

Affinities and architecture of Devonian trunks of *Prototaxites loganii*

G.J. Retallack¹

*Department of Geological Sciences, University of Oregon,
Eugene, Oregon 97403*

Ed Landing

*Department of Paleontology, New York State Museum,
222 Madison Avenue, Albany, New York 12230, and
Department of Earth and Environmental Sciences,
Lamont-Doherty Earth Observatory of Columbia
University, Palisades, New York 10964*

Abstract: Devonian fossil logs of *Prototaxites loganii* have been considered kelp-like aquatic algae, rolled up carpets of liverworts, enormous saprophytic fungal fruiting bodies or giant lichens. Algae and rolled liverwort models cannot explain the proportions and branching described here of a complete fossil of *Prototaxites loganii* from the Middle Devonian (386 Ma) Bellvale Sandstone on Schunnemunk Mountain, eastern New York. The “Schunnemunk tree” was 8.83 m long and had six branches, each about 1 m long and 9 cm diam, on the upper 1.2 m of the main axis. The coalified outermost layer of the Schunnemunk trunk and branches have isotopic compositions ($\delta^{13}\text{C}_{\text{PDB}}$) of $-25.03 \pm 0.13\%$ and $-26.17 \pm 0.69\%$, respectively. The outermost part of the trunk has poorly preserved invaginations above cortical nests of coccooid cells embraced by much-branched tubular cells. This histology is unlike algae, liverworts or vascular plants and most like lichen with coccooid chlorophyte phycobionts. *Prototaxites* has been placed within Basidiomycota but lacks clear dikaryan features. *Prototaxites* and its extinct order Nematophytales may belong within Mucoromycotina or Glomeromycota.

Key words: Chlorophyta, Devonian, Glomeromycota, lichen, New York, *Prototaxites*

INTRODUCTION

Prototaxites has long been an intriguingly enigmatic Devonian fossil. It was the size of a tree, but its permineralized histology is not that of a vascular land plant or of a decayed vascular plant. Its name suggests affinities with living yew (*Taxus*), but that was recognized early as incorrect because of its permineralized histology by Carruthers (1872) and accepted also by the author of the name *Prototaxites* (Dawson

1859, 1888; Penhallow 1889, 1893). Two other interpretations of *Prototaxites* as kelp-like aquatic alga (Schweitzer 1983) and rolled up carpets of liverworts (Graham et al. 2010) have been effectively falsified by Taylor et al. (2009, 2010) because of continuous dense tissues and shape like a load-bearing, tapering trunk. This study addresses two other interpretations of *Prototaxites* as enormous saprophytic fungal fruiting bodies (Hueber 2001, Boyce et al. 2007, Hobbie and Boyce 2010) or as giant lichen podetia (Retallack 1994, Selosse 2002). These two alternatives are tested herein by carbon isotopic analyses, thin section and scanning electron microscopic re-examination of an especially complete and well preserved example of *Prototaxites loganii* collected during the 19th century as the “Skunnemunk tree” (Ries 1897, Nevius 1900, Prosser 1902) and now in the New York State Museum in Albany. From the beginning the “Schunnemunk tree” (following revised place name) was known to be nonvascular: Penhallow (1893) prepared thin sections and described this fossil as “*Nematophyton crassum*”, then Clarke (1900 p 675) communicated Penhallow’s opinion in private correspondence to emend that to “*Nematophytum logani*”, and Hueber (2001) included it within *Prototaxites loganii* (extinct basidiomycotan fungal order Prototaxales). A revised higher classification is proposed by Edwards et al. (2013), who place *Prototaxites* and other enigmatic fossils, including *Nematohallus* and *Cosmochlaina*, in the extinct lichenized fungal order Nematophytales (Lang 1937). The Schunnemunk tree is unique in preserving outermost tissues. It also preserves branches arranged like those of other specimens of *Prototaxites loganii* (Heidtke 2006, Schindler and Wuttke 2006) and unlike Fibonacci branching of vascular plants.

MATERIALS AND METHODS

The long history of discovery and display of the Schunnemunk tree (*Prototaxites loganii*: NYSM 13793) in the New York State Museum, as well as its locality and geological setting are detailed (SUPPLEMENTARY DATA). The fossil was excavated from a small quarry 200 m southwest of the junction of Seven Springs and Seven Springs Mountain Roads north of Monroe, New York: 41.35560°N, 74.17876°W (Nevius 1900). The Schunnemunk tree was found within sandstones with trough cross bedding and claystone breccias characteristic of a fluvial paleochannel (Bridge 2000). The fossil site is within the middle Bellvale sandstone, which is at least Middle Devonian (early Givetian) based on marine fossils in the underlying Cornwall shale (Ries 1897). The overlying Skunnemunk Conglomerate

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¹ Corresponding author. Phone: 541 346 4558; Fax: 541 346 4692; E-mail: gregr@uoregon.edu

(formation name preserves outdated spelling) represents late Givetian progradation of the Catskill delta (Retallack and Huang 2011), so the likely age of the Schunnemunk tree is middle Givetian (ca. 386 Ma: Gradstein et al. 2012).

This article presents new photographs and measurements of the Schunnemunk tree, as well as observations from oriented petrographic thin sections. Freshly cut interior surfaces were sputter-coated with gold-palladium for examination under Zeiss Ultra 55 and FEI Helios D600 scanning electron microscopes, at the University of Oregon CAMCOR facility. Chips from the Schunnemunk tree and newly recovered branch compressions (NYSM 13531-2) were digested in 60% HF 24 h, then analyzed for organic carbon isotopic composition at the University of Hawaii by combustion in a Eurovector-element analyzer (EURO.EA3000) and analysis in an Isoprime continuous-flow stable isotope mass spectrometer. A compilation of published isotopic data for comparison with these 10 new analyses is included (SUPPLEMENTARY DATA), which can be compared with (SUPPLEMENTARY DATA) 31 early Paleozoic paleosols and alluvial sediments, 185 early Paleozoic fossil plants and 2426 living plants and fungi.

NEW OBSERVATIONS OF THE SCHUNNEMUNK TREE

Branches.—Nevius (1900) described and illustrated six branches, each at least 1 m long, attached to the apical 1.2 m of the “Schunnemunk tree” after complete excavation (FIG. 1A). Unlike the permineralized trunk, the branches were poorly preserved, friable, carbonaceous compressions and were not collected in 1898. The bases of the six branches are still visible on the permineralized trunk of the Schunnemunk tree (FIGS. 1C, D, 2A, B). Especially prominent are two long branches diverging from the apex of the trunk (FIG. 1C, D). Another two branches diverge from the side, and two more are represented by near-circular cross sections at the top of truncated longitudinal ridges in the trunk (FIG. 2A, B). Each branch of these pairs is slightly uneven in diameter. The basal part of the trunk has patches of adhering carbonaceous material (FIGS. 1E, I, 3A), with distinctive cell structures (FIG. 4). In contrast, the branch bases lack organic rinds, perhaps because they were broken during excavation.

The grain of external surfaces of the apical branches is fibrous with tubular cells, but the cross sections of both apical and subapical branches are granular and break conchoidally across the tubular cells to reveal concentric growth rings (FIG. 1C, D), revealed also by thin sections of permineralized parts of the Schunnemunk tree (FIG. 5C, D). The divergence between large tubular cells running up the trunk, but angled outward to feed branches, is clear also in other branching specimens of *Prototaxites loganii* illustrated by Altmeyer (1973), Schweitzer

(1983), Heidtke (2006) and Schindler and Wuttke (2006). Because of divergent orientations of permineralized tubular cells, the preserved branch bases are not accidental splitting or rotting of the trunk but are reflected in deep microstructure of the trunk. These branches of the Schunnemunk tree are not knots from shed branches, as illustrated for other specimens of *Prototaxites* by Dawson (1859). The apical branches have a smooth, divergent curve without abscission callus, cracking or deformation, and the lower branch scars coming outward from the trunk retain an undeformed near-circular outline. The branch base diameters and angles of divergence from the trunk are 101 mm and 30°, 111 mm and 20°, 93 mm and 20°, 95 mm and 25°, 105 mm and 20°, and 111 mm and 20° (SUPPLEMENTARY DATA). These are not the 60° angles of a space-optimizing, dichotomous, branching tree (Niklas 1997).

Branching of the Schunnemunk tree is best characterized by successive pairs of slightly unequal dichotomies (FIG. 2F). Fibonacci spiral arrangements of branch parastichies characteristic of vascular land plants (Douady and Couder 1996) are illustrated (FIG. 2E) but are a poor fit because they fail to predict branch positions and orientations observed on the Schunnemunk tree.

Parts of three branches matching the description of Nevius (1900) recovered from the quarry in 2011 are carbonaceous compressions (FIGS. 1F, G, 2C, D). These are 96, 79 and 89 mm diam (mean and standard deviation 88 ± 8.5 mm). Thus they are smaller but within the range of variation of the branch bases observed on the permineralized trunk (mean diameter and standard deviation 97.8 ± 10.4 mm). Like the fossil trunk, the newly collected branches have irregular transverse wrinkles (width 11.8 ± 3.2 mm for 33; SUPPLEMENTARY DATA), which in places overlap as flaps (FIG. 2C, D).

Subdermal invaginations and nests.—The outermost surface of the Schunnemunk tree is not preserved by silica permineralization like the central part (FIG. 5C, D) but is a carbonized compression disrupted by chalcedony mineralization of coal cleat. In areas unfractured by cleat, the outermost surface has invaginations spaced every millimeter or less over the outer surface (FIG. 3A). The narrow (0.2–0.3 mm) dermal invaginations are zones of the outermost dense tissues of the tree that lie directly outside less densely carbonized and larger (0.5–2 mm) nests of degraded equant cells (FIGS. 3C, D). This style of preservation of the outermost surface of *Prototaxites* does not show histological details but provides information useful for recognizing intact permineralized trunks.

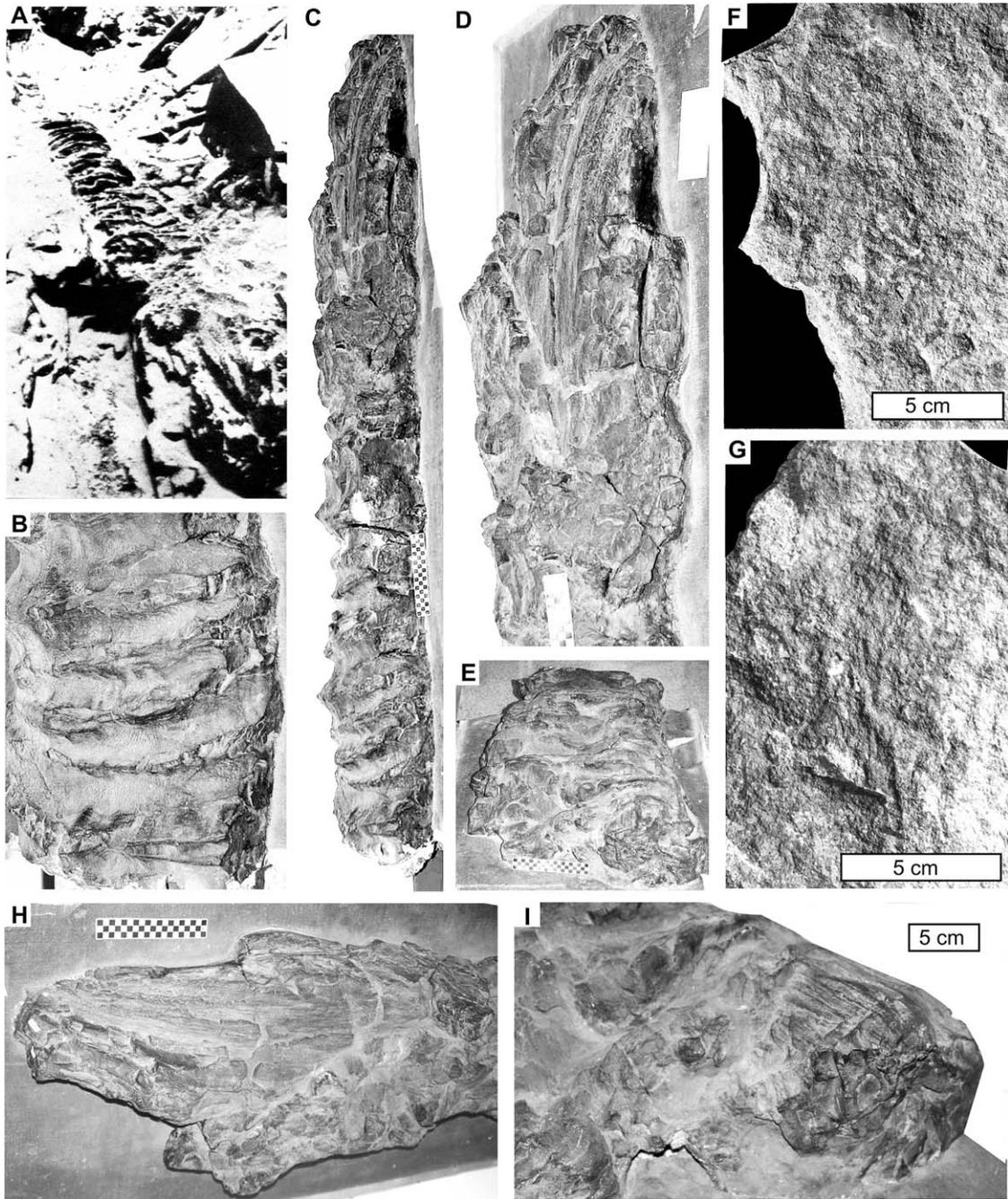


FIG. 1. Middle Devonian Schunnemunk tree (*Prototaxites loganii*; NYSM 13793). A. photograph at time of excavation during 1898, view to south from branched apex of trunk (from Nevius 1900); B–D. trunk with apex toward top; B. base with transverse wrinkles; C. overview of upper part of trunk; D. detail of apical branch bases; E. separate basal piece with vertical ridges; F, G. branches collected in 2011, NYSM17531 and 17532, respectively; H. oblique view of apical branch bases; I. oblique view of vertical flanges on basal piece. Scale C, D = 20 cm graduated in centimeters.

Dermal flanges.—The outer surface of the Schunnemunk tree is irregular in thin section, with branching tubular protuberances (FIG. 3E), local lumpy features (FIG. 3F) and triangular ridges (FIG. 3G). The tubular protuberances are similar to the thickest tubular cells

of permineralized parts of the trunk (FIG. 5C, D). Triangular ridges, here called dermal flanges, are formed from smaller opaque units, again comparable to an aggregation of thick tubular cells. These features have not been observed in other fossil trunks

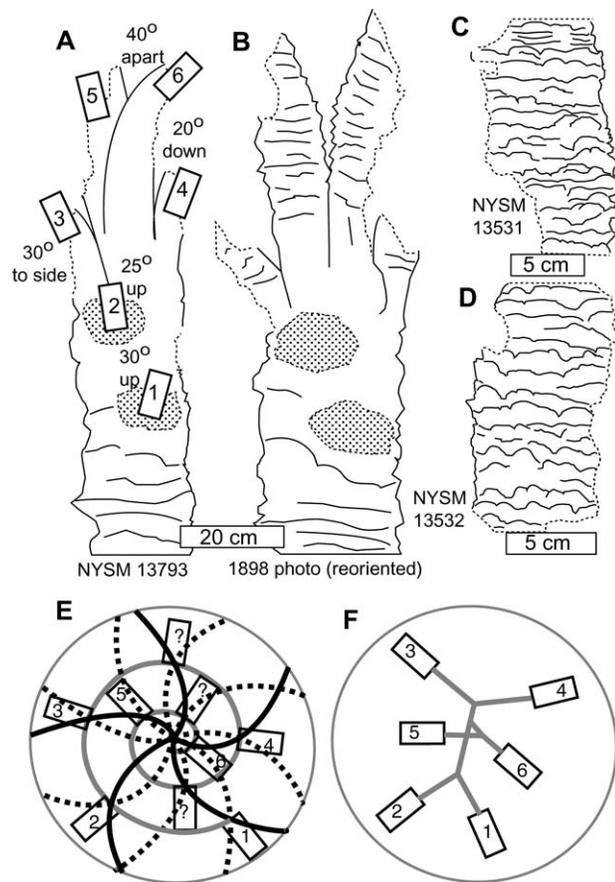


FIG. 2. Interpretive sketches of selected images of Fig. 1 of the Middle Devonian Schunnemunk tree (*Prototaxites loganii*). A. as preserved in NYSM 13793; B. as photographed in 1898; C, D. fossil branches found in the same quarry in 2011; E. a failed attempt to find Fibonacci patterns of branching; F. a more likely pattern of alternate dichotomy. Angles shown are intersection of midline of branches from midline of trunk, measured with protractor.

of *Prototaxites*, which either were stripped of outer tissues before burial or cleaned of carbonaceous material after collection (Altmeyer 1973, Hueber 2001, Heidtke 2006, Schindler and Wuttke 2006).

Subdermal vacuity.—A conspicuous gap, now 20–30 μm wide and 50–60 μm below the surface of the trunk, is here called a subdermal vacuity (FIG. 3F, G). The original width of this gap is unknown because it is unmineralized and would have been narrowed by burial compaction of the trunk. This gap follows the surface in all areas except those of the cortical nests composed of equant cells below cortical invaginations, which are poorly preserved in this kind of carbonaceous compression (FIG. 3A). The subdermal vacuity is thus an irregular planar feature just inside the outermost layer of the tree. This is not an accidentally addressed mat of vegetation or a flaking

of bark, because the vacuity maintains a constant thickness between regular cortical invaginations that pin it to the trunk. In contrast, mats or flakes would be expected to show varied width of flexuous detachment, unlike the brittle fractures of coal cleat also observed (FIG. 3A). Thus the subdermal vacuity is regarded as an original anatomical feature.

Coccoid cells.—Thin section and SEM examination of freshly cut portions of the carbonized cortex of the Schunnemunk tree revealed cortical nests of poorly preserved rounded carbonaceous bodies with radially arranged, poorly preserved filaments (FIG. 3B–D); 35 of these have an average diameter and standard deviation of $6 \pm 2 \mu\text{m}$ (3–10 μm). Under SEM, such coccoid cells are clustered around copiously branched tubular cells, again poorly preserved (FIG. 4); 59 of these yielded an average diameter and standard deviation of $5 \pm 2 \mu\text{m}$ (3–9 μm). Examination with SEM shows that some coccoid cells were misshapen by attached filaments (FIG. 4E) but others were well preserved and inflated, with shallow grooves and small papillae (FIG. 4F, G). This local variation in preservation quality matches observations of permineralized thin sections of the Schunnemunk tree (FIG. 5C, D). The coccoid cells (FIG. 4D–F) are attached to and surrounded by tubular branching cells (FIG. 4E), which branch toward the coccoid cells (FIG. 4A). The consistency of size of coccoid cells seen in thin section and SEM, attached branching tubular features and the variation in quality of coccoid preservation in SEM are evidence that these are biogenic structures and are not minerals or artifacts of opaque carbonization.

Rays and growth rings.—The carbonized outermost layer of the Schunnemunk tree is deformed by mineralized brittle cracks due to coal-cleat formation during burial (FIG. 3D) but also shows radial carbonaceous seams compacted into concertina-like organic partitions (FIG. 3G). Concentric growth rings composed of smaller diameter cells are apparent in broken branches of the Schunnemunk tree (FIG. 1C, D), but details of growth rings and their intersection by rays are better seen in other permineralized *Prototaxites*, in which they are radial empty zones, as wide as 1 mm (Hueber 2001). Summary diagrams of the relationship between growth rings, rays, branches, cortical nests and surface features are illustrated (FIG. 5A, B), largely based on the three-dimensional histological reconstruction of Hueber (2001).

Growth proportions.—Because the Schunnemunk tree was considered complete on excavation (Ries 1897, Nevius 1900), it is evidence of the original proportions of the entire organism. The allometric relation-

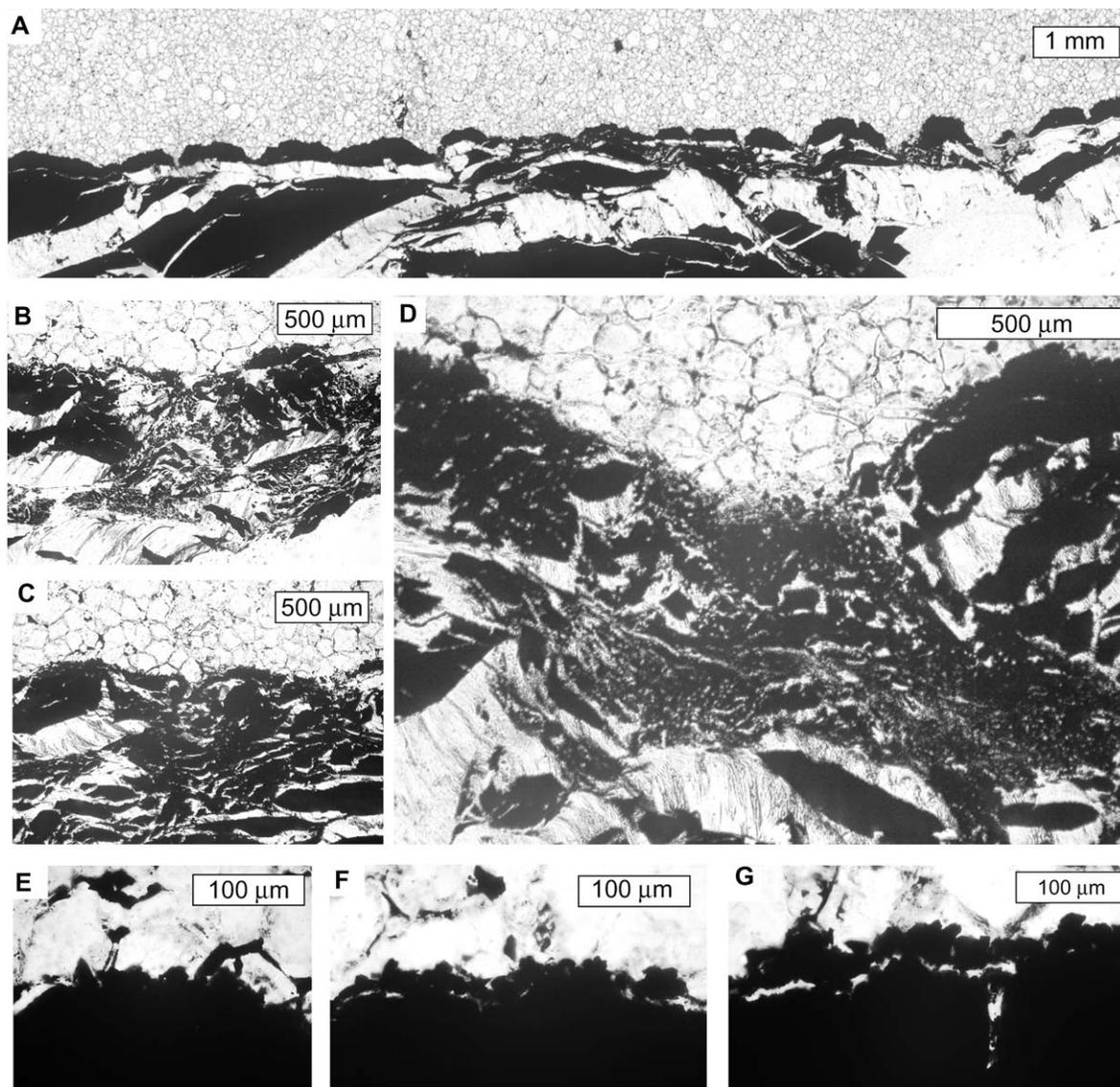


FIG. 3. Thin sections oriented transverse to long axis of Schunnemunk tree (*Prototaxites loganii*; NYSM 13697) and its sandstone matrix (above). A. Surface invaginations and nests of poorly preserved equant cells in outermost carbonized tissues; B, D. enlarged view of three nests of equant and less coalified cells. E. tubular protuberances into sandy matrix; F, G. details of subdermal vacuity oriented horizontal. All specimens are carbonized and disrupted by mineral growth of chalcedony, unlike silica permineralization of central part of the trunk. These features can be interpreted as a lichen algal layer (subdermal vacuity and cortical nests).

ship between diameter at breast height (B in m at a height of 1.4 m) and tree height (H in m) of 670 species of living tracheophytes can be predicted by the formula (after Niklas 1994): $H = 21.9B^{0.896}$. At 36 cm diam at 1.4 m above the base; the predicted height of the Schunnemunk tree with this equation is 8.77 ± 0.9 m. This is close to the measured height of 8.83 m on excavation (Ries 1897). Thus the stout tapering trunk of the Schunnemunk tree is comparable in proportions to load-bearing trees, such as those of pine and oak. Other nematophyte fossils have similar growth proportions (SUPPLEMENTARY DATA).

Carbon isotopic composition.—Newly discovered branch compressions from the site of the Schunnemunk tree had an isotopic composition of $-26.17 \pm 0.69\text{‰}$, which is indistinguishable from the outer carbonized layer of the Schunnemunk tree of $-25.03 \pm 0.13\text{‰}$ (SUPPLEMENTARY DATA). These values are comparable to a wide variety of fossil and modern organisms using or feeding on organisms with the C3 photosynthetic pathway (Smith and Griffiths 1998, Boyce et al. 2007) and with Devonian and older organic matter in alluvial sediments and paleosols (SUPPLEMENTARY DATA).

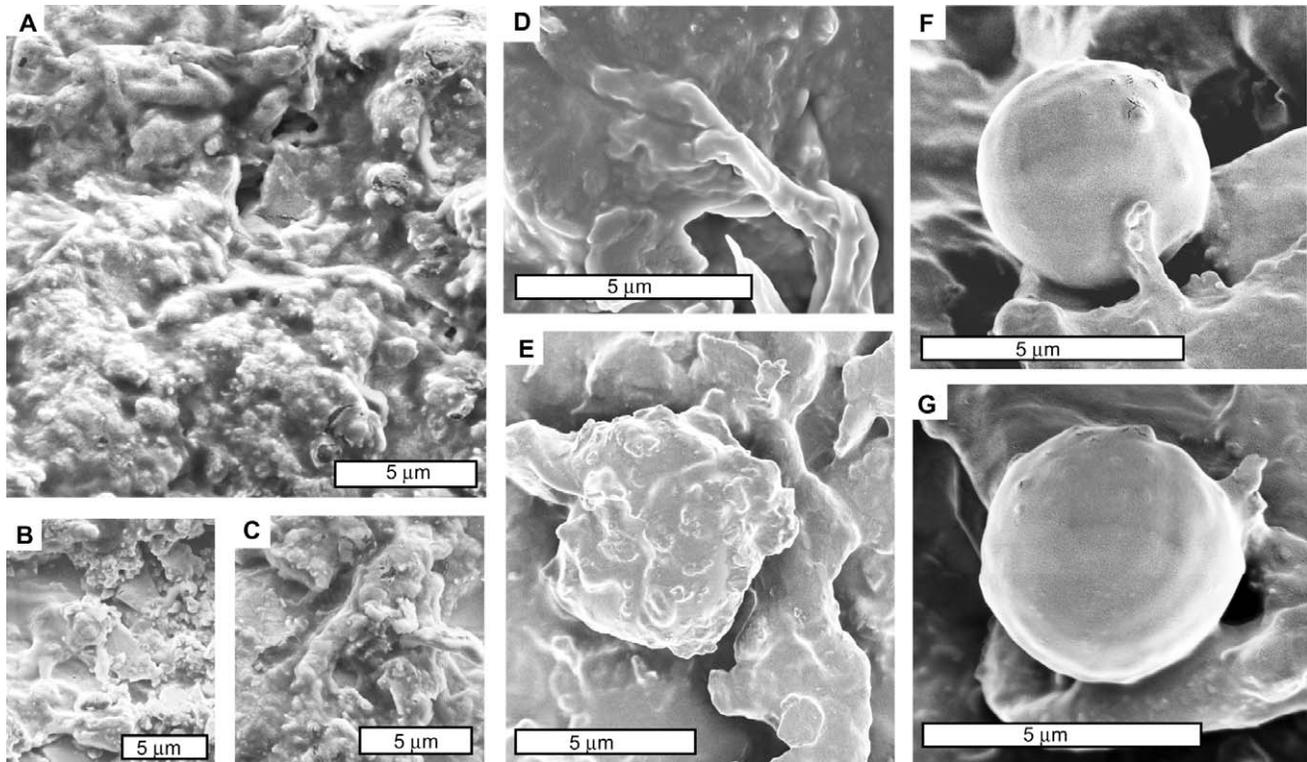


FIG. 4. Scanning electron micrographs of outermost cortical nests in carbonized tissue of Schunnemunk tree (*Prototaxites loganii*; NYSM 13697). A–C. clusters of coccoid cells surrounded by tubular cells; D. tubular cells branching copiously toward coccoid cells; E. deformed coccoid cell enwrapped in branching tubular cell; F, G. coccoid cell with attached tubular cells. These features can be interpreted as coccoid eukaryotic algal photobionts and haustorial hyphae of lichen.

FUNGAL FRUITING BODY OR LICHEN?

Retallack (1994, 2007) argued from the resistance to burial compaction of tubular cells of *Prototaxites* that it had a strong biopolymer, such as chitin found in fungal hyphae, and that rounded vacuities within cortical nests once included coccoid photobionts. Selosse (2002) elaborated on this lichen interpretation with nutritional arguments that such a large fungus needed a larger reservoir of organic carbon than associated early land plants, unless it was lichenized. The nutritional argument finds support in discovery of *Prototaxites*-like rhizomorphs in carbon-lean, red paleosols (Driese and Mora 2001, Hillier et al. 2008). In contrast, Hueber (2001) argued from detailed histological examination that *Prototaxites* was a large basidiomycotan fruiting body. Study of carbon isotopes was used as evidence of saprophytism by Boyce et al. (2007) and Hobbie and Boyce (2010) and of mixotrophy by Graham et al. (2010). Additional histological, morphological and carbon isotopic evidence on the question of lichenization versus saprophytism-mixotrophy is detailed below.

Histology.—A difficulty in considering basidiocarp versus lichen interpretations of *Prototaxites* is different

terminology for mushrooms and lichens (outlined in SUPPLEMENTARY DATA). Hueber's (2001) basidiomycota terminology contrasts with lichen terminology used here and with nongenetic terminology used in previous paragraphs.

Coccoidal carbonaceous bodies of cortical nests near cortical invaginations in *Prototaxites* are poorly preserved but might have been functional photobionts (FIGS. 4B–D, 5E–G). Like phycobionts of lichens (Amadjian 1967, Brodo et al. 2001), these coccoid cells are surrounded and penetrated by branching hyphae. Coccoids are unlikely to represent fungal attack of unicellular yeasts (Hutchison and Barron 1996), algae (Hutchison and Barron 1997) or bacterial colonies (Barron 1988) because coccoids were common within the carbonaceous thallus of a freshly cut fossil, not found in the sediment matrix or at the edges of the fossil. They are not preserved in the subdermal vacuity (FIG. 3F, G), which might have housed another photobiont not preserved, comparable with modern lichens that have two or more photobionts (Hawksworth 1988). They are not preserved within interior cortical nests of carbonized and permineralized specimens (FIG. 5B), which presumably was too deep within the trunk for light penetration.

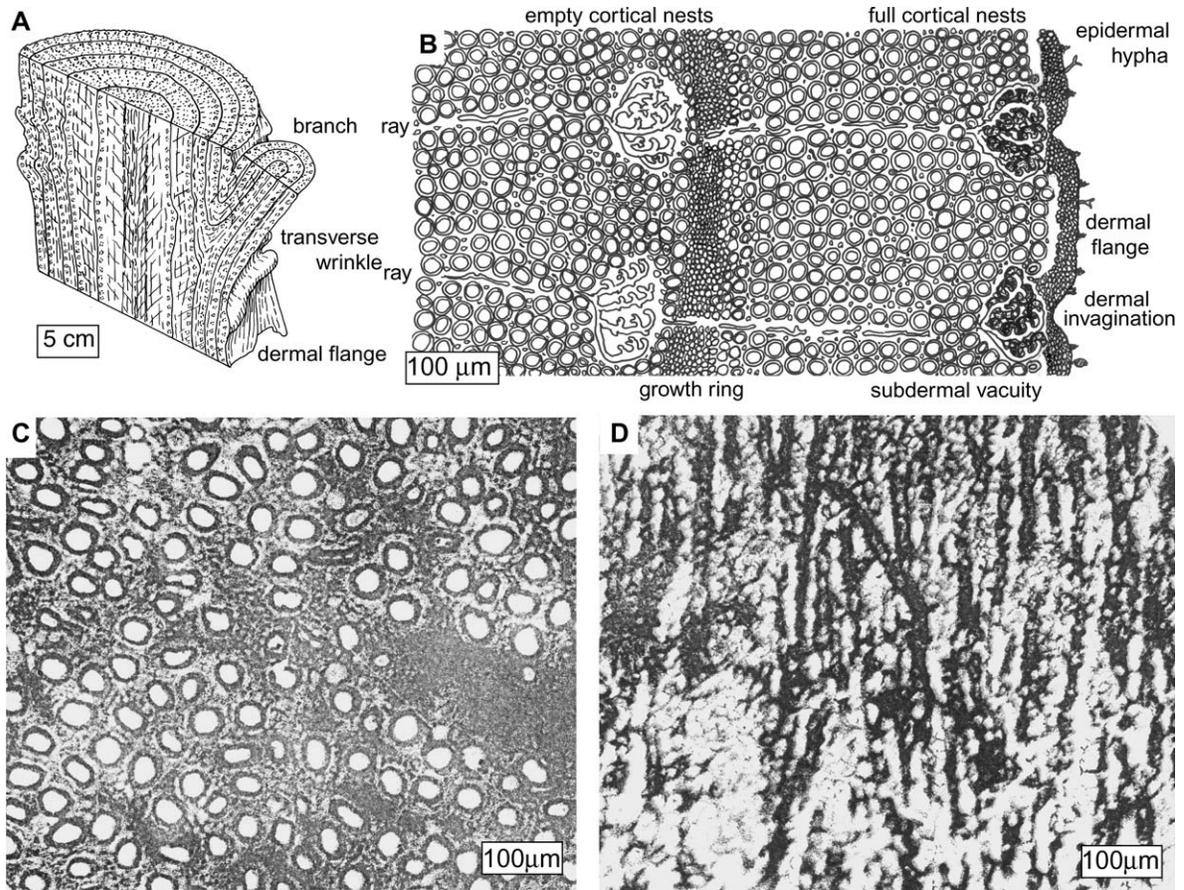


FIG. 5. Interpretive sketches and photomicrographs of the Schunnemunk tree (*Prototaxites loganii*: NYSM 13793) based on observations of branches and exterior presented here and interior histology documented by Hueber (2001); A. interpreted arrangement of branches, rays and growth rings; B. interpreted histology of single outer growth zone in transverse section; C, D. thin sections in transverse (C) and tangential (D) orientation, showing local cell disruption (not septae) due to quartz recrystallization (after Penhallow 1893).

Small (3–10 μm diam) fossil coccoid photobionts in outer cortical nests (FIGS. 4E–G) could be an indication of former coccoid cyanobacteria (now mostly 2.5–10 μm) rather than coccoid algae (now 10–25 μm). However, these measurements of Schopf (1991) provide a rule of thumb for Precambrian microfossils and come from free-living cells but do not apply to lichen photobionts. Eukaryotic lichen photobionts, such as *Hyalococcus*, *Myrmecia*, *Picochlorum*, *Palmellococcus*, *Pseudococcomyxa* and *Trebouxia*, are commonly less than 10 μm diam when freshly isolated from lichens but subsequently grow in culture medium to 25 μm or more, typical of free-living eukaryotic cells (Amadjian 1967, Henley et al. 2004). While eukaryotic photobionts are smaller within lichens than when cultured, cyanobacterial photobionts are larger within lichens than when free living (Ahmadjian 1967). Thus the size of coccoid cells in the Schunnemunk tree is most like that of eukaryotic unicellular algae in modern lichens.

A key prediction of Hueber's (2001) suggestion that *Prototaxites loganii* was a saprophytic thallus of a basidiomycotan is that the outermost tissues, when discovered, would prove to be a hymenium. Our thin sections of the carbonized cortex (FIG. 3) failed to reveal cell palisades comparable with hymenia. Although the preservation is thoroughly carbonized, the shapes of the spaces within the cortex are more like periclinal hyphae than radial hymenial cells. There also is no indication of gills or other hymenial structures on the putative branches (FIG. 1F, G). Hueber's (2001 fig. 13) possible spiculate protosterigma are not in groups of two, four or eight and lack a preserved metabasidium or terminal basidiospores. The spiculate terminations also are similar to phialides or mucronate hyphopodia, such as those of Ascomycota (Minter et al. 1983, Luttell 1989, Mueller et al. 1991, Sung and Spatafora 2004) but lack attached conidia. Attachment of these thin-walled spiculate cells to the hyphae of *Prototaxites* is unclear

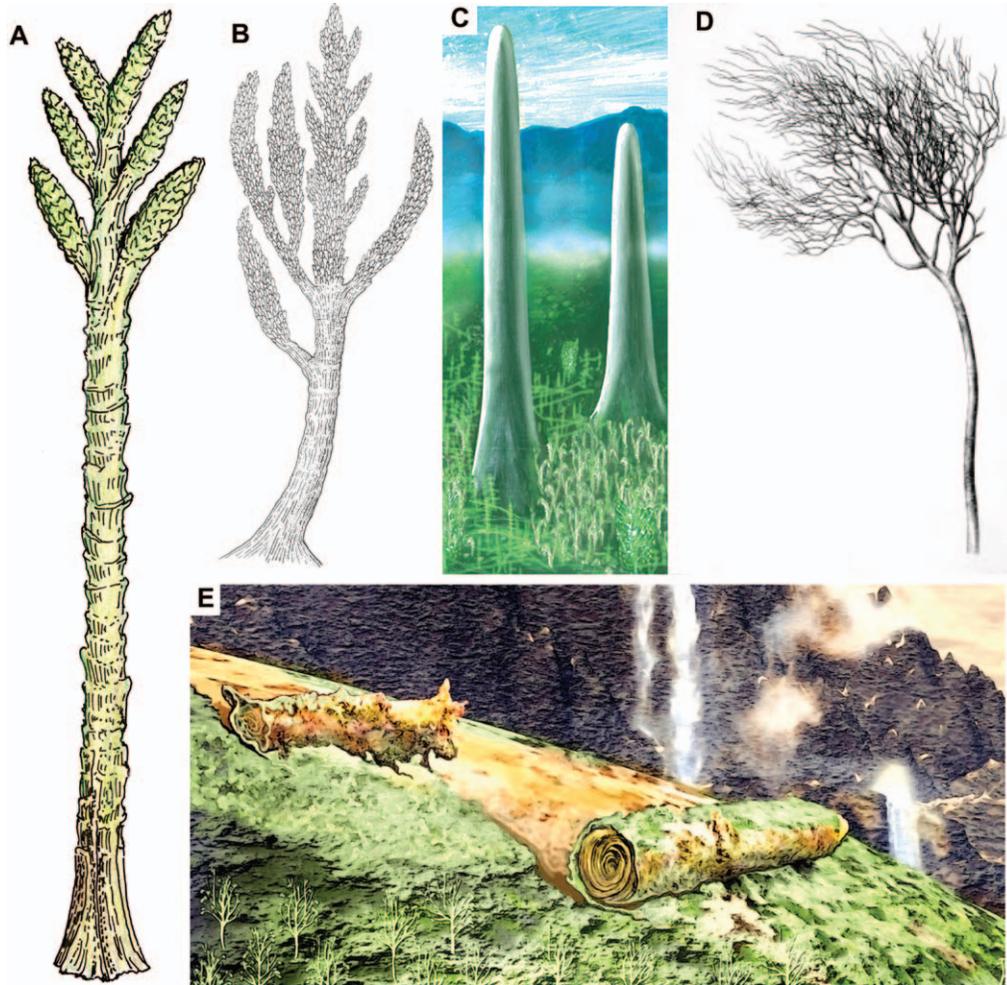


FIG. 6. Reconstructions of *Prototaxites loganii*; A. this paper; B. Dawson (1888); C. Mary Parrish for Hueber (2001); D. Schweitzer (1983) but here regarded as *Mosellophyton hefteri*; E. Kandis Elliot for Linda Graham et al. (2010). Images (C–E) are reprinted with permission from the Smithsonian Institution, Linda Graham and Schweitzerbart Science Publishers, respectively.

(Hueber 2001), and they might have been parasitic or symbiotic unrelated fungi.

Subdermal invaginations of the Schunnemunk tree might have been thinning to allow unimpeded illumination of photobionts in subdermal nests, comparable with epicortical pores of lichens (Brodo et al. 2001). These dermal invaginations are original features of the thallus, distinct from arthropod borings documented within *Prototaxites loganii* by Hueber (2001) and Labandeira (2007). The invaginations have a floor above an irregular cavity filled with hollow spherical cells (FIG. 3B–D), whereas borings are open to the outside, commonly have a uniform width throughout and are filled with solid, ellipsoidal fraas pellets. Subdermal invaginations and vacuities also are unlikely to have resulted from damage by predepositional transport of the Schunnemunk tree. Dermal invaginations are not scratches or gouges formed during deposition because they are

morphologically irregular over deep cortical nests and numerous examples are scattered evenly over the outer surface of the fossil (FIG. 3A).

Morphology.—Hueber's (2001) concept of *Prototaxites* as an unbranched basidiocarp (FIG. 6C) is falsified by the branching Schunnemunk tree (FIGS. 1, 2). Successive slightly uneven bifurcation of large branch meristems in the Schunnemunk tree (FIG. 3F) are comparable with branching in lichens, such as *Cladina subtenuis* (Ascomycota: Hammer 1997, 2000), and in fungal fruiting bodies, such as *Clavaria* (Burt 1922, Petersen 1964). This uneven branching is distinct from dichotomous or monopodial branching in algae and land plants (Taylor et al. 2009).

Other nematophyte trunks also have branches or knots. Especially similar is a specimen of *Prototaxites loganii* from Wirschweiler, Germany, (Heidtke 2006, Schindler and Wuttke 2006) with two permineralized

apices diverging at a low angle like the apex of the Schunnemunk tree. Other branched nematophytes include “*Prototaxites/Nematasketum*” and “cf. *Nematasketum*” (both of Edwards and Axe 2012), *Mosellophyton hefteri* (Schaarschmidt 1974, Schweitzer 1983) and coalified nematophyte rhizomorphs (Argast 1992). Although *M. hefteri* (Schaarschmidt 1974) was assigned to *Prototaxites* (a genus for permineralized remains) by Schweitzer (1983), compressed remains here are referred to the original genus *Mosellophyton* of Schaarschmidt (1974) because their branches are more slender and copiously branched than those demonstrated here and by Dawson (1888), Schindler and Wuttke (2006) and Heidtke (2006) for *Prototaxites*.

Wrinkles on the branches (FIGS. 1F, G, 2C, D) and stem of the Schunnemunk tree (FIGS. 1B, C) are comparable with waves of hyphal orientation in thin sections of other *Prototaxites* specimens (Altmeyer 1973, Hueber 2001) and do not reflect peeling of an external layer. They are not artifacts of jointing of the matrix because the fossil quarry lacks jointing with such fine spacing (SUPPLEMENTARY DATA). Similar shelves and flaps of lichens are called squamules, which are irregular projections and roll-like structures of thallus that increase photosynthetic surface area (McCune and Rosentreter 2007). Comparable transverse flaps also were shown in reconstructions of *Prototaxites* by Dawson (1888). Such leaf-like and wrinkled morphology also is widespread in algal thalli (Taylor et al. 2009) and fungal fruiting bodies (Burt 1922).

Isotopic composition.—Boyce et al. (2007) compared the wide variance of isotopic composition (-15.7 to -28.4‰ $\delta^{13}\text{C}$) for different specimens of *Prototaxites loganii* from Quebec and New Brunswick, Canada, with variance in the isotopic composition of saprophytic fungi in glacial outwash of Washington, USA, (Hobbie and Boyce 2010) and suggested that some individuals grew by saprotrophy on vascular land plants and others on aquatic algae or cyanobacteria (hypothesis 1). A similar hypothesis of mixotrophy in the liverwort hypothesis of Graham et al. (2010) also proposes that isotopic variation reflects different organic substrates. Neither hypothesis uniquely explains the spread of isotopic values.

Another possibility is that some Quebec *Prototaxites* grew around and engulfed liverwort or hornwort fragments but others engulfed vascular land plants. This could be envisaged as an isotopically varied substrate (as in hypothesis 1), but fine preservation of cell structure in fragments of a variety of other land plants within trunks of *Prototaxites* (Hueber 2001) is evidence that they were not consumed but instead were overgrown without assimilation (hypothesis 2).

Other hypotheses for isotopic variability come from lichenization, as proposed for *Prototaxites* by Retallack (1994) and Selosse (2002). Lichens with cyanobacterial photobionts such as *Nostoc* and *Gloeocapsa* are isotopically heavy (Smith et al. 1998), comparable to Kranz anatomy (C_4) plants (Vogel et al. 1977). In contrast, lichens with chlorophyte photobionts, such as *Trebouxia*, are isotopically light, comparable with Calvin-Benson cycle (C_3) plants (Smith and Griffiths 1998). Individual lichen species of several clades (Lecanoromycetes, Lichinomycetes) are photosymbiodemes or chimeras, in having multiple and changing photobionts (Hawksworth 1988, Smith et al. 1998, Aptroot and Schumm 2010). The thallus form and species of lichens are determined by the fungus, not the photobiont (Brodo et al. 2001), but carbon isotopic composition is determined by the photobiont. Divergent carbon isotopic compositions thus can arise from different photobionts of chimeric individuals of the same species (hypothesis 3).

Single species of lichen (*Lichina pygmaea*) approach C_3 isotopic composition when growing in air but conserve CO_2 in a manner comparable with Crassulacean acid metabolism (CAM; Mooney et al. 1977) when submerged in water (Raven et al. 1990). Algae, hornworts and liverworts also develop CO_2 -conserving photosynthetic pathways (Raven et al. 2002, Fletcher et al. 2004) when that gas is limited by submergence. This produces hypothesis 4, in which *Prototaxites* may have been like modern mangroves or swamp cypresses that thrive both submerged and emergent or comparable Devonian cladoxyl fossil trees *Wattieza* cf. *W. casasioi*, found in both well drained and waterlogged marine-influenced paleosols (Retallack and Huang 2010).

Thus there are four viable hypotheses for the wide range of carbon isotopic compositions observed in *Prototaxites loganii* by Boyce et al. (2007) and clear evidence for only inclusion without assimilation (hypothesis 2) of other plants (Hueber 2001 pl. VII figs. 1, 2). The other hypotheses could be tested by combined histological-isotopic studies and by studies of *Prototaxites*-bearing paleosols for isotopic variation, near-marine, waterlogged or well drained conditions (Driese and Mora 2001, Hillier et al. 2008). Our compilation found the greatest variance in a single living lichen species in the maritime lichen *Lichina pygmaea* (-9.72 to -15.47‰ $\delta^{13}\text{C}$; Raven et al. 1990) and the epiphytic lichen *Hypogymnia physodes* (-21.07 to -25.35‰ $\delta^{13}\text{C}$; Smith and Griffiths 1998). Only three of the 20 reported carbon isotope analyses of *Prototaxites* are within the CAM or C_4 photosynthetic range (Boyce et al. 2007). Isotopic composition and variation in composition does not uniquely support interpretation of *Prototaxites* as a saprophyte.

Carbon isotope composition of the Schunnemunk tree is comparable with that of a wide variety of Calvin-Benson cycle (C_3) plants and lichens with chlorophyte photobionts, such as *Trebouxia* (Smith and Griffiths 1998). In contrast, modern lichens with cyanobacterial photobionts such as *Nostoc* and *Gloeocapsa* are isotopically heavy and comparable with Kranz anatomy (C_4) plants (Smith et al. 1998). A final line of evidence for photobiont affinities is organic chemical composition of *Prototaxites*, which clusters with algae rather than vascular land plants (Niklas 1976a, b).

HIGHER TAXONOMY OF *PROTOTAXITES*

We agree with inclusion of *Prototaxites* by Edwards et al. (2013) within the extinct order Nematophytales but are not persuaded by Hueber's (2001) inclusion of *Prototaxites* and its extinct order within Basidiomycota, because most of the tubular cells are aseptate. Because evidence from the Schunnemunk tree now indicates that *Prototaxites loganii* was lichenized, Hueber's (2001) interpretation as giant basidiocarps needs to be reassessed in terms of lichen mycobiont affinities. For example, partial clamp connections of Hueber's (2001 pl. VIa) are lateral lobes of cells found both near septae-like true basidiomycotan clamp connections but also well away from septae. These resemble appressoria of lichens (Brodo et al. 2001). Flanged septal pores of *Prototaxites* lack additional compelling details of basidiomycotan dolipores, as indicated by Schmid (1976), and also are comparable with septal pores of Mucorales. Small, highly branched cells were interpreted as basidiomycotan dendrophyses (ramose cystidia) by Hueber (2001 p 145), despite his counter-observation, "They are not freely dispersed in the hymenium as in a modern fungus but appear to line the inner walls of large thin-walled generative hyphae." Hartig nets of ectomycorrhizal fungi *Laccaria amethystina* and *Lactarius subsulcis* (Basidiomycota) on beech (*Fagus sylvatica*: Brand and Agerer 1986, taf. 6c) are similar but also external and have fewer tapered and splayed hyphal ends. Similar cell-penetrating structures are haustoria of parasitic *Discinella schimperi* (Ascomycota) on moss (*Sphagnum squarrosum*: Redhead and Spicer 1981 fig. 6.8). Thus the highly branched cells within some hyphae of *Prototaxites* (Hueber 2001 pl. VIId) might belong to another parasitic or symbiotic fungus.

Hueber (2001 fig. 5B) compared curling and enclosing hyphae within cortical nests of *Prototaxites loganii* with spreading clusters of hyphae in the bracket fungus *Coltrichia* (Basidiomycota), but in that fungus the copiously branching hyphae are scattered among large, straight hyphae and not clustered in nests (Corner 1991). Furthermore, hyphae within the

cortical nests of *P. loganii* are curled inward, open-ended and frayed, not branched with acute end walls like the short-branched hyphae of *Coltrichia* (Corner 1991). Cortical nests of another extinct nematophyte *Nematasketum* are full of degraded spherical to ovoid masses of organic matter embraced by inwardly curled hyphae (Edwards and Axe 2012). These also are comparable with cortical nests of the Schunnemunk tree (FIG. 3B–D), whereas coltricioid clusters of bracket fungi branch into elongate open spaces (Corner 1991). Cortical nests may be regarded as overgrown internal cephalodia and subdermal nests as photosynthetic internal cephalodia within lichen terminology.

Also counting against basidiomycota affinities of *Prototaxites* is the lack of evidence for definitive Devonian Basidiomycota in the diverse early Devonian fungal flora of the Rhynie chert (Taylor and Taylor 2000; Taylor et al. 2004, 2006) and the lack of basidiospores in Silurian-Devonian palynofloras (Wellman 2006, Beck and Strother 2008). In contrast, lichens with aseptate hyphae and cyanobacterial symbionts have been found in the Rhynie chert (Taylor et al. 1997), as well as in Precambrian rocks (Yuan et al. 2005). Stalked spheres (*Germinosphaera*) and isolated spheres (*Leiosphaeridium*), comparable with spores and vesicles of Glomerales (Pirozynski and Dalpé 1989), are common in Ordovician (Redecker et al. 2000), Silurian (Beck and Strother 2008) and Devonian (Wellman 2006) palynofloras within the age range of *Prototaxites* and comparable fossils (SUPPLEMENTARY DATA). Glomeralean affinities of leiospheres are not universally accepted because they also are similar to marine algal cysts (Moczyłowska et al. 2011). Nevertheless, there remains no convincing spore or megafossil evidence for Devonian or older Basidiomycota (Berbee and Taylor 2010).

These observations favor the placement of Nematophytales within the phylum Glomeromycota or the subphylum Mucoromycotina (unassigned phylum of Hibbett et al. 2007: formerly "Zygomycota"), or both, because the wide hyphae of *Prototaxites* are aseptate, like the former, but the narrow and curling hyphae are sparsely septate, as in the latter. *Prototaxites* may have included several species of fungus, in addition to fungal parasites, as in many modern lichens (Hawksworth 1988). Modern symbiotic glomeromycotans include living *Geosiphon pyriformis* (Archaeosporales, Glomeromycota: Schüßler 2012; Retallack et al. 2013a, b), which lacks a solid thallus and has expanded terminal mycelial cells ("bladders") enclosing heterocystic cyanobacterial photosymbionts of *Nostoc punctiforme*. Such "endolichens" differ from ordinary lichens, which have haustorial capture of photobionts (Brodo et al. 2001), and lichens have been defined to exclude endosymbiotic organisms

such as *Geosiphon* (Hawksworth and Honegger 1994). *Geosiphon*-like fossils as old as 2200 Ma are now known (Retallack et al. 2013a, b). Thallose lichenized Glomeromycota include permineralized lichens (unnamed) from the Ediacaran (550 Ma) Doushantuo formation near Weng'an, China, (Yuan et al. 2005) and diffuse lichen-like Mucoromycotina include *Winfrenatia reticulata* from the early Devonian (410 Ma), Rhynie chert of Scotland (Taylor et al. 1997). The reticulate mycobiont and cyanobacterial phycobiont of *Winfrenatia* is very different from *Prototaxites*, which has yet to yield anything like zygospores. Extinct lichenized fossil Glomeromycota and Mucoromycotina are surprising for fungal phyla now known largely as mycorrhizae and pin molds, respectively. Because large aseptate hyphae are the principal structural elements of *Prototaxites*, our preference is to place *Prototaxites* and Nematophytas provisionally within Glomeromycota.

GROWTH MODEL FOR *PROTOTAXITES*

Prototaxites was a large perennial structure with distinct growth rings, which overgrew injury and photosynthetic tissue, generally comparable with growth zonation of crustose lichens (Hill 1981) and trees (Hueber 2001). Our description here of the outermost layers of the trunk enables reconsideration of its growth.

A possible growth mechanism outlined by Hueber (2001) is that *Prototaxites* added hymenial or vegetative increments from hyphal elaboration of the exterior, as in *Lachnocladium zonatum* and *Clavaria pistillaris* (both Basidiomycota). A second possibility is that the subdermal vacuity of *Prototaxites* housed a meristematic tissue comparable with the bifacial or unifacial vascular cambium of land plants. Vascular cambium and phloem are rarely preserved in permineralized plants and are notable when found (Decombeix et al. 2010). Both hymenial and meristematic growth zones are unlikely because of three observations: (i) highly variable width of single growth rings, which appear eccentric in different directions for consecutive rings (Schweitzer 1983 pl. 3 fig. 1), (ii) delayed repair of breaches in undamaged growth rings after as many as 10 growth increments (Hueber 2001 pl. VII figs. 5, 6) and (iii) common small inclusions of vascular land plants (Hueber 2001 pl. VII figs. 1, 2). Individual tree rings can be slightly eccentric in the same direction throughout a branch, as in compression wood (Westing 1965, Schweingruber 2007), but *Prototaxites* trunks have many different directions of more extreme eccentricity (Schweitzer 1983) than known in living trees. Breaches in growth rings that were repaired after many increments are unusual in showing no damage of the subjacent ring

and a persistent seam between subsequent rings down to carbonized masses at the base of the seam (Hueber 2001 pl. VII, figs. 5, 6). Delays of as many as 10 rings before covering of the seam may be from long-lived epiphytic outgrowths, now represented by decayed carbonaceous masses at the base of the seams. Fungal tissues incorporate nearby plants more readily than the bark-protected cambium of tracheophyte trees.

A third alternative, proposed and preferred here, is that growth rings were an episodic sheathing of the entire trunk from a basal hypothallus, like radial growth of crustose lichens that extend in different directions depending on growing-season moisture or illumination and engulf small obstacles (Hooker 1980, Hill 1981). Sheathing scaffolding from a hypothallus might have been a loose prosoplectenchyma of aseptate hyphae, as demonstrated for another Devonian lichen, *Winfrenatia reticulata* (Taylor et al. 1997). Such a loose network could engulf adhering small fragments before filling in with paraplectenchyma and enmeshing hyphae and finishing of the exterior. Such a hypothallus also may explain the absence of knots from shed branches on the Schunnemunk tree, although such features have been documented for other specimens of *Prototaxites* by Dawson (1859). Thus young trees of *Prototaxites* also might have been branched, but branches then were shed and engulfed by hypothallial growth additions. Varied thickness of rings by this hypothesis could reflect filling of knots from shed branches, damage by boring or burrowing or fertilization by fecal pellets lower down on the trunk. Borings and fecal pellets have been documented for *Prototaxites loganii* by Labandiera (2007). The rays in the trunk of *Prototaxites* are without parallel in living fungi and lichens and might have been channels where "pushing hyphae" thrust "travelling algae" (postulated for some modern lichens by Nienberg 1926) outward into the newly sheathing hypothallial growth ring. Photobionts entrapped within the tall trunks of *Prototaxites* would have become less productive as they became isolated from light. Perhaps appressoria grip then was relaxed, and released algae were buoyed by outward hyphal growth into these empty spaces. The concept of "pushing hyphae" is controversial for modern lichens, which are low enough to engulf new algal symbionts (Hill 1981). Growth rings in crustose lichens and bracket fungi are often annual, but there are too many exceptions (Hooker 1980, Hueber 2001) for this to be assumed also for *Prototaxites*.

SYNECOLOGY OF *PROTOTAXITES*

Our reconstruction of Middle Devonian *Prototaxites loganii* as a branching, tree-sized lichen (FIG. 7A)

would have been the largest known free-standing lichen or fungus ever. "Free-standing" is an important distinction because the largest known living fungi are supported by or dependent on trees and soil. The fungal mycelia of honey mushrooms (*Armillaria ostoyae*) cover up to 9.7 km² of soil but form mushrooms only about 3 cm diam (Smith et al. 1992). Attached bracket fungus (*Fomitopsis officinalis*) on vascular plant tree trunks can reach lengths of 1 m (Blanchette et al. 1992), and Methuselah's beard lichen (*Usnea longissima*) hangs at least 3 m from 30 m tall trees (Brodo et al. 2000). The largest free-standing mushroom (*Termitomyces titanicus*) is 1 m tall and 1 m diameter (Wood and Thomas 1989), and the tallest podetiate lichens are 18 cm tall *Cladonia maxima* colonies (Brodo et al. 2001). At 8.83 m the Schunnemunk tree was much bigger, and known relationships between stem diameter and height (SUPPLEMENTARY FIG. 4, SUPPLEMENTARY TABLE IV) can be used to estimate that other massive trunks of *Prototaxites loganii* were 22.3 ± 0.9 m tall (Saudi Arabian specimens of Hueber 2001, dated to Givetian).

Prototaxites loganii and other prototaxaleans towered over land plants before and during their Late Silurian to Early Devonian increase in size and abundance. In rocks of age comparable with the Schunnemunk tree (Middle Givetian), cladoxyls (*Duisbergia* sp.) from the Catskill front have been estimated to have been only 2.9 ± 0.9 m tall and progymnosperms (*Svalbardia* sp.) only 1.9 ± 0.9 m tall (Retallack and Huang 2011). Later, during the Devonian (earliest Frasnian), cladoxyls (*Wattieza* sp. cf. *W. casasi*) might have been 10.7 ± 0.9 m tall and progymnosperms (*Callixylon* sp.) perhaps 4.0 ± 0.9 m (Retallack and Huang 2011). *Pitus primaeva*, seed fern trunks, from the Early Carboniferous (341 Ma) Middle Border Group of Kingwater, Scotland, were 26.6 ± 0.9 m tall (Retallack and Dilcher 1988). *Pitus primaeva* is the oldest fossil known to have been taller than *Prototaxites*, and no geologically younger nematophytaleans are known (SUPPLEMENTARY TABLE V). Direct competition between *Prototaxites* and vascular land plants is revealed by inclusion of undecayed vertical plant fragments within *Prototaxites* trunks (Hueber 2001 pl. VII figs. 1, 2). Lichens are currently overgrown by vascular land plants in all environments except sites of hard substrate, cold temperature or low nutrients (Retallack 1992). The fastest current growth rates of podetiate lichens (*Cladonia* spp.) grazed by reindeer (*Rangifer tarandus*) are 3–5 mm·y⁻¹ (Pegau 1968, Lindsay 1975), much slower than those of vascular land plants (160–3160 mm·y⁻¹; Coley 1988). Huge lichens such as *Prototaxites* thus could have prevailed before Middle Devonian evolu-

tion of tree-sized vascular land plants (Retallack and Huang 2011).

Prototaxites lived at a time of many other fungi, best known from the Early Devonian Rhynie chert of Scotland, which has yielded fossils of saprophytic chytrids and oomycotans, mycoparasitic chytrids, phytoparasitic chytrids and pyrenomycete ascomycotans, glomeralean arbuscular endomycorrhizae and reticulate mucoromycotinan lichens (Taylor et al. 1997, 2004, 2006, 2009; Taylor and Taylor 2000; Krings et al. 2010). Finely branching structures within *Prototaxites* regarded as dendrophyses by Hueber (2001) and carbonized remains within long-lived growth disruptions (Huber 2001 pl. VII figs. 5, 6) might have been haustoria and thalli, respectively of other symbiotic or parasitic fungi. *Prototaxites* interpreted as a saprophyte would have been dependent on large amounts of plant and other organic matter in the soil (Hueber 2001, Boyce et al. 2007), but *Prototaxites* interpreted as a lichen would have generated much of its own nutrition from symbiotic photobionts independent of substrate. Nematophytes are prime suspects for unusually large and diffuse rhizomorph systems seen in red, organic-lean Silurian and Devonian paleosols (Driese and Mora 2001, Hillier et al. 2008).

CONCLUSIONS

Our new reconstruction is more like that of Dawson (1888 fig. 6B) than other reconstructions (FIG. 6C–E). Dawson (1859, 1888) inferred branches from his documentation of knots and small axes of comparable diameter and would not have known of the Schunnemunk tree because it was fully excavated by 1895 (Ries 1897, Prosser 1902). Dawson's reconstruction is more like a candelabra cactus (*Euphorbia ingens*) or saguaro cactus (*Cereus giganteus*) than our reconstruction, which is more like a sparsely branched boojum (*Fouquieria columnaris*; Benson 1982). Although comparable in architecture with modern succulents, *Prototaxites loganii* was not a flimsy succulent but a dense organism (Hueber 2001). We also could not find a Fibonacci pattern of parastichies for the branches (FIG. 2E), which in *Prototaxites* are more like the uneven-paired branching seen in lichens (*Cladina subtenuis*; Hammer 1997, 2000).

Prototaxites loganii was a unique organism without exact parallel in the modern world, and we agree with Edwards et al. (2013) that it should be placed in the extinct order Nematophytales. Because there is no clear evidence of clamp connections, sterigmata or dendrophyses, Hueber's (2001) inclusion of *Prototaxites* in Basidiomycota is considered doubtful. The wide

hyphae of *Prototaxites* are aseptate as in Glomeromycota and the narrow and curling hyphae are porate and sparsely septate as in Mucoromycotina. Prototaxales could be placed within either or both taxa like other multispecies lichens (Hawksworth 1988), but structural dominance of large aseptate hyphae inclines us to provisionally prefer Glomeromycota.

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