity of weathering on land and greater nutrient delivery to the ocean explain stepwise increases in depth and thoroughness of marine bioturbation (Bottjer and Ausich, 1986).

8. Mycotrophic hypothesis

A Silurian-Devonian canopy of lichens fed by extensive mycelia supports the mycotrophic hypothesis of Pirozynski and Malloch (1975), that colonization of land by plants required nutrition from fungal mycorrhizae. These essential symbionts of most land plants are mainly glomalean fungi of the phylum Glomeromycota (Hibbett et al., 2007), and not Oomycota as originally envisaged (Pirozynski and Malloch, 1975). The mycotrophic hypothesis was also originally linked to the idea that multicellular aquatic green algae colonized the land. Stebbins and Hill (1980) have argued that archegoniate land plants evolved from fully terrestrial, small, soil algae, with three dimensional thalli and conjugation rather than zoospores. Both conjugation and fungal mycotrophism are more effective on land than in water (Hawksworth, 2000). Precambrian fungal spores (Retallack, 2015d; Loron et al., 2019), and *Geosiphon*-like problematic fossils (Retallack et al., 2013) are also evidence for long term exploitation of soils by fungal mycelia. The current compilation (Fig. 8) now demonstrates that fungal above-ground biomass represented by nematophytes, as well as mycelial biomass inferred from depth of soil carbonate, exceeded biomass and rooting depth of tracheophytes from late Ordovician to early Devonian.

Studies of ecological succession in western North American calcareous desert soils show the following stages: 1, bare soil; 2, large filamentous cyanobacteria such as *Microcoleus vaginatus*; 3, gelatinous lichens such as *Collema coccophorum*; 4, squamulose lichens such as *Psora cerebriformis*; 5, crustose lichens such as *Diploschistes scruposus*; 6, liverworts such as *Cephaloziella divaricata*; 7, short mosses such as *Bryum argenteum*; 8, foliose lichens such as *Xanthoparmelia convoluta*; 9, tall mosses such as *Syntrichia ruralis*; 10, fruticose lichens such as *Aspicilia filiformis*; 11, early successional angiosperms such as *Chrysothamnus nauseus*; and 12, late successional angiosperms such as *Artemisia tridentata*

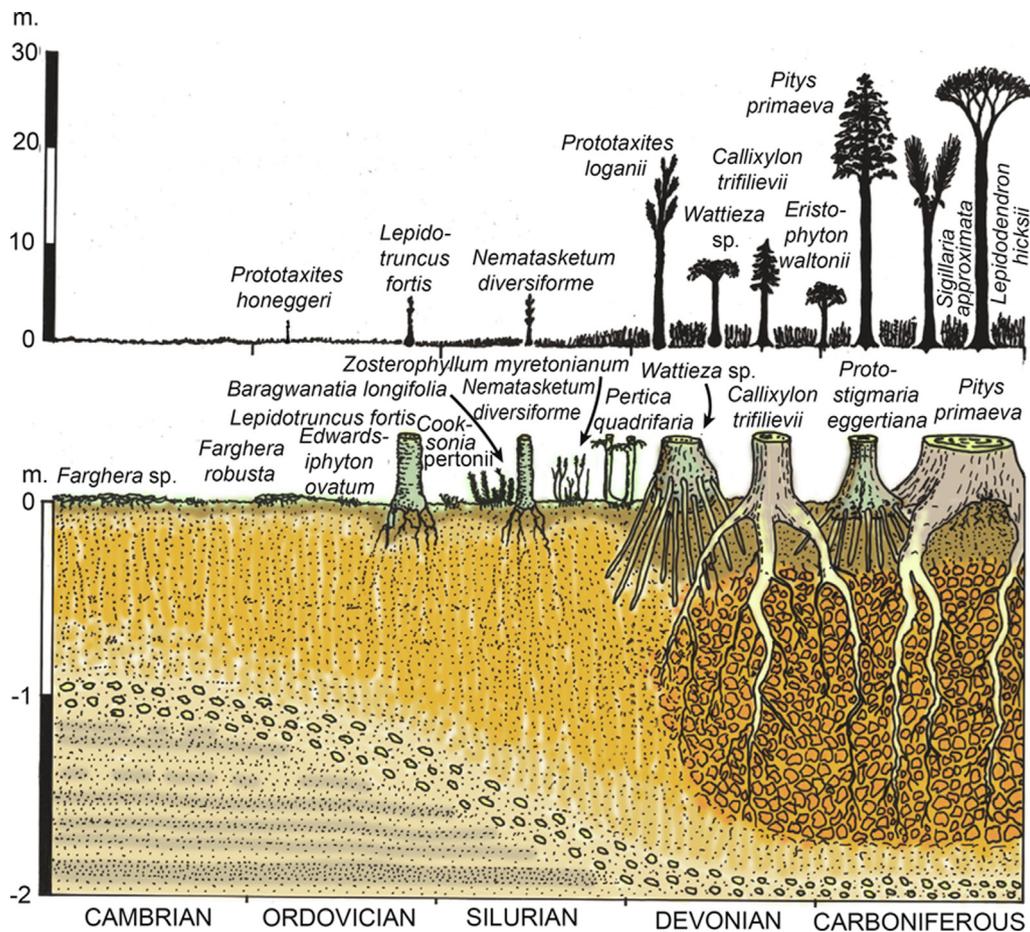


Fig. 10. Early Palaeozoic non-marine tiering, showing maximum depth of Bk (rounded white nodules), of mycelial bioturbation (dotted vertical lines) and rhizoids and roots (solid lines). Cambrian to Silurian soils have simple profiles (A-Bk or A-Bw-Bk) homogenized by cracking, rhizines and mycelia (Retallack, 2009a, 2015a,b), but Devonian and later soils have more complex profiles (A-Bt-Bk), with a slickensided hackly (blocky, argillic, or Bt) horizon created by tapering woody roots (Retallack, 2011a; Retallack & Huang, 2011). Stumps are based on actual fossils; *Farghera sp.* (Retallack, 2011b), *Farghera robusta* (Retallack, 2009b), *Edwardsiphyton ovatum* (Retallack, 2020), *Lepidotruncus fortis* (Fritsch, 1908), *Cooksonia pertonii* (Clea & Thomas, 1995), *Nematasketum diversiforme* (Edwards and Axe, 2012), *Zosterophyllum myretonianum* (Clea & Thomas, 1995), *Pertica quadrifaria* (Allen and Gastaldo, 2006), *Wattieza sp.* (Stein et al. 2007), *Callixylon trifilievii* (Snigirevskaya, 1984), *Protostigmalaria eggertiana* (Jennings, 1975), *Pityis primaeva* (Retallack & Dlicher, 1988).

(Rosentreter, 1984). This ecological succession may be recapitulating Precambrian communities of lichens and microbes on land, with cyanobacterial stage 2 reached very early in Earth history, lichen stage 3 by the Paleoproterozoic (Retallack et al., 2013), non-vascular land plant stage 6 by Ordovician (Retallack, 2015a, 2020), and the vascular plant stage 11 by Silurian (Retallack, 2015b). Microbial conditioning is essential for the plant colonization of desert soils today, and may also have been essential for the colonization of land by non-vascular, then vascular plants, and finally trees during the Paleozoic.

Another modern analog for lichen canopies are polar desert vegetation of tundra regions, where lichens such as copiously branching *Cladonia stellaris*, up to 40 cm tall, dominate (64% total biomass) vascular plants such as *Dryas octopetala* and *Betula nana*. Lichens are the principal food source for large caribou herds (Moser et al., 1979; Gough et al., 2008), as well as shelter from wind chill and frost for dwarf angiosperms and bryophytes.

9. Conclusions

This new view of terrestrial ecosystems reaching more deeply into their substrate and higher in their fluid medium than communities of the sea floor (Figs. 9 and 10) supports the general argument of Bambach (1993) and Servais et al. (2019) that increased

biomass, diversity and muscularity of early Palaeozoic marine communities, and increased diversity of marine phytoplankton were fueled by increased primary productivity and chemical weathering on land. Advances in bulk and reach of Ordovician life on land preceded and supplied nutrients to evolutionary advances of life in the sea. Furthermore, fungal hyphae reached both higher and deeper than early land plants for much of the early Palaeozoic. Critical to the success of early plants on land was the mycelial networks and shelter of lichenized fungi.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gr.2022.01.010>.

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