Article

Enigmatic fossil plants with three-dimensional, arborescent-growth architecture from the earliest Carboniferous of New Brunswick, Canada

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SUMMARY

The evolution of arborescence in Devonian plants, followed by their architectural radiation in the Carboniferous, is a transition fundamental to Earth-system processes and ecological development. However, this evolutionary transition in trees is based on preserved trunks, of which only a few known specimens possess crowns. We describe Mississippian-aged (Tournaisian) trees with a unique three-dimensional crown morphology from New Brunswick, Canada. The trees were preserved by earthquake-induced, catastrophic burial of lake-margin vegetation. The tree architecture consists of an unbranched, 16-cm-diameter trunk with compound leaves arranged in spirals of ~13 and compressed into ~14 cm of vertical trunk length. Compound leaves in the upper ~0.75 m of the trunk measure >1.75 m in length and preserve alternately arranged secondary laterals beginning at 0.5 m from the trunk; the area below the trunk bears only persistent leaf bases. The principal specimen lacks either apical or basal sections, although an apex is preserved in another. Apically, the leaves become less relaxed toward horizontal and are borne straight at an acute angle at the crown. The compact leaf organization and leaf length created a crown volume of >20–30 m^3. This growth strategy likely maximized light interception and reduced resource competition from groundcover. From their growth morphology, canopy size, and volume, we propose that these fossils represent the earliest evidence of arborescent subcanopy-tiering. Moreover, although systematically unresolved, this specimen shows that Early Carboniferous vegetation was more complex than realized, signaling that it was a time of experimental, possibly transitional and varied, growth architectures.

INTRODUCTION

Trees (e.g., *Wattieza*/*Eospermatopteris*[1]; hereafter, *Wattieza*) first appear in the Mid-Devonian ~393–383 Ma,[2] although modern woody trees, typified by *Archaeopteris*, don't appear until about 10 million years later.[2] Evidence of arborescence is based primarily on mudcast, sandcast, or permineralized stumps or extensive rooting structures in paleosols (fossilized soils[3]). Under unique preservational circumstances, these early trees were fossilized with rooting-and-crown structures attached to their trunks.[1,4] Permineralized boles of varying dimensions are common in the fossil record following the production of extensive secondary xylem and wood evolution. Yet, the number of examples remains low, restricted to a few dozen transported logs spanning tens of millions of years. As with logs found in recent woody accumulations,[5,6] these trunks generally lack bases and/or rootstocks and are without canopies.

Intact trees remain rare in the Paleozoic record until their preservation in peat-forming forests of the latest Early Carboniferous (Serpukhovian[7]). At ~350 Ma, trees become more common as stumps with intact rooting structures,[8] or trunks buried *in situ* to heights of 5–7 m with rooting structures[9] or canopy branches.[10] Growth architectures of these taxa, assigned to spore-bearing (e.g., lycophytes, pteridophytes, and equisetaleans) and seed-bearing (gymnosperm) groups across the systematic spectrum, are well documented[11] and form the basis for Late Paleozoic forest reconstructions. However, prior discussions of Tournaisian species diversity[12–14] have not focused on floral architecture and broader ecological structure, and it remains unclear how these have been conceived. Therefore,
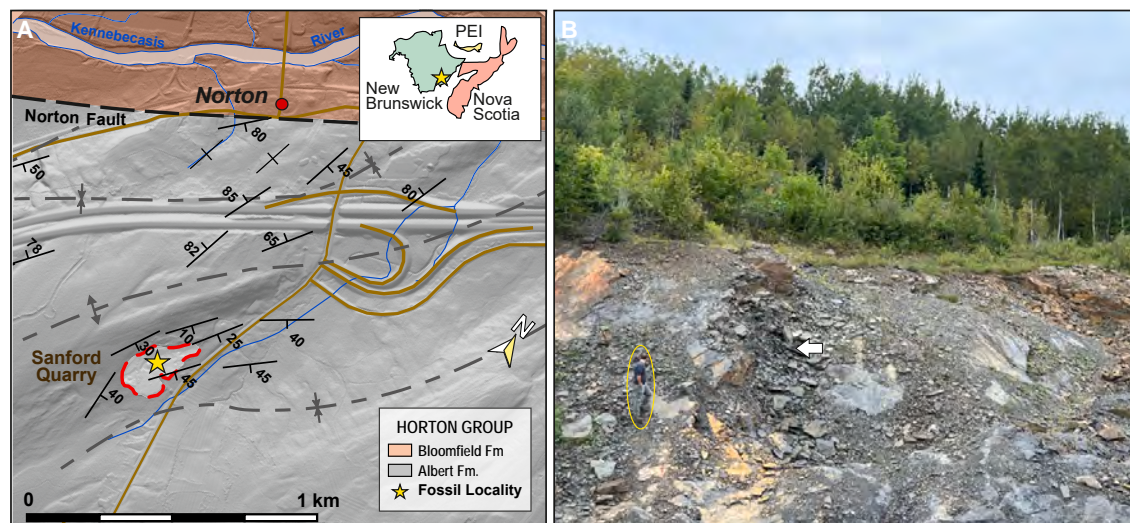
Figure 1. Sanford Quarry locality, New Brunswick, Canada

(A) Geologic map of Upper Devonian-Lower Carboniferous strata exposed around Norton (red dot) and the Sanford Quarry (yellow star; N 45.627786°, W 65.691610°). Scale in km. Inset: Canadian Maritime Provinces.

(B) August 2023 quarry exposure where white arrow shows the location of primary tree crown. M. Stimson (yellow ellipse) for scale.

although tree-growth architectures of the Middle-Late Devonian are bookended by Late Carboniferous taxa, there is a dearth of data from Mississippian specimens about tree-growth architecture (e.g., *Pitus* and *Protopitys*) and ecosystem structure.

We present a new tree-crown architecture based on exceptional three-dimensional specimens from a Tournaisian (~359–347 Ma) rift lake in New Brunswick, Canada. These fossils display an extraordinarily dense spiral-branching pattern and produced long, functional, compound leaves retained along a narrow trunk, resulting in a tree-crown volume of >20–30 m³. The scale of this plant's form indicates a growth strategy of maximizing light interception and reducing resource competition from ground cover. From the trunk-and-canopy dimensions at the time of burial, the plant's stature conforms to that of a subcanopy element.

Geological setting

Specimens come from Sanford Quarry, New Brunswick, Canada (Figure 1A), belong to the Hiram Brook Member,[15] Albert Formation, and are Tournaisian based on palynostratigraphy (see supplemental information). The Sanford Quarry succession (Figure 1B; N 45.627786, W 65.691610) accumulated in a rift-lake setting and comprises deep and marginal-lake shoreface and delta-top deposits.[16,17] Fossils occur in an ~1.5 m thick gray sandstone-and-siltstone over a limited area (Figure 1B). The succession represents slump-block sedimentation resulting from earthquake activity. Here, trees with attached lateral compound leaves are preserved with disarticulated plant axes, pinnae, and pinnules.

RESULTS

Five trees are preserved in close proximity, with the most complete specimen serving as the basis for the current report. The fossiliferous block (Figures 2A–2C), excavated at ~2.3 m

long × ~2.0 m wide, is at the New Brunswick Museum (NBM), Saint John. One trunk, showing the apical region, remains *in situ* but is to be excavated and curated at NBM along with other megafossils and palynological samples.

The principal specimen is a monopodial trunk, 12–16 cm wide, extending for 2.25 m in length (Figures 2A, 3, and 4; NBMG 22403). It is missing both a base and apex, but another, narrower trunk (7–8 cm diameter) with attached leaves retains the apex (Figure 2B). Compound-leaf petioles depart from the lower middle trunk and continue apically; petioles are partially preserved or absent in the lower part of the specimen. Petioles/rachides are three-dimensionally preserved (Figure 2C) and organized into tightly compressed spirals. Leaves depart at an acute angle, curve outward ~5–6 cm, and project up to 1.75 m in length distal to the trunk. Leaves are truncated by the edge of the block. The first *in situ* secondary laterals occur ~0.5 m distal to the petiole base. No evidence exists of attached laminate structures in the principal specimen. An isolated petiole with attached second- and third-order rachides lies adjacent to several leaves of the large trunk (Figure 5E), with petiole features identical to the principal specimen. Poorly preserved laminae conform to *Sphenopteridium*[18] (Figure 4F) and occur in close proximity to parts of the tree.

Preservational modes

The tree exhibits an array of pre-burial decay states resulting in two preservational modes that are adpression[19] and mud-filled casts of hollowed voids (Figures 2, 3, 4, and 5). Post-burial (secondary) alteration includes calcite crystallization around organic matter (Figure 2D). Adpression typifies the basal trunk, where coalified leaf bases occur (Figures 2A and 3A). Commonly, coalification remains were sloughed off during excavation and investigation, leaving leaf-base impressions (Figures 2A and 3B). Coalified tissues cover petioles in the upper trunk (Figure 3B). Mud-filled hollowed axes (portions of the trunk and petioles)
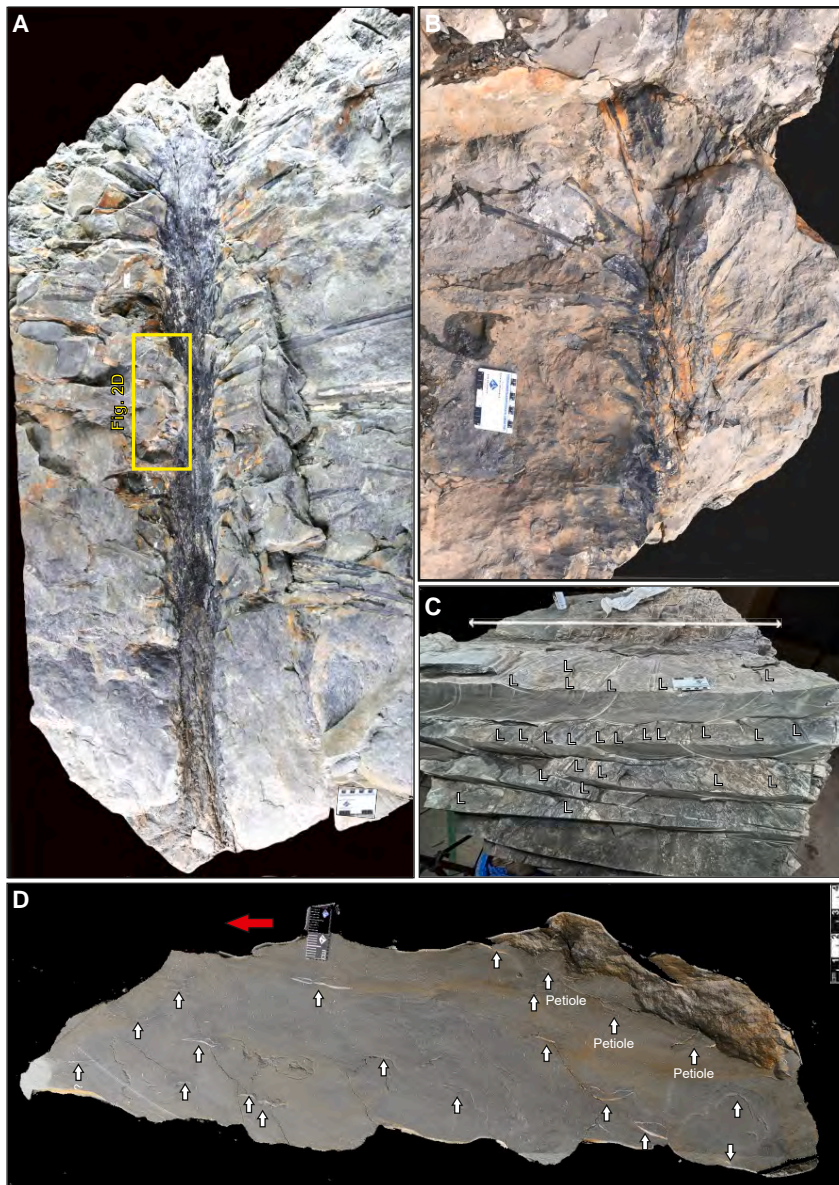
Figure 2. Tournaisian tree with spirally arranged compound leaves

(A) Block surface showing contorted (decayed) leaf bases on lower trunk and upper trunk encircled with near-perpendicularly oriented petioles. Yellow rectangle counterpart in (D). NBM 22403/1. Scale in cm and inches.

(B) Metashape model using field images of uppermost 20+ cm of NBM 23141 with preserved tree apex. Petiolar orientation ranges from ∼45° below the apex to ∼30° at the apical terminus. All leaves are incomplete. Scale in cm and inches.

(C) Lateral oblique view of curated block where a surficial trunk (double arrow line) is surrounded by petioles (L) preserved on multiple layers, demonstrating 3D preservation. NBM 22403/1. Scale in cm and inches.

(D) Tangential longitudinal surface of sectioned and polished counterpart (Figure 4A) showing petiolar density and disposition (white arrows) along a 36 cm interval. Here, petioles are either partially mudcast or without mud-fill and outlined in, or identified by, a calcite envelope in response to decay and cation interaction after burial. Red arrow points toward apex. Scale in cm/mm. NBM 22403/3.

are interior casts, with petiolar castings ranging from complete, or near complete, fills (Figures 4B and 4C) to incomplete structures (Figure 2E). Petiolar cross-sectional geometries are best seen in the former states (Figure 4B).
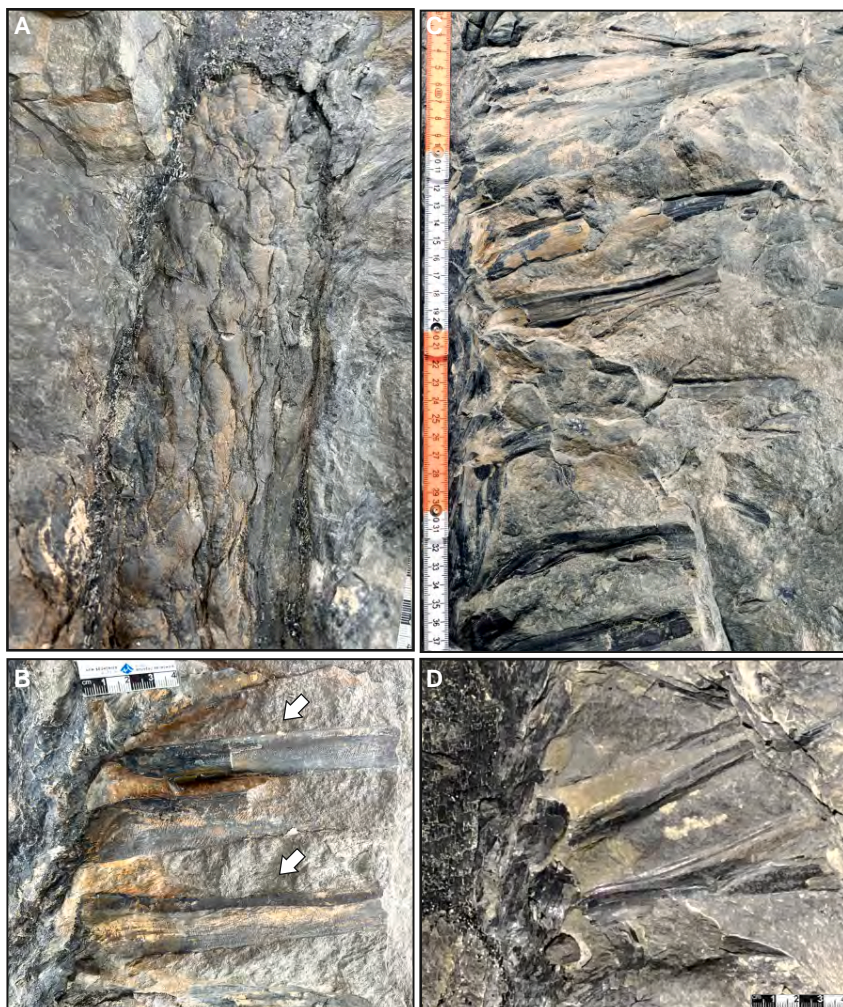
Tree trunk characteristics

The maximum, exposed, monopodial-trunk width is ∼16 cm near the specimen's top, whereas near the base it is ∼12 cm, resulting from decay and tissue collapse, leaving leaf bases distorted and crowded (Figure 2A). Distinct differences are manifest in the lower and upper trunk. Surficial features in the lower trunk are in convex relief, representing elliptical, poorly preserved leaf bases (Figure 3A). Their convex relief may reflect either the subepidermal organization of original cortical tissues or the degree to which mud filled voids after decay. Leaf bases are slightly compressed laterally, a decay feature, measuring ∼6.5 cm in length and ∼2 cm in width (Figure 3A), and are best preserved

directly below where the lowest compound-leaf departs the trunk. Leaf bases are unrecognizable at the specimen's base, whereas they are obscured in the upper trunk by the retention of compound leaves. No evidence exists that leaves were oriented downward, parallel to the trunk, forming a non-functional leaf skirt.

Compound leaves and petiole geometry

Compound leaves and basal (broken) petioles cover the upper 0.75 m of the trunk. Petiolar bases are decurrent, depart at an ∼45° angle, and extend upward for ∼7 cm before changing their orientation (100°–115°) and extend distally. Leaf features are a function of (1) orientation in the siltstone matrix, (2) extent of decay and infill, and (3) post-burial vertical compression following burial (Figure 2C). The angle of departure toward the growing apex becomes more acute, ultimately approaching ≤ 20° (Figure 2B). Adjacent to the trunk, petioles are 2.7–3 cm wide (Figures 3B and 3C), tapering to ∼2 cm in the first ∼10 cm, and then to 1.5–2 cm distally. A distinctive medial groove occurs on the adaxial surface (Figures 3C, 3D, 4C, 5A, 5C, and 5D) in the proximal petiole, reflected as a cordate geometry in cross-section (Figure 4B). Distally, the cross-sectional geometry becomes reniform before transitioning to triangular-ovate (Figure 6C). Axes are ∼1 cm in width at a distance of ∼1.7 m (Figure 4A). All axes exhibit fine longitudinal striations (Figure 5B), indicating a resilience of peripheral cells that maintained petiolar cross-sectional shape during sediment infill and before compression and sediment dewatering.

Thirteen laterals depart along only ∼14 cm of trunk length (Figures 2A, 3, and 4A). These are in a non-Fibonacci, estimated

compound, non-dichotomizing leaves over a trunk interval of only 0.75 m, and another specimen (Figure 2B) extends compound leaves to the apex (Figure 6A). Based on the rate of leaf-diameter reduction distal to the trunk, we estimate that each leaf grew ~1 m more before termination, resulting in a length of 2.5–3 m. Hence, the trunk plus laterals likely attained a 5–6 m diameter and had a calculated cylindrical volume of at least 20–30 m^3.

Systematics and diagnosis
Systematics
Class *Incertae sedis*.

Sanfordiacaulis densifolia gen. et sp. nov. Gastaldo et al.

Etymology
Generic name derives from the quarry locality and its owner, Laurie Sanford. The species epithet derives from the tight, compact organization of compound leaves.

Holotype
NBMG Collection 22403/1 part and counterpart to trunk 22403/2; (NBM, New Brunswick E2K 1E5, Canada; Figure 2A).

Locality, horizon, and age
Sanford Quarry, Norton, New Brunswick, Canada. Grid Ref: N 45.627786, W 65.691610. Stratigraphy: Hiram Brook Member, Albert Formation, Horton Group. Age: Carboniferous, late Tournaisian, eastern Canada *Spelaeotriletes cabotii* subzone of the *Vallatisporites vallatus* Biozone/Europe upper part of the *Spelaeotriletes pretiosus-Raistrickia clavata* (PC) Biozone, ~355–350.5 Ma (Figure S1).

Combined generic and specific diagnosis
Adpression and mudcast arborescent fossil. Monopodial (pseudomonopodial) trunk, compound undichotomized leaves in vertically compressed (estimated) 1/13 phyllotaxis. Base missing. Leaf bases are in proximal trunk, and attached leaves are along distal trunk. Petioles depart at ~45° angle, reflex to ~90°, extending >1.7 m. Finely striate petiole and rachis; strong, tapering, longitudinal medial groove reflects cross-sectional cordate to triangle to elliptical geometries distally. Secondaries with flared base arise ~0.5 m distally; pinnae

1/13, very tightly compressed and dense spiral (Figure 3A), and it is estimated that the 75 cm of foliated trunk bore >200 laterals, based on measurements of petiole distribution (see supplemental information). All laterals are incomplete. Surficial examples are preserved for >1.7 m in length and relaxed to an ~90° angle distal to the trunk. Although surfaces are finely striate (Figure 5B), there is no evidence of strong supportive fibrous tissues.

Secondary laterals
Second-order, alternating laterals appear 50 cm along the leaf and depart at a 90° angle (Figures 3A, 3C, and 3D); no third- or higher-order axes appear on the principal specimen. Secondary laterals, each with a flared base (Figure 5D), are 3–4 mm in width and preserved for 3–4 cm. Some petioles (Figure 4A) exhibit alternating secondary axes (Figure 5A), and an associated petiole with two orders of laterals (Figure 5E) exemplifies leaf complexity. In only one case is a laminate photosynthetic structure preserved in attachment to a rachis with features identical to those of the principal specimen (Figure 5F).

Model reconstruction
Applying the non-woody allometric equation of Niklas,[20] the buried principal specimen attained a minimum height of 2.65 m (Figure 6). This specimen (Figure 2A) exhibits >200 (estimated)

Figure 4. Trunk and petiolar features

(A) Trunk and basal parts of leaves (right; NBM 22403/1) with adjacent block showing their continuation, indicating that leaves were longer than shown on main block. The counterpart removed and sectioned in Figure 2D originates from the upper right (NBM 22403/2). Scale in cm and inches. NBM 22403-3.

(B) Petiole cross-sections proximal to the trunk exhibiting a heart-shaped geometry with an adaxial depression appearing as a longitudinal furrow in compressions. Scale in mm. NBM 23142.

(C) Mudcast petiole proximal to the trunk showing adaxial groove and fine striations. NBM 22403/2. Scale in cm and mm.

and pinnules unknown. Associated pinnules assigned to *Sphenopteridium*.

DISCUSSION

The end-Devonian saw the onset of a transition in arborescent vegetation[21] from Middle Devonian landscapes, dominated by spore-bearing cladoxylaleans (e.g., *Wattieza*[1] and *Calamophyton/Duisbergia*[4]) and progymnosperms (e.g., *Archaeopteris*[22]), to the addition of gymnosperms (e.g., *Calamopitys*[23]). In contrast, Mississippian megafloras became populated by club mosses (e.g., cf. *Lepidodendropsis*[24]), horsetails (e.g., *Archaeocalamites*[25]), various gymnosperms, and rare leptosporangiate and marattialean ferns.[18] These plants assembled in

systematically diverse communities, unlike today.[26] The growth architectures of several groups are well-established from adpressions, whereas other organization-and-growth habits are reconstructed solely from anatomically preserved, often small and fragmentary, permineralized specimens attributed to trees/shrubs and vines. Tall trunks without preserved crowns are reported in *Pitus* and *Protopitys* (Figure 7).

Our understanding of many Mid-Devonian to Early Carboniferous trees comes from a handful of localities scattered globally. Stumps and stump fields of Middle-Late Devonian,[2,38–40] Mississippian,[8,41] and Early-Middle Pennsylvanian[10,42] trees are, in general, restricted to coastal wetlands. Here, cast or permineralized bole heights are limited <1 m or more,[43] and stump fields with rooting are limited to areas exposed over a few hundreds
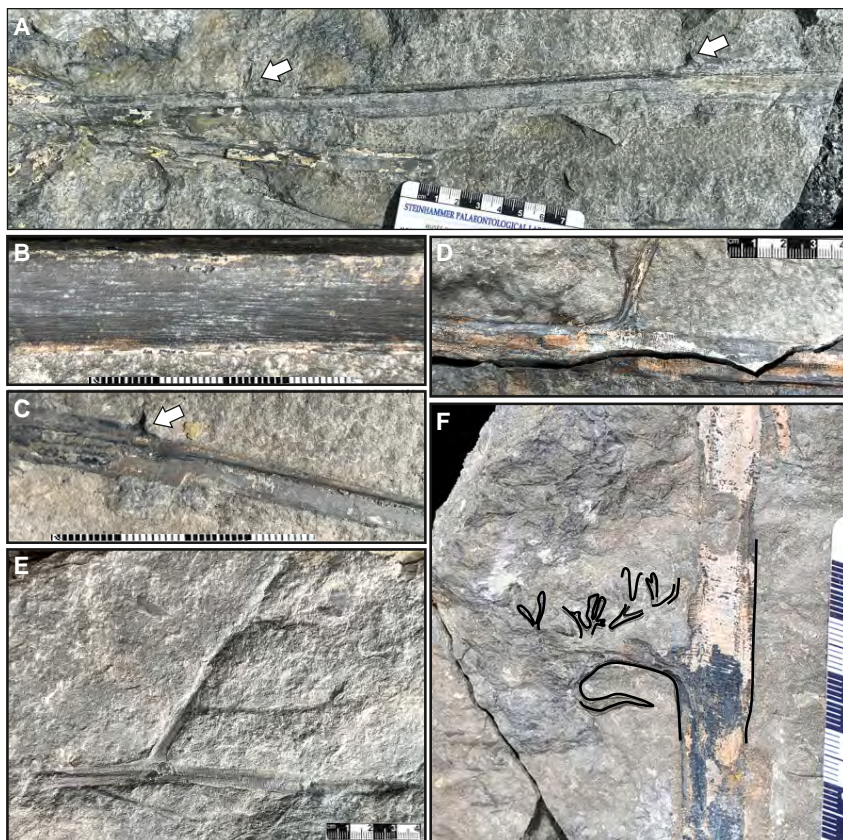
Figure 5. Evidence of compound leaves and pinnules. NBM 22403/2

(A) Portions of two leaves in close spatial proximity. Arrows indicate bases of second-order laterals departing from upper axis. Scale in cm and mm.

(B) Petiole/rachis detail showing fine striations and adaxial groove (top). Scale in mm.

(C) Leaf rachis with white arrow indicating departure of another lateral. Scale in mm.

(D) Longer second-order lateral departing from rachis. Scale in cm and mm.

(E) Isolated rachis on large block with second- and third-order laterals. Scale in cm and mm.

(F) Rachis with poorly preserved, *Sphenopteridium*-like, pinnules (black outline) departing from second-order axes. Scale in cm and mm.

of square meters.[2,42] Woody, often permineralized long logs >10 m[31,44–46] are in river deposits rather than in growth position, preserving neither roots nor crown. Their architectural reconstructions are based on branch anatomy.[47] Entire plants are preserved under unusual and exotic taphonomic circumstances.[2,4,9,10] Yet, to date, no arborescent Mississippian taxon is known where the trunk and crown are preserved together. As such, the architectural organization of *S. densifolia* contrasts with previously described Paleozoic trees (Figure 7).

Late Paleozoic tree architectures and ecological implications

Our perception of Late Paleozoic landscapes, their vegetation, growth architectures, and ecological relationships is restricted to several windows of exceptionally preserved fossils (Fossil Lagerstätten). Here, stumps, trunks, and complete or nearly complete plants occur, and include the oldest Devonian stumps in Gilboa, New York, USA. These plants are assigned to *Wattieza*[48] in the enigmatic Cladoxylales[49] (Figure 7). Individual trees in mixed-age, monodominant stands[48] are reconstructed at heights of 8 m,[1] topped by a whorled crown of forked branches. Only one whole *Wattieza* tree is known. Crown branches were deciduous, as evidenced by branch scars below the apex, restricting the functional branching structures to the plant apex. A monodominant cladoxylalean landscape may have precluded subcanopy elements, although groundcover and/or lianas of an enigmatic rhizomatous progymnosperm, *Tetraxylopteris*, were present.[48] A smaller Middle Devonian cladoxylalean

tree, *Calamophyton* (= *Duisbergia*), ~5 Ma older, of Lindlar, Germany,[4] had a similar growth habit. Here, whole plants, including rootstocks and crowns, exhibit the same architecture as *Wattieza*, albeit smaller (~2.5 m height). Reconstructions of the Lindlar forest[50] are of a dense, even-aged cladoxylalean canopy with light breaks colonized by immature plants, apparently without evidence of an obvious subcanopy element.

Wood appears in Early Devonian lignophytes,[51] although extensive production of secondary xylem is first found in the progymnosperm *Archaeopteris* (wood = *Callixylon*), a pseudomonopodial tree.[47] Permineralized, decorticated *Callixylon* trunks, up to 11 m in length,[46] occur in river and open-marine deposits, without rootstocks or crowns. *In situ* tree bases with attached rootstocks[2] are reported from one Middle Devonian locality, Gilboa Quarry, NY. *Archaeopteris* bases co-occur with *Wattieza* rootstocks. Here, a unique solution of using the largest root diameter as a proxy for diameter-breast-height, *Archaeopteris* is estimated to have reached heights of 11 and 30 m.[2] Smaller *Wattieza* rootstocks in high density in-and-around the progymnosperm trees imply a tiered forest structure. All other *Archaeopteris* woodlands are reconstructed as systematically mixed[2] or gallery forests.[52] Although Late Devonian systematic diversity was relatively high compared with older assemblages, ground-cover ferns (*Rhacophyton* and *Gillespiea*), cormose lycophytes (e.g., *Lepidodendropsis* and *Lepidosigillaria*), and cupulate gymnosperms (*Elkinsia* and *Moresnetia*) continued to dominate. To date, there exists no evidence for subcanopy taxa in these communities. Rather, ecological partitioning appears to be bimodal wherein groundcover was overtopped by a tall canopy. *Archaeopteris* survived into the Mississippian whereupon other woody forest taxa replaced it[53] (Figure 7).

The systematic affinities of two Mississippian woody progymnosperms—*Pitus* and *Protopitys*—remain uncertain.[4,31,54] These taxa are found either as transported and isolated, prostrate, permineralized trunks,[21] or as isolated stumps.[55] Both are reconstructed as large trees, reaching 20 m in height (Figure 7), with successive orders of terminal branches, some
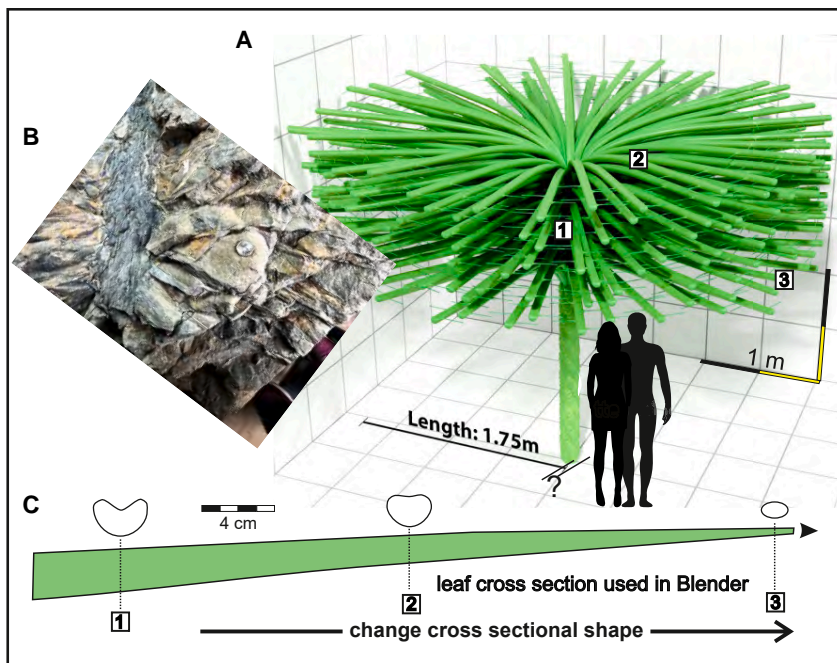
Figure 6. *Sanfordiacaulis densifolia* reconstruction

(A) Scaled reconstruction of *S. densifolia* consisting of a monopodial trunk surrounded by compound leaves in an estimated 1/13 phyllotaxis; base of trunk unknown. Change in petiolar cross-sectional geometry (see Figure 4) used in Blender model. Global average male height (1.75 m) and female height (1.6 m) are scaled adjacent to the tree for illustrative purposes. Scale in meters.

(B) Insert showing the multi-level departure of mudcast laterals for comparative purposes. NBM 22403/1. Coin for scale.

(C) Changes in proximal to distal petiole/rachis cross-sectional geometries. Numbers correlate to leaf position in (A).

reconstructed in an opposite, two-rowed arrangement.[21] Unlike coastal lycophyte-forested wetlands,[25,56] Early to Middle-Mississippian (Tournaisian-Viséan) forests have been reconstructed as even-aged stands.[57] The development of a robust subcanopy likely accompanied the expansion of peat- and non-peat-accumulating Mississippian (Viséan) coastal wetlands[57] with a burst of innovation and systematic diversification.

Late Mississippian (Serpukhovian) and Early Pennsylvanian (Bashkirian) forests are well documented due to coal mining from the Industrial Revolution onward.[11] *In situ* landscapes, either as a consequence of coseismic subsidence[9] or burial under volcanic ash,[58] provide direct insights into tree architectures and forest structure. Stumps, trunks, and crown elements of lycophytes, sphenophytes, ferns, and gymnosperms are found *in situ* or associated in these unique taphonomic settings. Each group exhibits a distinctive growth strategy. Immature monopodial lycophyte trunks are surrounded by 1-m long, spirally arranged leaves, and mature genera exhibit various lateral branching and crown architectures. Regardless, arborescent taxa exhibit a dichotomous growth pattern[59] (Figure 7). Several sphenophyte architectural models appear in the literature,[37,60] but all depict a monopodial trunk with whorled branches at successive nodes (Figure 7). Marattialean (eusporangiate) ferns become common and exhibit either a distichous or spiral arrangement of crown leaves; fossils are assigned to the compression taxa *Megaphyton* and *Caulopteris*,[32] respectively. The permineralized tree-fern taxon, *Psaronius*, exhibits a 2/7 phyllotaxy,[33] attaining heights that place it in the subcanopy.[61] In the late Viséan, medullosan pteridosperms are preserved as monocultures[35,62] and exhibit various growth architectures. Taxa in the subcanopy attained heights of ≥5 m (Figure 7) in localities where entire plants are preserved.[63] Other gymnosperms in the pre-conifer Cordaitales also are monopodial trees. Growth heights range from small trees to towering canopy elements of 48.5 m.[64,65] Orthogonal branches originate in opposite pairs or irregular

whorls, where 4–7 branches may have developed at any level. Members of the pre-conifer group grew across the continental landscape, with architectures reflecting mangrove,[66] small-to-medium understory trees,[65] to emergent canopy elements.[64] Creepers and lianas of various systematic affinity occupied both ground-cover and upper tiers, respectively. We must acknowledge a fact, which applies throughout the paleobotanical literature and rarely discussed, that the features recorded in any single plant-fossil assemblage reflect a point in time when this biomass was transferred from the living community to depositional burial site.[67] Hence, plant reconstructions reflect the ontogenetic stage of each in its life cycle at that time and may not represent the fully mature plant. Recurrent observations of plant groups over space (different geographic settings) and time (hundreds of thousands to millions of years) have yielded data on the Late Paleozoic ecological position(s) occupied by these taxa. Yet, until now, no direct physical evidence exists for Early Mississippian plants with a subcanopy stature.

The discovery of *S. densifolia*, with a conservative calculated height of >2.65 m, places it in a similar, second-tier position as Late Mississippian and Pennsylvanian-age understory pteridophytes and pteridosperms (Figure 7). Given that the maturation state of *S. densifolia* is unknown prior to burial in the Tournaisian rift lake, its height suggests a position as a second-tier forest element. As such, these plants would have been separated vertically from canopy components resulting in woodland stratification. Such stratification in modern forests is shown to be advantageous, resulting in optimized light and CO_2 utilization, benefiting both pollination and dispersal, as well as leading to enhanced structural integrity of the forest itself.[68,69] Stratification increases the range of microclimates and microenvironments, which influence the spread of forests. Vertical stratification in modern ecosystems also increases the structural complexity of all biotic elements, including impacting bacterial and fungal substrates and affecting invertebrate and vertebrate herbivory and shelter resources. The evolution of sun-and-shade leaves, with their impacts on mechanical and biochemical leaf characteristics, may also be linked to stratification.[69] And, the evolution of a tiered canopy would have influenced wildfire activity where a subcanopy tier potentially acted as a
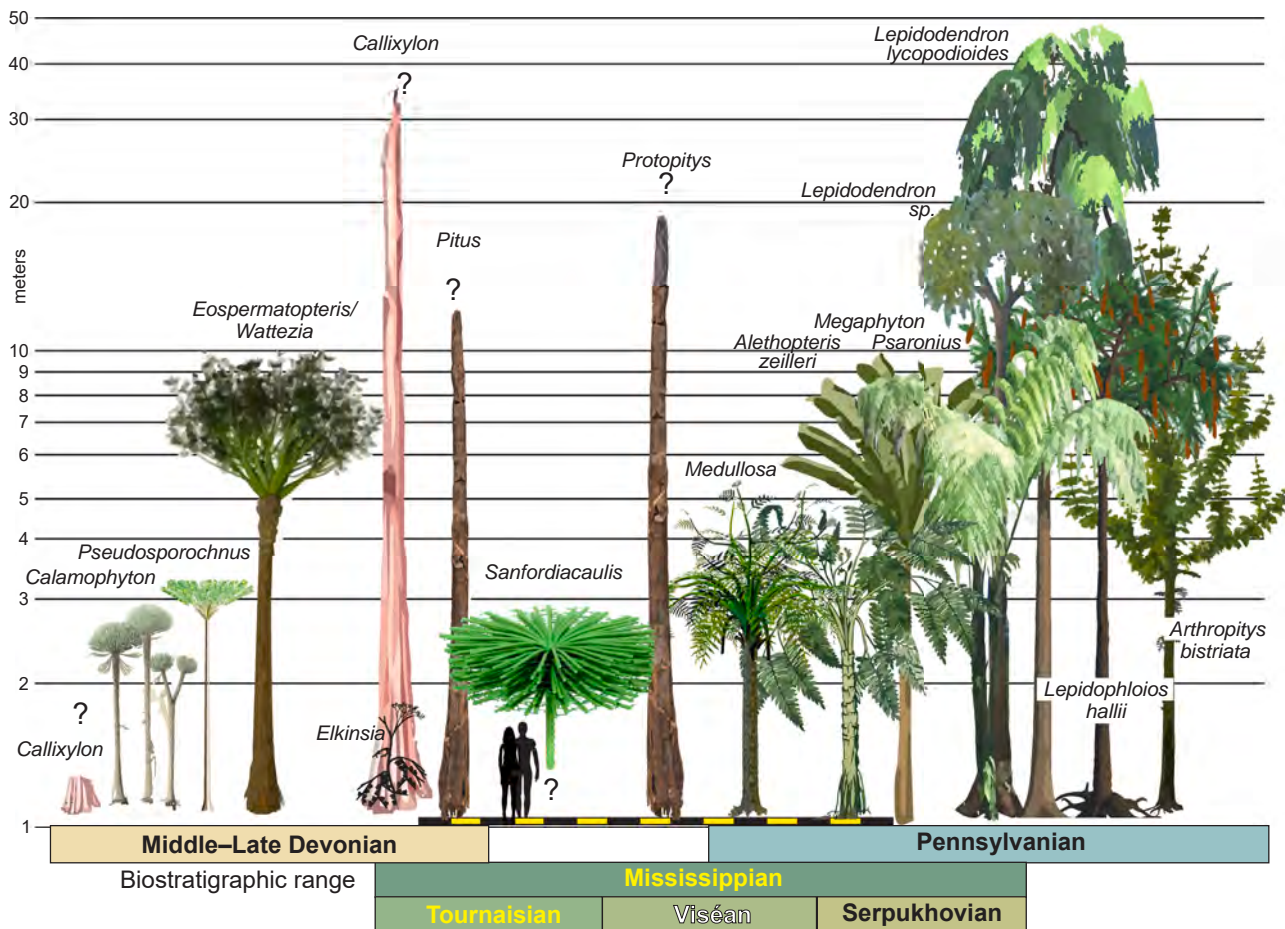
Figure 7. Actual and reconstructed tree heights and biostratigraphic ranges of Middle Devonian to Pennsylvanian trees
Plants depicted based on fossils preserved with either trunks, trunks with attached crowns, or forest elements buried in growth position. Plant reconstructions are Cladoxylales: *Calamophyton*,[4] *Pseudosporochnus*,[27] and *Eospermatopteris/Wattieza*[1]; Progymnosperms: *Callixylon*,[2,28,29] *Pitus*,[30] and *Protopitys*[31]; Ferns: *Megaphyton*[32] and *Psaronius*[33]; Gymnosperms: *Elkinsia*,[34] *Medullosa*,[35] and *Alethopteris zeilleri*[36]; Lycophytes: *Lepidodendron* sp., *L. lycopodioides*, and *Lepidophloios hallii*[10]; and Equisetales: *Arthropitys bistrata*.[37] Horizontal scale in meters; $\log_{10}$ vertical scale. Plants arranged in chronostratigraphic order according to geologic intervals in which they are reported. Trees that colonized landscapes at two successive geologic intervals are shown as overlapping the time scale. Hence, *Callixylon* and *Pitus* are known from both the Late Devonian and Early Mississippian; *Medullosa*, *Alethopteris*, and *Psaronius* are reported first in the middle Mississippian (Viséan) and continue into the Pennsylvanian. Horizontal scale in 0.5 m; vertical log scale.

ladder fuel promoting the spread of ground fires to the crown.[70,71] It is in the Tournaisian that widespread fires start to be documented and the concentration of charcoal, recorded in mire settings, jumps dramatically from pre-Carboniferous levels.[72]

Phyllotaxis, leaf function, and architectural analogs
Many plants follow a common 3/8 Fibonacci phyllotaxis.[73] The same 3/8 phyllotaxis occurs in Carboniferous pteridosperms,[74] cordaites,[75] and ferns, with leaf organization in the latter also ranging from 2/5,[76] 2/7 and 2/9,[33] to 3/5.[77] In contrast, lycophytes and sphenophytes develop bijugate spirals that exhibit highly variable phyllotaxis.[73] Several Late Paleozoic plants, though, are reported with non-Fibonacci phyllotaxis, including the Early Devonian *Asteroxylon*[78] and the late Tournaisian *Oxroadia gracilis*,[79,80] both lycophytes. Hence, the phyllotaxis in *S. densifolia* is another example of a fossil plant, a tree, with a non-Fibonacci phyllotaxis.

All leaves attached to the trunk of *S. densifolia* were likely physiologically functional when moved to the lake bottom. We interpret this feature based on the fact that: (1) every lateral is maintained in a quasi-orthogonal orientation; (2) abscised leaves are represented only by their bases; and (3) there is no evidence of a non-functional leaf "skirt" as seen in modern plants. The attached, compound, and incomplete leaves have a long petiole, and alternating secondary laterals do not develop until >0.5 m distance from the trunk (Figure 5). Changes in petiolar geometry are similar to those in modern, non-woody leaves up to and exceeding 10 m in length (e.g., *Nypa*[81] and *Raphia*[82]). Although photosynthetic laminae are not attached to the principal specimen of *S. densifolia*, poorly preserved, systematically inconclusive microlaminae (cf. *Sphenopteridium*) occur attached to secondary laterals of other specimens (Figure 5F). *Sanfordiacaulis*'s distinctive, compact, and extensive phyllotaxis likely functioned to maximize photosynthesis of this very large plant, acting as a light harvester,[83] and blocking sunlight to the forest floor.

Maximizing light capture may mean that the plant: (1) occupied a subcanopy position where light filtration was decreased by the canopy; (2) developed an architecture to curtail groundcover growth for greater efficiency in acquiring nutrients in a low-nutrient soil; and (3) evolved a compensatory mechanism for small-and-fimbriate laminae that were photosynthetically inefficient.

Sanfordiacaulis's growth architecture is similar to two recent tropical tree-growth models.[83] Cook's model is typified by a monopodial trunk producing a crown of spirally arranged leaves and reproductive structures, while persistent leaf scars are retained on the trunk following their loss. This model is found in tree ferns (Marattiaceae), cycads, and a few monocot-and-dicot families. Corner's model typifies tree ferns in the Cyatheaceae and Dicksoniaceae, cycads, monocots, and dicot families. Here, a monopodial trunk produces either a spiral or decussate phyllotaxis, compound leaves appear to be branches, and leaf scars remain after abscission. Crown leaves in both models are: (1) restricted to a short terminal section below the apex; (2) self-supporting, with lengths >20 m (*Raphia regalis*[82]); and (3) similar in cross-sectional petiole shapes as *S. densifolia*. The phyllotaxis-and-leaf distribution along the Tournaisian plant, though, is distinctly different from either model, indicating an evolutionary innovation that may mark the timing of subcanopy radiation and diversification. Hence, Mississippian vegetation displays greater variation in stem-and-leaf architectures earlier than previously realized.

Plant affinity

Late Paleozoic compound-leaf architectures were not constrained to any specific clade. In general, ferns (Pteridophytales) and seed-fern gymnosperms (Pteridospermales) differed in basic leaf architectures, although systematic placement depends on spore- or seed-producing structures, respectively. For example, the wood of *Archaeopteris, Callixylon*, was considered gymnospermous due to its conifer-like anatomy, although the plant bore spirally arranged "fern-like" leaves around a woody rachis.[84] Subsequent studies recognized that only the ultimate laminate units were leaves (megaphylls), arranged in a 1/3 phyllotaxis around a lateral branch system,[84] and the taxon's systematic position was reinterpreted when the tree was found to be free-sporing and not seed-bearing.[85] Further analyses have demonstrated a pseudomonopodial growth strategy.[47] Hence, the presence of any leaf architecture in Late Paleozoic plants cannot be taken, in isolation, as indicative of their systematic affiliation based on characteristics of plants in the modern flora.

In general, Late Paleozoic fern leaves differ from seed ferns. Fern leaves have an unbranched medial axis (petiole/rachis) bearing secondary and/or tertiary axes (pinnae), with photosynthetic laminae (pinnules).[86] Structural integrity of non-woody petioles is maintained by thickened, sub-epidermal lignified cells. In contrast, many seed-fern petioles depart the main axis and divide into two equal forked rachides from which secondaries and tertiaries develop. Depending on the clade, either reinforcing transverse sclerenchymatous bands (Lyginopteridales) or longitudinal fibers (Medullosales) are present. Structural integrity also may be maintained by woody tissues. Pinnules vary in their development and placement. In the absence of attached photosynthetic pinnules, reproductive structures, or internal anatomy, we are unable to confirm the systematic position of *S. densifolia*. Yet, the presence of a spirally arranged phyllotaxis of compound leaves, with a central rachis and secondary laterals, restricted to the upper trunk apparently presages growth architectures of tree-fern lineages (Marattiaceae and Cyathaceae) that persist to the present in tropical and subtropical forests.

Conclusions

Empirical evidence reveals an increasing tripartite-tiering forest structure beginning in the Middle Devonian and expanding in the Late Mississippian. Our new data suggest the Mississippian as a time interval when the subcanopy ecological niche was likely exploited and confirm it as an under-recognized period of new evolutionary strategy contributing to broader Late Paleozoic plant diversification. The discovery of three-dimensionally preserved Tournaisian trees provides evidence of subcanopy plant heights in the Early Mississippian and evidences a greater variation in both stem-and-leaf architectures earlier than realized. At a reconstructed height of ~3 m, *Sanfordiacaulis densifolia* exhibits an exotic dense growth architecture where compound leaves: (1) are arranged in an estimated 1/13 phyllotaxis; (2) are functionally persistent over a long trunk interval; and (3) extend >2 m from the axis, resulting in an estimated crown volume of 20–30 m^3. This evolutionary architecture presages the growth architectures of tree-fern lineages (Marattiaceae and Cyathaceae) that persist to the present tropical and subtropical forests. The plant's exceptional and environmentally atypical preservation resulted from an uncommon set of geological circumstances where earthquake-induced slumping of marginal rift-lake soils transferred whole trees, leaf litters, and sediments to lake depths where they were buried, entombed, and preserved.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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REFERENCES

1. Stein, W.E., Mannolini, F., Hernick, L.V., Landing, E., and Berry, C.M. (2007). Giant cladoxylopsid trees resolve the enigma of the Earth's earliest forest stumps at Gilboa. Nature *446*, 904–907.

2. Stein, W.E., Berry, C.M., Morris, J.L., Hernick, L.V., Mannolini, F., Ver Straeten, C., Landing, E., Marshall, J.E.A., Wellman, C.H., Beerling, D.J., et al. (2020). Mid-Devonian *Archaeopteris* roots signal revolutionary change in earliest fossil forests. Curr. Biol. *30*, 421–431.e2.

3. Stein, W.E., Berry, C.M., Hernick, L.V., and Mannolini, F. (2021). The classic mid-Devonian *Eospermatopteris* localities, Gilboa NY, USA. Rev. Palaeobot. Palynol. *295*, 104520.

4. Giesen, P., and Berry, C.M. (2013). Reconstruction and growth of the early tree *Calamophyton* (Pseudosporochnales, Cladoxylopsida) based on exceptionally complete specimens from Lindlar, Germany (Mid-Devonian): Organic connection of *Calamophyton* branches and *Duisbergia* trunks. Int. J. Plant Sci. *174*, 665–686.

5. Gastaldo, R.A. (2004). The relationship between bedform and log orientation in a Paleogene fluvial channel, Weißelster basin, Germany: Implications for the use of coarse woody debris for paleocurrent analysis. Palaios *19*, 595–606.

6. Gastaldo, R.A., and Degges, C.W. (2007). Sedimentology and Paleontology of a Carboniferous Log Jam. Int. J. Coal Geol. *69*, 103–118.

7. Strullu-Derrien, C., Spencer, A.R.T., Cleal, C.J., and Leshyk, V.O. (2022). The 330–320 Million-Year-Old Tranchée des Malécots (Chaudefonds-sur-Layon, south of the Armorican Massif, France): a rare geoheritage site containing in situ palaeobotanical remains. Geoheritage *14*, 42.

8. Gastaldo, R.A. (1986). An explanation for lycopod configuration, 'Fossil Grove' Victoria Park, Glasgow. Scott. J. Geol. *22*, 77–83.

9. Gastaldo, R.A., Stevanovic-Walls, I., and Ware, W.N. (2004). *In situ*, erect forests are evidence for large-magnitude, coseismic base-level changes within Pennsylvanian cyclothems of the Black Warrior Basin, USA. AAPG Stud. Geol. *51*, 219–238.

10. Opluštil, S., Pšenička, J., Bek, J., Wang, J., Feng, Z., Libertín, M., Šimůnek, Z., Bureš, J., and Drábková, J. (2014). T0 peat-forming plant assemblage preserved in growth position by volcanic ash-fall: A case study from the Middle Pennsylvanian of the Czech Republic. Bull. Geosci. *89*, 773–818.

11. Gastaldo, R.A., Bamford, M., Calder, J., DiMichele, W.A., Iannuzzi, R., Jasper, A., Kerp, H., McLoughlin, S., Opluštil, S., Pfefferkorn, H.W., et al. (2020). The non-analog vegetation of the Late Paleozoic icehouse–hothouse and their coal-forming forested environments. In Nature Through Time, E. Martinetto, E. Tschopp, and R.A. Gastaldo, eds. (Springer Nature), pp. 291–316.

12. Bateman, R.M., and Scott, A.C. (1990). A reappraisal of the Dinantian floras at Oxroad Bay, East Lothian, Scotland. 2. Volcanicity, palaeoenvironments and palaeoecology. Earth Environ. Sci. Trans. R. Soc. Edinb. *81*, 161–194.

13. Prestianni, C., Rustán, J.J., Balseiro, D., Vaccari, E., Sterren, A.F., Steemans, P., Rubinstein, C., and Astini, R.A. (2015). Early seed plants from Western Gondwana: Paleobiogeographical and ecological implications based on Tournaisian (Lower Carboniferous) records from Argentina. Palaeogeogr. Palaeoclimatol. Palaeoecol. *417*, 210–219.

14. Bateman, R.M., Stevens, L.G., and Hilton, J. (2016). Stratigraphy, palaeoenvironments and palaeoecology of the Loch Humphrey Burn Lagerstätte and other Mississippian palaeobotanical localities of the Kilpatrick Hills, southwest Scotland. PeerJ *4*, e1700.

15. Carter, D.C., and Pickerill, R.K. (1985). Lithostratigraphy of the late Devonian–Early Carboniferous Horton Group of the Moncton Subbasin, southern New Brunswick. Atl. Geol. *21*, 11–24.

16. Pickerill, R.K. (1992). Carboniferous nonmarine invertebrate ichnocoenoses from southern New Brunswick, eastern Canada. Ichnos *2*, 21–35.

17. Keighley, D.K. (2008). A lacustrine shoreface succession in the Albert Formation, Moncton Basin, New Brunswick. Bull. Can. Petrol. Geol. *56*, 235–258.

18. Hübers, M., Bomfleur, B., Krings, M., Pott, C., and Kerp, H. (2014). A reappraisal of Mississippian (Tournaisian and Viséan) adpression floras from central and northwestern Europe. Zitteliana *54*, 39–52.

19. Shute, C.H., and Cleal, C.J. (1987). Palaeobotany in museums. Geol. Curator *4*, 553–559.

20. Niklas, K.J. (1994). Predicting the height of fossil plant remains: an allometric approach to an old problem. Am. J. Bot. *81*, 1235–1242.

21. Decombeix, A.-L., Meyer-Berthaud, B., and Galtier, J. (2011). Transitional changes in arborescent lignophytes at the Devonian–Carboniferous boundary. J. Geol. Soc. *168*, 547–557.

22. Marshall, J.E.A., Holterhoff, P.F., El-Abdallah, S.R., Matsunaga, K.K.S., Bronson, A.W., and Tomescu, A.M.F. (2022). The archaeopterid forests of Lower Frasnian (Upper Devonian) westernmost Laurentia: Biota and depositional environment of the Maywood Formation in northern Wyoming as reflected by palynoflora, macroflora, fauna, and sedimentology. Int. J. Plant Sci. *183*, 465–492.

23. Galtier, J., and Meyer-Berthaud, B. (2006). The diversification of early arborescent seed ferns. J. Torrey Bot. Soc. *133*, 7–19.

24. Gensel, P.G., and Pigg, K.B. (2010). An arborescent lycopsid from the Lower Carboniferous Price Formation, southwestern Virginia, USA and the problem of species delimitation. Int. J. Coal Geol. *83*, 132–145.

25. Rygel, M.C., Calder, J.H., Gibling, M.R., Gingras, M.K., and Melrose, C.S.A. (2006). Tournaisian forested wetlands in the Horton Group of Atlantic Canada. Geol. Soc. Am. Spec. Pap. *399*, 103–126.

26. DiMichele, W.D., Gastaldo, R.A., and Pfefferkorn, H.W., Biodiversity Partitioning in the Late Carboniferous and its implications for ecosystem assembly.Proceedings of the California Academy of Sciences, v. 56, suppl. 1, no. 4, p. 24-41.

27. Dambreville, A., Meyer-Berthaud, B., Barczi, J.-F., Decombeix, A.-L., Griffon, S., and Rey, H. (2018). Using architecture modeling of the Devonian tree *Pseudosporochnus* to compute its biomass. In Transformative Paleobotany, M. Krings, C.J. Harper, N.R. Cúneo, and G.W. Rothwell, eds. (Academic Press), pp. 35–47.

28. Arnold, C.A. (1931). On *Callixylon newberryi* (Dawson) Elkins et Weiland. Contr. Mus. Paleontol. Univ. Mich. *4*, 207–232.

29. Wilson, L.R. (1958). Oklahoma's oldest fossil trees. Okla. Geol. Notes *18*, 173–176.

30. Lyon, G. (1873). Discovery of a new fossil tree in Craigleith Quarry, Edinburgh. Trans. Edinb. Geol. Soc. *2*, 219–220.

31. Decombeix, A.-L., Galtier, J., and Prestianni, C. (2015). The Early Carboniferous progymnosperm *Protopitys*: new data on vegetative and

fertile structures, and on its geographic and stratigraphic distribution. Hist. Biol. *27*, 345–354.

32. Pfefferkorn, H.W. (1976). Pennsylvania tree fern compressions *Caulopteris*, *Megaphyton*, and *Artisophyton* gen. nov. in Illinois. Ill. State Geol. Surv. Circ. *492*, 1–31.

33. Morgan, J. (1959). The morphology and anatomy of American species of *Psaronius*. Ill. Biol. Monogr. *27*, 1–107.

34. Serbet, R., and Rothwell, G.W. (1992). Characterizing the most primitive seed ferns. I. A reconstruction of *Elkinsia polymorpha*. Int. J. Plant Sci. *153*, 602–621.

35. Wnuk, C., and Pfefferkorn, H.W. (1984). The life habits and paleoecology of Middle Pennsylvanian medullosan pteridosperms based on an *in situ* assemblage from the Bernice Basin (Sullivan County, Pennsylvania, U.S.A.). Rev. Palaeobot. Palynol. *41*, 329–351.

36. Zodrow, E.L. (2007). Reconstructed tree fern *Alethopteris zeilleri* (Carboniferous, Medullosales). Int. J. Coal Geol. *69*, 68–89.

37. Rößler, R., Feng, Z., and Noll, R. (2012). The largest calamite and its growth architecture — *Arthropitys bistriata* from the Early Permian Petrified Forest of Chemnitz. Rev. Palaeobot. Palynol. *185*, 64–78.

38. Driese, S.G., Mora, C.I., and Elick, J.M. (1997). Morphology and taphonomy of root and stump casts of the earliest trees (Middle to Late Devonian), Pennsylvania and New York, U.S.A. PALAIOS *12*, 524–537.

39. Berry, C.M., and Marshall, J.E.A. (2015). Lycopsid forests in the early Late Devonian paleoequatorial zone of Svalbard. Geology *43*, 1043–1046.

40. Wang, D., Qin, M., Liu, L., Liu, L., Zhou, Y., Zhang, Y., Huang, P., Xue, J., Zhang, S., and Meng, M. (2019). The most extensive Devonian fossil forest with small lycopsid trees bearing the earliest stigmarian roots. Curr. Biol. *29*, 2604–2615.e2.

41. MacGregor, M., and Walton, J. (1948). The Story of the Fossil Grove of Glasgow Public Parks and Botanical Gardens, Glasgow (Glasgow Public Parks and Botanic Gardens Department), p. 32.

42. Gastaldo, R.A. (1986). Implications on the paleoecology of autochthonous Carboniferous lycopods in clastic sedimentary environments. Palaeogeogr. Palaeoclimatol. Palaeoecol. *53*, 191–212.

43. Goldring, W. (1927). The oldest known petrified forest. Sci. Mon. *24*, 514–526.

44. Meyer-Berthaud, B., Wendt, J., and Galtier, J. (1997). First record of a large *Callixylon* trunk from the late Devonian of Gondwana. Geol. Mag. *134*, 847–853.

45. Gooding, P., Smath, R., Eble, C.F., and Ettensohn, F.R. (2016). A Devonian Callixylon log of the Archaeopteris tree found in Marion County, Kentucky. AAPG East. Sect. Mtg,, 90258.

46. Cullen, A., Hull, D., and Turko, M. (2021). An intact thirty-four foot long petrified log in the Woodford Shale, Oklahoma: A question of preserving geological heritage. Shale Shaker *72*, 118–129.

47. Trivett, M.L. (1993). An architectural analysis of *Archaeopteris*, a fossil tree with pseudomonopodial and opportunistic adventitious growth. Bot. J. Linn. Soc. *111*, 301–329.

48. Stein, W.E., Berry, C.M., Hernick, L.V., and Mannolini, F. (2012). Surprisingly complex community discovered in the mid-Devonian fossil forest at Gilboa. Nature *483*, 78–81.

49. Durieux, T., Lopez, M.A., Bronson, A.W., and Tomescu, A.M.F. (2021). A new phylogeny of the cladoxylopsid plexus: contribution of an early cladoxylopsid from the Lower Devonian (Emsian) of Quebec. Am. J. Bot. *108*, 2066–2095.

50. Giesen, P., and Berry, C.M. (2015). Der älteste Wald der Welt – die einzigartige mitteldevonische Pflanzenfundstelle Lindlar. Archäol. Rheinl. *2015*, 42–44.

51. Gerrienne, P., Gensel, P.G., Strullu-Derrien, C., Lardeux, H., Steemans, P., and Prestianni, C. (2011). A simple type of wood in two Early Devonian plants. Science *333*, 837.

52. Cressler, W. (2006). Plant paleoecology of the Late Devonian Red Hill locality, north-central Pennsylvania, an *Archaeopteris*-dominated wetland plant community and early tetrapod site. Geol. Soc. Am. Spec. Pap. *399*, 79–102.

53. Decombeix, A.-L., Meyer-Berthaud, B., Rowe, N., and Galtier, J. (2005). Diversity of large woody lignophytes preceding the extinction of *Archaeopteris*: New data from the middle Tournaisian of Thuringia (Germany). Rev. Palaeobot. Palynol. *137*, 69–82.

54. Falcon-Lang, H.J., and Galtier, J. (2010). Anatomically-preserved tree-trunks in late Mississippian (Serpukhovian, late Pendleian-Arnsbergian) braided fluvial channel facies, near Searston, southwest Newfoundland, Canada. Rev. Palaeobot. Palynol. *160*, 154–162.

55. Decombeix, A.-L. (2007). Origine et évolution des arbres chez les lignophytes du Paléozoïque. PhD thesis (Université Montpellier II).

56. Leslie, A.B., and Pfefferkorn, H.W. (2010). Fossil floras from the Emma Fiord Formation (Viséan, Mississippian) of the Canadian Arctic Archipelago and their paleoenvironmental context. Rev. Palaeobot. Palynol. *159*, 195–203.

57. Alekseeva, T.V., Mitenko, G.V., and Alekseev, A.O. (2021). The ecology of a late Viséan forest at Catcraig (East Lothian, Scotland) based on multi-proxy study of paleosol and root-casts. Palaeoworld *30*, 62–71.

58. Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimunek, Z., Drábková, J., and Dašková, J. (2009). A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved *in situ* in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic. Rev. Palaeobot. Palynol. *155*, 234–274.

59. Boyce, C.K., and DiMichele, W.A. (2016). Arborescent lycopsid productivity and lifespan: Constraining the possibilities. Rev. Palaeobot. Palynol. *227*, 97–110.

60. Hirmer, M. (1927). Handbuch der Pälaobotanik. Band I: Thallophyta Bryophyta Pteridophyta. R. (Oldenburg Verlag), pp. 1–724.

61. Zhou, W.-M., D'Antonio, M.P., Boyce, C.K., and Wang, J. (2021). An upright psaroniaceous stump and two surrounding pecopteroids from the early Permian Wuda Tuff Flora. Palaeoworld *30*, 451–460.

62. DiMichele, W.A., Elrick, S.D., and Nelson, W.J. (2017). Vegetational zonation in a swamp forest, Middle Pennsylvanian, Illinois Basin, U.S.A., indicates niche differentiation in a wetland plant community. Palaeogeogr. Palaeoclimatol. Palaeoecol. *487*, 71–92.

63. Gastaldo, R.A., Stevanović-Walls, I.M., Ware, W.N., and Greb, S.F. (2004). Community heterogeneity of Early Pennsylvanian peat mires. Geology *32*, 693–696.

64. Falcon-Lang, H.J., and Bashforth, A.R. (2005). Morphology, anatomy, and upland ecology of large cordaitalean trees from the Middle Pennsylvanian of Newfoundland. Rev. Palaeobot. Palynol. *135*, 223–243.

65. Falcon-Lang, H.J. (2005). Small cordaitalean trees in a marine-influenced coastal habitat in the Pennsylvanian Joggins Formation, Nova Scotia. J. Geol. Soc. *162*, 485–500.

66. Raymond, A., Lambert, L., Costanza, S., Slone, E.J., and Cutlip, P.C. (2010). Cordaiteans in paleotropical wetlands: An ecological re-evaluation. Int. J. Coal Geol. *83*, 248–265.

67. Behrensmeyer, A.K., Kidwell, S.M., and Gastaldo, R.A. (2000). Taphonomy and Paleobiology. Paleobiology *26*, 103–147.

68. Smith, A.P. (1973). Stratification of temperature and tropical forests. Am. Nat. *107*, 671–683.

69. Shaw, D.C. (2004). Vertical organization of canopy biota. In Forest Canopies, M.D. Lowman, and H.B. Rinker, eds. (Elsevier), pp. 73–101.

70. Scott, A.C. (2020). Fire: A Very Short Introduction (Oxford University Press), p. 176.

71. Scott, A.C., and Glasspool, I.J. (2006). The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. Proc. Natl. Acad. Sci. USA *103*, 10861–10865.

72. Glasspool, I.J., and Scott, A.C. (2010). Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. Nature Geosci. *3*, 627–630.

73. Okabe, T., Ishida, A., and Yoshimura, J. (2019). The unified rule of phyllotaxis explaining both spiral and non-spiral arrangements. J. R. Soc. Interface 16, 20180850.

74. Luthardt, L., Merbitz, M., Fridland, E., and Rößler, R. (2022). Upside-down in volcanic ash: crown reconstruction of the early Permian seed fern Medullosa stellata with attached foliated fronds. PeerJ 10, e13051.

75. Bureš, J., Šimůnek, Z., Pšenička, J., Bek, J., Drábková, J., and Bruthansová, J. (2023). Fertile cordaitalean leafy branch with in situ pollen from the volcanic Whetstone Horizon (Radnice Member, early Moscovian, Plzeň Basin, Czech Republic). Rev. Palaeobot. Palynol. 315, 104903.

76. Rößler, R. (2000). The Late Palaeozoic tree fern Psaronius – an ecosystem unto itself. Rev. Palaeobot. Palynol. 108, 55–74.

77. Gastaldo, R.A. (1990). Earliest evidence for helical crown configuration in a Carboniferous tree of uncertain affinity. J. Paleontol. 64, 146–151.

78. Turner, H.A., Humpage, M., Kerp, H., and Hetherington, A.J. (2023). Leaves and sporangia developed in rare non-Fibonacci spirals in early leafy plants. Science 380, 1188–1192.

79. Bateman, R.M. (1992). Morphometric reconstruction, palaeobiology and phylogeny of Oxroadia gracilis Alvin emend. and O. conferta sp. nov.: Anatomically-preserved rhizomorphic lycopsids from the Dinantian of Oxroad Bay, SE Scotland. Palaeontogr. Abt. B 228, 29–103.

80. Bateman, R.M., and Rothwell, G.W. (1990). A reappraisal of the Dinantian floras at Oxroad Bay, East Lothian, Scotland. 1. Floristics and the development of whole-plant concepts. Earth Environ. Sci. Trans. R. Soc. Edinb. 81, 127–159.

81. Widodo, P., Sukarsa, Herawati, W., Hidayah, H.A., Chasanah, T., and Proklamasiningsi, E. (2020). Distribution and characteristics of Nypa Palm (Nypa fruticans Wurmb.) in southern part of Cilacap Regency. IOP Conf. Ser. Earth Environ. Sci. 550, 12010.

82. Hallé, F. (1977). The longest leaf in palms? Principes 21, 18.

83. Hallé, F., Oldemann, R.A.A., and Tomlinson, P.B. (1978). Tropical Trees and Forests: An Architectural Analysis (Springer Verlag), p. 463.

84. Beck, C.B. (1962). Reconstructions of Archaeopteris, and further consideration of its phylogenetic position. Am. J. Bot. 49, 373–382.

85. Scheckler, S.E. (1978). Ontogeny of progymnosperms. II. Shoots of Upper Devonian Archaeopteridales. Can. J. Bot. 56, 3136–3170.

86. Galtier, J. (2010). The origins and early evolution of the megaphyllous leaf. Int. J. Plant Sci. 171, 641–661.

87. Gibling, M., Culshaw, N., Pascucci, V., Waldron, J., and Rygel, M. (2019). The Maritimes Basin of Atlantic Canada: Basin Creation and Destruction during the Paleozoic Assembly of Pangea, A.D. Miall, ed. (Elsevier B.V.), pp. 267–314.

88. King, O.A., MacRae, R.A., Stimson, M.R., Hinds, S., Park, A., and McLean, D. (2022). Palynology of the Albert Formation of New Brunswick. Geol. Assoc. Canada-Mineral. Assoc. Canada Abst. 45, 126.

89. Higgs, K.T., Clayton, G., and Keegan, J.B. (1988). Stratigraphic and systematic palynology of the Tournaisian rocks of Ireland. Geological Survey of Ireland 7, 1–93.

90. Clayton, G., Higgs, K., Keegan, J.B., and Sevastopulo, G.D. (1978). Correlation of the palynological zonation of the Dinantian of the British Isles. Palinologia 1, 137–147.

91. Higgs, K.T., Dreesen, R., Dusar, M., and Streel, M. (1992). Palynostratigraphy of the Tournaisian (Hastarian) rocks in the Namur Synclinorium, West Flanders, Belgium. Rev. Palaeobot. Palynol. 72, 149–158.

92. Higgs, K.T. (1996). Taxonomy and systematic study of some Tournaisian (Hastarian) spores from Belgium. Rev. Palaeobot. Palynol. 93, 269–297.

93. Lucas, S.G., Schneider, J.W., Nikolaeva, S., and Wang, X. (2022). The Carboniferous timescale: an introduction. Geol. Soc. Lond. Spec. Publ. 512, 1–17.

94. Austin, R.L., Conil, R., and Rhodes, F.H.T. (1973). Recognition of the Tournaisian-Viséan boundary in North America and Britain. Ann. Soc. Géol Belg. 96, 165–188.

95. Waldron, J.W.F., Giles, P.S., and Thomas, A.K. (2017). Correlation chart for Late Devonian to Permian stratified rocks of the Maritimes Basin, Atlantic Canada: Nova Scotia. Dept. Energy Open File Rep, 2017-02, p. 12. https://energy.novascotia.ca/sites/default/files/files/NSDOE%20Open%20File%20Report%202017-02%20-%20Supporting%20Notes(2).pdf.

96. Rex, G.M., and Chaloner, W.G. (1983). The experimental formation of plant compression fossils. Palaeontology 26, 231–252.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Main tree, large block	New Brunswick Museum of Natural History	NBMG 22403-1
Main tree, counter-part to trunk	New Brunswick Museum of Natural History	NBMG 22403-2
Main tree Figure 4A	New Brunswick Museum of Natural History	NBMG 22403-3
Palynological Slides	New Brunswick Museum of Natural History	22SAN-04A, 22SAN-04B, 22SAN-05, 22SAN-06, 22SAN-07, 22SAN-08, 22SAN-11
Software and algorithms		
Blender 3D modelling software	https://www.blender.org/	Blender 3.6.4 LTS

RESOURCE AVAILABILITY

Lead contact
Further information and requests for resources should be directed to, and will be fulfilled by, the lead contact, Robert A. Gastaldo (robert.gastaldo@colby.edu).

Materials availability
All fossils analyzed as part of this study have been deposited at the New Brunswick Museum of Natural History, and are publicly available as of the date of publication, with the exception of the specimen figured in Figure 2C, which remains *in situ* in the Sanford Quarry (private property). Palynological samples: 22SAN-04A, 22SAN-04B, 22SAN-05, 22SAN-06, 22SAN-07, 22SAN-08, 22SAN-11 are deposited at NBMNH.

Data and code availability
Field and collection data are available from the New Brunswick Museum, Saint John, Canada.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Sanford Quarry
Sanford Quarry is located adjacent to the Southfield Road in Norton, New Brunswick, Canada. Grid Ref: N45.627786, W 65.691610. As of this writing, the quarry exposure is limited to the Western highwall with exposure in the floor of the quarry. The fossils come from the Hiram Brook Member, Albert Formation, Horton Group. As of writing, the quarry only exposes the Hiram Brook Member. As this is an active quarry, the outcrop is continuously changing. Based on available data, we interpret that this interval of the Hiram Brook Member is situated near the top of the Albert Formation, close to its time-transgressive contact with the overlying Bloomfield Formation.

The Sanford Quarry is situated in the Moncton Subbasin for which the sediment provenance is not currently known. This subbasin extends west laterally from Moncton and Albert County to the western shore of Grand Bay before pinching out. In-and-around Norton, the lithostratigraphy consists, from oldest to youngest, of the Memramcook, Albert and Bloomfield formations of the Horton Group. These were deposited unconformably on the basement grabens of the Maritimes Basin during the Devonian (Famennian) to Lower Carboniferous (Tournaisian) periods.[87]

The quarry succession is subdivided into four lithologic units. Unit 1 is a basal, stratigraphic package dominated by beds of very fine sandstone, siltstone, and, mudstone that is at least 90 cm thick. Symmetrical wave-ripple bedforms are present as well as common mudcracks. Bedding plane surfaces preserve microbially-induced sedimentary structures (MISS) including microbial wrinkles and microbial induced "elephant skin textures". Plants are absent from the basal unit but invertebrate trace fossils are common. Unit 1 is interpreted as being marginal lacustrine and is not affected by softsediment deformation as found in the overlying Unit 2. The fossil plant bearing horizon is found in Unit 2, interpreted as an earthquake-induced slump horizon. The unit is a 60-to-140 cm thick

package that sits conformably over Unit 1. Unit 2 is comprised of light-to-medium grey sandstone and siltstone with abundant articulated and disarticulated plant fossils. Although cross-bedding is pervasive in sandstone beds, virtually all of the unit exhibits signs of soft-sediment deformation including convolute bedding, load casting, load pouches, and load balls (ball-and-pillow structures) at scales varying from centimeter to large meter-scale beds. Unit 3 has a distinctive coarser grainsize, and is pyrite-nodule bearing, brownish-colored, massive, and a less carbonaceous sandstone that has large wrinkled MISS areas on its upper bounding surface. While the top surface of this bed is relatively planar across the entire quarry, the basal contact is wavey and has a pointed cuspate surface, a continuation of the deformational features observed in the underlying carbonaceous sandstones. Unit 3 shows no sign of significant syn-sedimentary deformation and, thus, is interpreted to post-date the phase of deformation. Unit 4 terminates the succession and overlies Unit 3 with a sharp conformable contact. The maximum thickness of Unit 4 is at least 5.65 m in outcrop, found in the eastern floor of the quarry. The top of the section is not exposed; hence, the true thickness of this unit is unknown. Unit 4 is dominated by featureless or, less commonly, laminated, dark grey mudstone and siltstone that is pyrite rich. Overall, this mudstone-dominated unit likely represents a return to deeper-water lacustrine conditions.

METHOD DETAILS

Measured sections in the quarry exposure were recorded at the decimeter or finer scale and followed standard stratigraphic methodologies. Lithologic field descriptions followed standard protocols and included grain size, Munsell color, bed contacts, bed thickness, primary and secondary sedimentary structures, and fossil content. Palynological samples were collected from fine-grained, organic-rich lithologies, and megafloral and ichnofossil identifications followed standard practices.

Materials

Macrofloral remains continue to be excavated using standard hammer-and-chisel field techniques, supplemented by heavy equipment capable of accessing and moving large blocks of rock. Palynological samples (22SAN-04A, 22SAN-04B, 22SAN-05, 22SAN-06, 22SAN-07, 22SAN-08, 22SAN-11) originate from successive horizons in the succession, and were processed using standard techniques.

All palynological samples provided abundant organic material that is dominated by vitrinite in various stages of degradation, with lesser inertinite. Miospores occur in all samples, being abundant in all but samples 22SAN-4A and 22SAN-07. Preservation of miospores is variable, and very poor to poor in all samples other than 22SAN-05 and 22SAN-11 where preservation is moderate to good. The poor state of preservation means that many taxa are only identified to generic level, and are mainly recognizable as simple, laevigate forms assigned to *Calamospora* spp., *Punctatisporites* spp. and *Retusotriletes* spp. Less common are (amongst others) *Pustulatisporites gibberosus*, *Spelaeotriletes balteatus*, *S. cabotii*, *S. galearis*, *Vallatisporites vallatus*, *Verrucosisporites nitidus*, and *Waltzispora polita*. A fairly diverse accessory assemblage includes *Acanthotriletes hacquebardii*, *Claytonispora distincta*, *Claytonispora rarisetosa*, *Crassispora trychera*, *C.* cf. *trychera*, *Cristatisporites matthewsii*, *Cyrtospora cristifera*, *Densosporites regalis*, *D. spitsbergensis*, *Grandispora impensa*, *G. senticosa*, *Granulatisporites microgranifer*, *Murospora dubitata*, *Neoraistrickia loganensis*, *Pustulatisporites dolbii*, *Rugospora flexuosa*, *R. minuta*, *R. polyptycha*, *Spelaeotriletes crustatus*, *S. pretiosus*, *Vallatisporites galearis*, and *V. verrucosus*.

Biozone Interpretation: Eastern Canada

The assemblages are very similar in composition and are most likely all assignable to the *Spelaeotriletes cabottii* subzone of the *Vallatisporites vallatus* Biozone of Lower Carboniferous age (Figure S1). Records of scarce *Crassispora trychera* along with relatively common *Spelaeotriletes cabottii* and *Vallatisporites vallatus* indicate this palynozone. Records of species which might limit the upper range of this interpretation are limited. Only one specimen of *Leiozonotriletes insignatus* was recorded (22SAN-04B) along with a questionably identified specimen of *Apiculiretusispora hystrichosus*? (22SAN-06) and a comparison record of *Schopfites* cf. *augustus* (22SAN-08). Occurrences of *Claytonispora distincta* along with *Crassispora trychera* are in keeping with observations by King et al.[88] in which the stratigraphical range of *C. distincta* is seen to extend above the range base of *C. trychera*. Records from Sanford Quarry indicate that the same may be true for *Claytonispora rarisetosa*.

Biozone Interpretation: European Comparisons

The overall composition of the assemblages with *Claytonispora distincta*, *Cyrtospora cristifera*, *Densosporites spitsbergensis*, *Granulatisporites microgranifer*, *Spelaeotriletes balteatus*, *S. pretiosus*, *Rugospora polyptycha*, *Vallatisporites vallatus*, *V. verrucosus*, and *Verrucosisporites nitidus* indicates correlation with the late Tournaisian *Spelaeotriletes pretiosus-Raistrickia clavata* (PC) Biozone of Higgs et al.[89] The records of *Crassispora trychera* in samples at and above 22SAN-04B indicate the highest part of the PC Biozone.[90] The range base of *C. trychera* in the samples may only be apparent: a specimen assigned to *C.* cf. *trychera* was recorded from the poorly preserved material from 22SAN-06. In the highest sample (22SAN-11) the presence of *Cyrtospora cristifera* and the absence of *Raistrickia clavigera* indicate that the overlying *Raistrickia clavigera-Auroraspora macra* (CM) Biozone is not proven in the section. The base of the PC Biozone in Ireland lies just below the boundary between the *Polygnathus spicatus* and the *Polygnathus inornatus* conodont biozones.[89] In northwest Belgium, the lower part of the PC Biozone has been described from the Llandelies and Orient formations where it is associated with the mid Tournaisian Upper *Siphonodella crenulata* Conodont Biozone.[91,92] Lucas et al.[93] estimate the position of this conodont biozone at 352 to 355 Ma. The uppermost part of the PC Biozone in Ireland occurs in the late Tournaisian

Pseudopolygnathus multistriatus Conodont Biozone[89] which is correlated with the North American *P. multistriatus* Biozone.[94] Lucas et al.[93] indicate an age of circa 350.5 to 351 Ma for this biozone. Thus, an approximate age range of the PC Biozone is 350.5 to 355 Ma, of which the present material would lie within the younger part, which is in agreement with the age estimate of Waldron et al.[95]

Estimate of Phyllotaxis

Phyllotaxis was estimated using the size, shape, angle of disposition, and organization of leaf bases as illustrated in Figure 3A. This trunk section exhibits their best features, although decay and compression are evident in several areas. Rex and Chaloner[96] demonstrated experimentally that megafossil compression occurs only in the z-dimension. This is because hydrostatic pore-water pressures retain plant dimensions in the x and y planes during compression. Their experiments were undertaken on foam-rubber models, whereas decayed-and-softened plant tissues may show some lateral displacement in response to stress and dewatering over the duration of compaction. Identifiable leaf bases on the compressed trunk were measured across a distance of 10 cm, which serves as the diameter on which phyllotaxis is estimated. This dimension was used decompress a trunk of the same diameter constructed of pliable duct insulation (Figure S2). Three partial leaf-base spirals (green, blue, pinkish-red) as seen in Figure 3A were printed out at scale and pasted these onto the trunk. Black horizontal lines are spaced 10 cm apart to maintain the distance between two vertically adjacent leaf bases as found on the specimen. The distribution of leaf bases around the wrapped insulation results in individual, vertically stacked spirals as seen in successive rotations of the model trunk. The lower green-leaf spiral begins with leaf base [1] with the successive spiral also labeled as [1]; this single spiral consists of 14 leaf bases. The middle blue-leaf spiral begins with the number [6] with the beginning of the successive spiral also numbered [6]; the spiral count here is 13. The third reddish-pink spiral begins with leaf base [1], with the successive spiral also numbered as [1]. This spiral consists of 12 leaves, although there is an obvious gap where a leaf base might be located. We note spaces that exist in each spiral are a consequence of using only the number of leaf bases of each partially exposed spiral as in Figure 3A. Due to the impartial nature of leaf-base spirals, we provide only a phyllotaxis estimate of 1:13, a non-Fibonacci series. We estimate approximately 47 leaf bases exist over a trunk distance of 13.5 cm which, when extrapolated to a trunk length of 75 cm, results in >250 leaves over this vertical height.

QUANTIFICATION AND STATISTICAL ANALYSIS

No statistical analyses were conducted during the course of this project.

Supplemental Information

Enigmatic fossil plants with three-dimensional,

arborescent-growth architecture from the earliest

Carboniferous of New Brunswick, Canada

Robert A. Gastaldo, Patricia G. Gensel, Ian J. Glasspool, Steven J. Hinds, Olivia A. King, Duncan McLean, Adrian F. Park, Matthew R. Stimson, and Timothy Stonesifer

System	Subsystem		Biozones Hacquebard (1972) Richardson & McGregor (1986) Utting et al. (1989, 2010)	Dolby in St. Peter & Johnson (2009)
Mississippian	Upper	Kinderscoutian to Chokierian	////// Regional Unconformity //////	
		Arnsbergian	*R. carnosus*	
		Pendleian	*G. spinosa—I. magnificus*	
		330.0 ± 0.2 Ma		
	Middle	Brigantian	*Z. acadiensis—K. triradiatus*	
		Asbian	*K. stephanephorus*	
		Holkerian		
		Arundian	*L. pusilla—D. columbaris*	
		Chadian		
		346.7 ± 0.4 Ma		
	Lower	Tournaisian	*C. decorus—R. clavigera*	5
			S. pretiosus	4
			V. vallatus *S. cabottii* subzone	3B
				3A
			V. vallatus *C. diatincta—C. rarisetosa* subzone	2B
				2A
				1D
				1C
			E. rotatus—I. explanatus	1B
				1A
		358.9 ± 0.4 Ma		
Devonian	Upper		*R. lepidophyta—V. nitidua*	
			V. pusillites—R. lepidophyta	
			R. flexuosa—G. cornuta	
			T. rotatus—G. gracilis	

Figure S1. Late Devonian–Mississippian palynostratigraphical biozonation of the Carboniferous of Maritimes Canada. Related to STARMethods.

Palynozones follow Hacquebard[S1], Richardson and McGregor[S2], Utting et al.[S3, S4], and Dolby in St. Peter and Johnson[S5]. Age assignment of palynozone 3 according to Waldron et al.[S6].
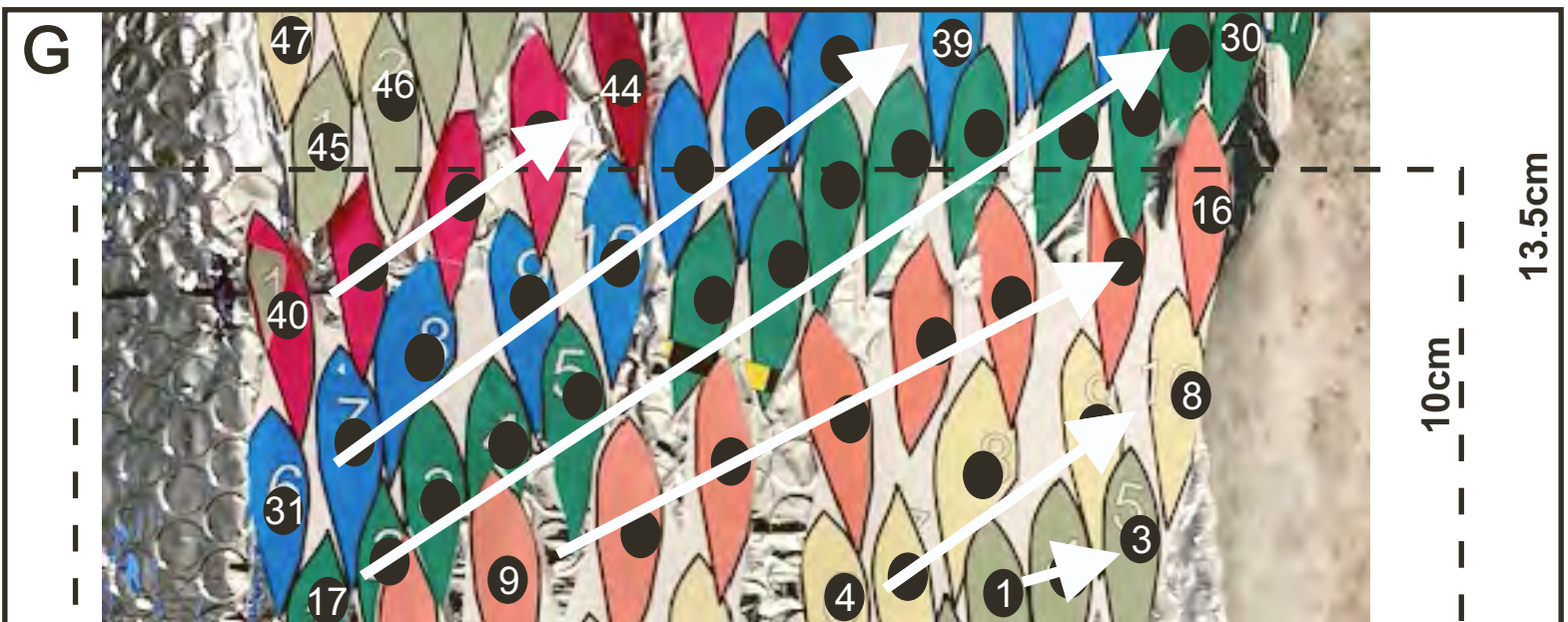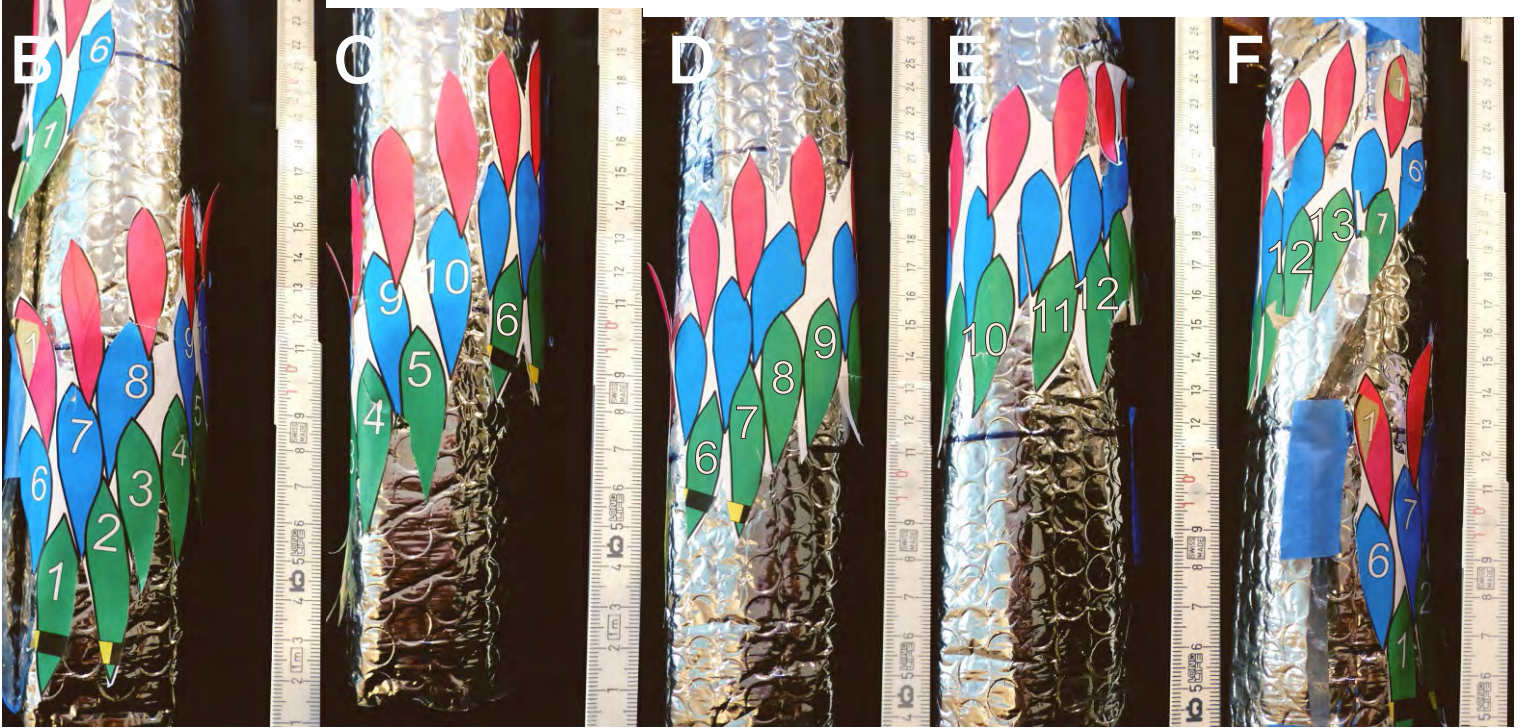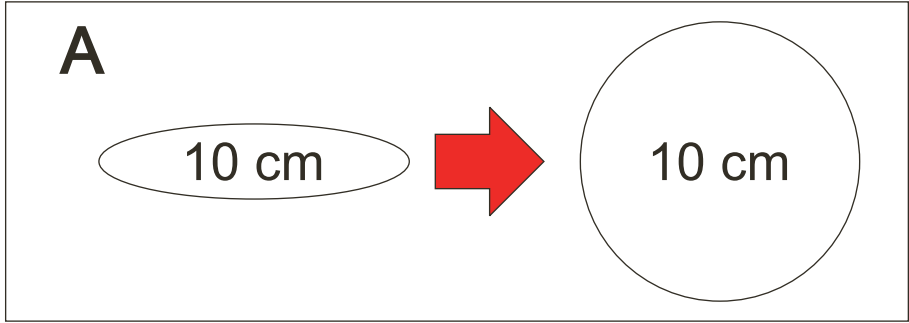
Figure S2 - Methodology used to estimate *Sanfordiacaulis densifolia* phyllotaxis. Related to STARMethods.

(A) Ten centimeter compressed trunk is decompressed to a circumference of 31.42 cm.

(B–F) Partial leaf-base spirals illustrated in Figure 3A are overlain onto the scaled trunk model and this configuration is repeated around the axis until a phyllotaxis is realized (see STARMethods). The realized phyllotaxis of the green-leaf bases is 1:13, encompassing 13.5 cm of vertical trunk distance.

(G) The unfurled model illustrating the estimated number of leaf bases (N = 46) encircling the trunk over a vertical distance of 13.5 cm. Extrapolating this number to 75 cm of preserved trunk over which leaves depart the axis results in an estimate of 256 leaves comprising the subapical leaf count, each of which is interpreted to have been functional at the time of transfer to the rift-lake sediment-water interface.

Supplemental References

S1. Hacquebard, P.A. (1972). The Carboniferous of eastern Canada. 7th Carbon. Congr. Krefeld. Compt. Rend. 1. 69–90.

S2. Richardson, J.B., and McGregor, D.C. (1986). Silurian and Devonian spores zones of the Old Red Sandstone Continent and adjacent regions. Geol. Surv. Can. Bull. 364, p. 1–79.

S3. Utting, J., Keppie, J.D., and Giles, P.S. (1989). Palynology and stratigraphy of the Lower Carboniferous Horton Group, Nova Scotia. Geol. Surv. Can. Bull. 396, p. 117-143.

S4. Utting, J., Giles, P.S., and Dolby, G. (2010). Palynostratigraphy of Mississippian and Pennsylvanian rocks, Joggins area, Nova Scotia and New Brunswick, Canada. Palynology 34, p. 43-89. DOI: 10.1080/01916121003620569

S5. St. Peter, C.J., and Johnston, S.C. (2009). Stratigraphic and Structural History of the Late Paleozoic Maritimes Basin in South Eastern New Brunswick, Canada. New Brun. Geol. Surv. Br. Mem. 3, 348 p.

S6. Waldron, J.W.F., Giles, P.S., and Thomas, A.K. (2017). Correlation chart for Late Devonian to Permian stratified rocks of the Maritimes Basin, Atlantic Canada: Nova Scotia. Dept. Energy Open File Rep. 2017-02, 12 p.