

Current Biology

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

Highlights

- Extensively preserved, ~350 Ma trunk with protracted crown morphology
- Early Carboniferous growth architecture presages modern fern lineages
- Densely arrayed compound leaves provide expansive photosynthetic surface and cover
- Fossils preserved as a consequence of earthquake-induced burial in ancient rift lake

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In brief

Newly discovered tree fossils from ~350 Ma in New Brunswick, Canada, are architecturally unique, and Gastaldo et al. interpret them to presage modern tree-fern lineage growth forms. These fossils, preserved by earthquake-induced burial in an Early Carboniferous rift lake, may represent early evidence of a subcanopy forest niche.

Article

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

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<https://doi.org/10.1016/j.cub.2024.01.011>

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 $>20\text{--}30\text{ m}^3$. 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 $\sim 393\text{--}383$ 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 soils³). 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 (Serpukhovian⁷). 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 structures⁹ 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 documented¹¹ 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,

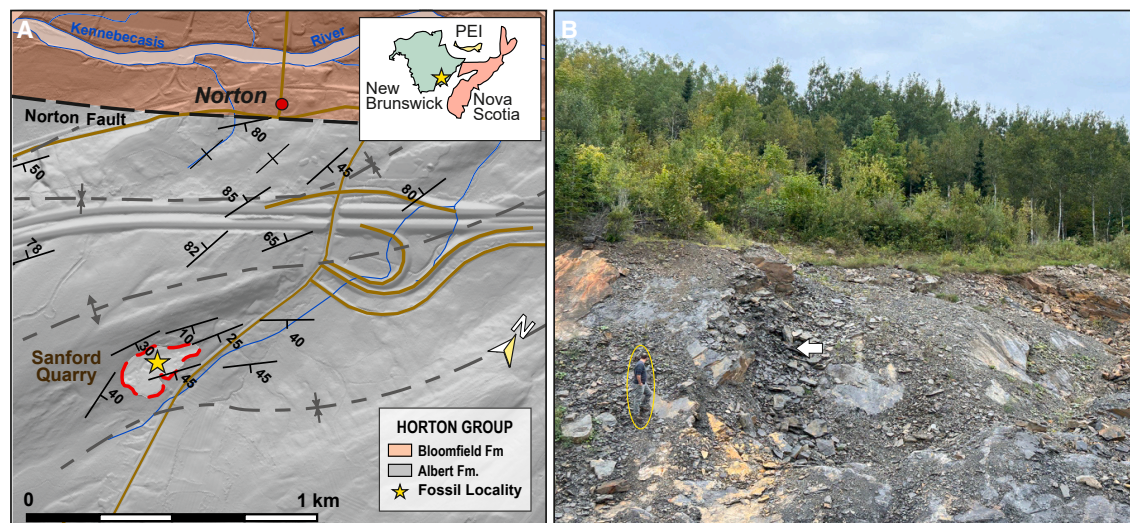


Figure 1. Sanford Quarry locality, New Brunswick, Canada

(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 adpression¹⁹ 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)

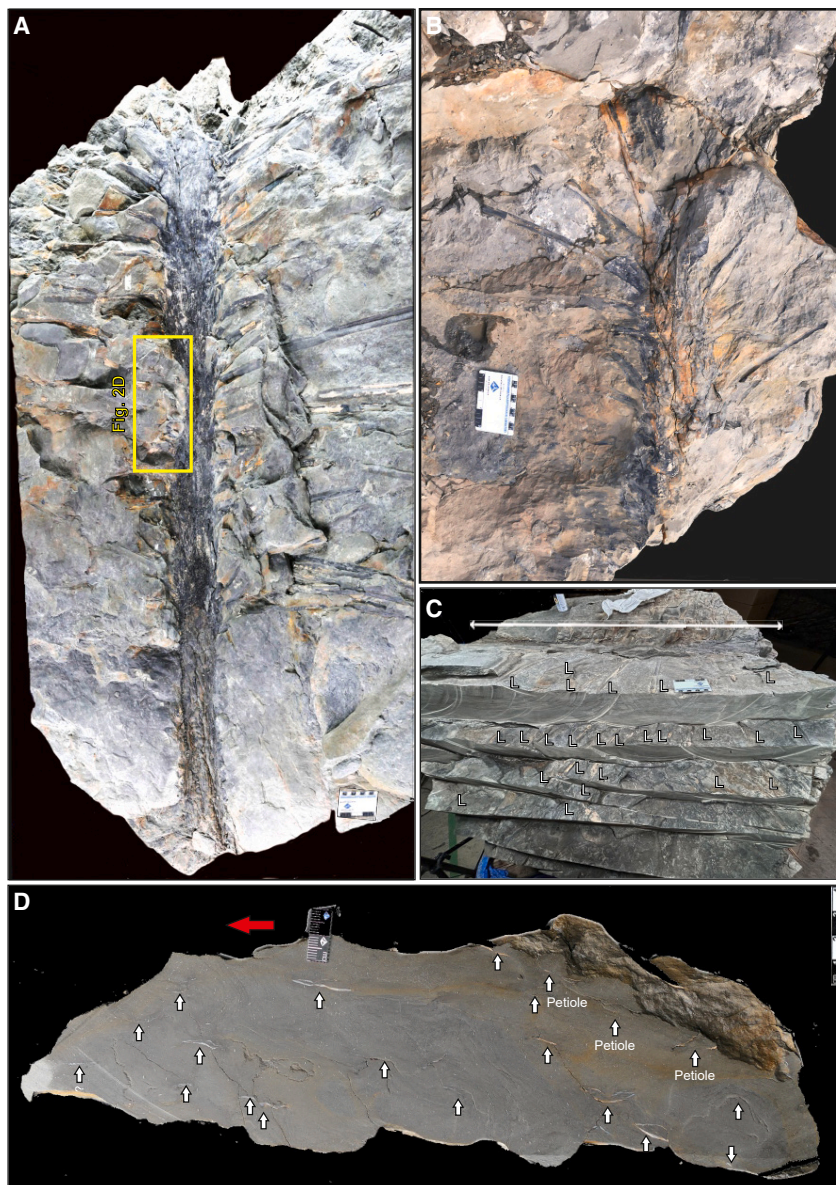


Figure 2. Tournaisian tree with spirally arranged compound leaves

(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 $\sim 45^\circ$ below the apex to $\sim 30^\circ$ 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.

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 $\sim 45^\circ$ 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 $\leq 20^\circ$ (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

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 sub-epidermal 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

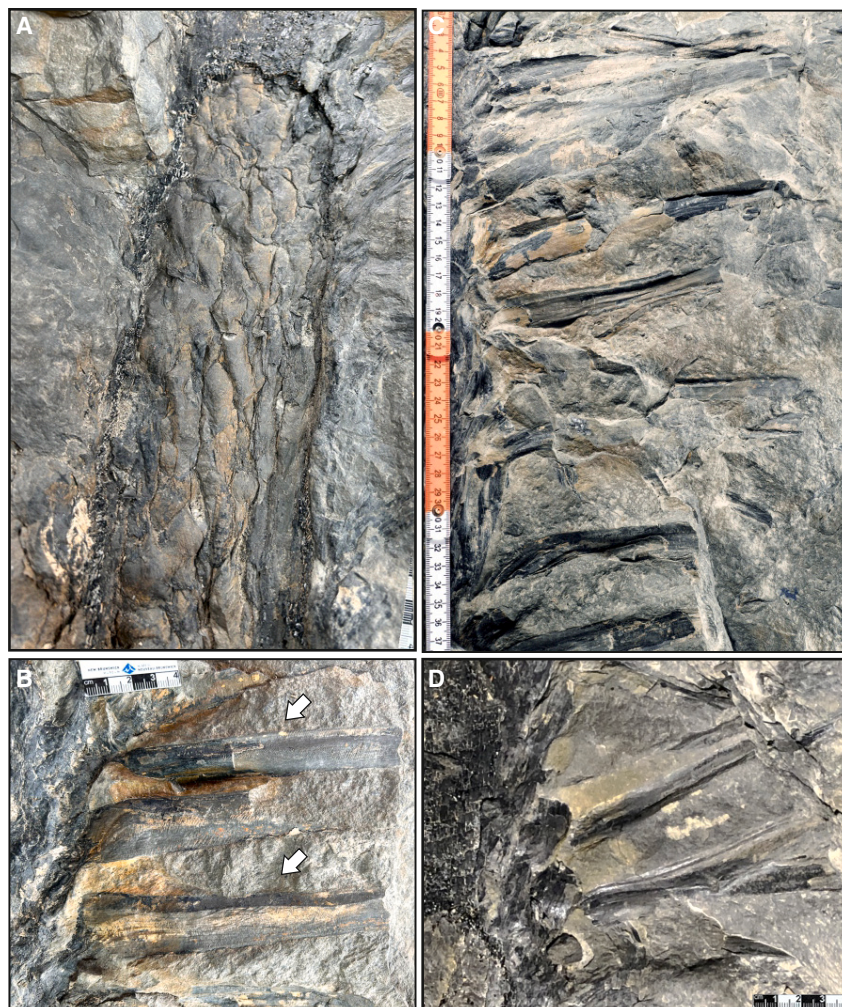


Figure 3. Trunk and petiole features. NBM 22403/1

(A) An ~40 cm interval showing helically arranged, mudcast petiole bases in an estimated 1/13 phyllotaxy with coalified and mudcast petioles departing side of the trunk. Scale in cm and mm.
(B) Finely striated and adaxially grooved petioles diverge ~90° to the trunk (white arrows) beneath the apex; petioles are without secondaries. Scale in cm/mm.
(C) Petioles diverge from trunk at ~90° angle. Scale in cm and mm.
(D) Divergence of petioles in dimensions reflecting their spiral arrangement. Strong longitudinal ridges mirror the petiole cross-sectional geometry, and striated petioles may exhibit transverse markings, similar to coal cleat, from tectonism. Scale in cm and mm.

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 m³.

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 *Spelaotritiles cabotii* subzone of the *Vallatisporites vallatus* Biozone/Europe upper part of the *Spelaotritiles 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)

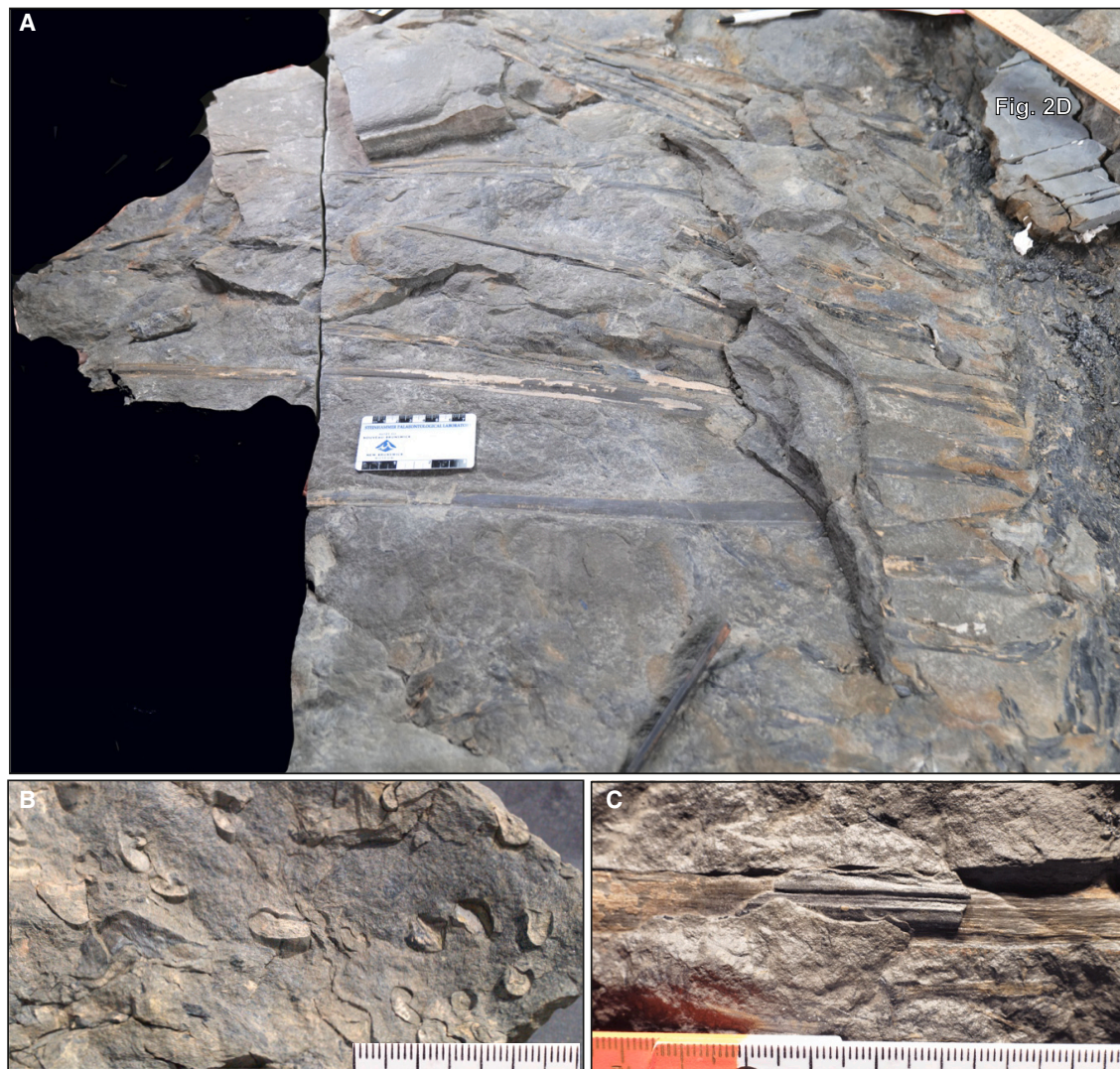


Figure 4. Trunk and petiolar features

(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 vegetation²¹ 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

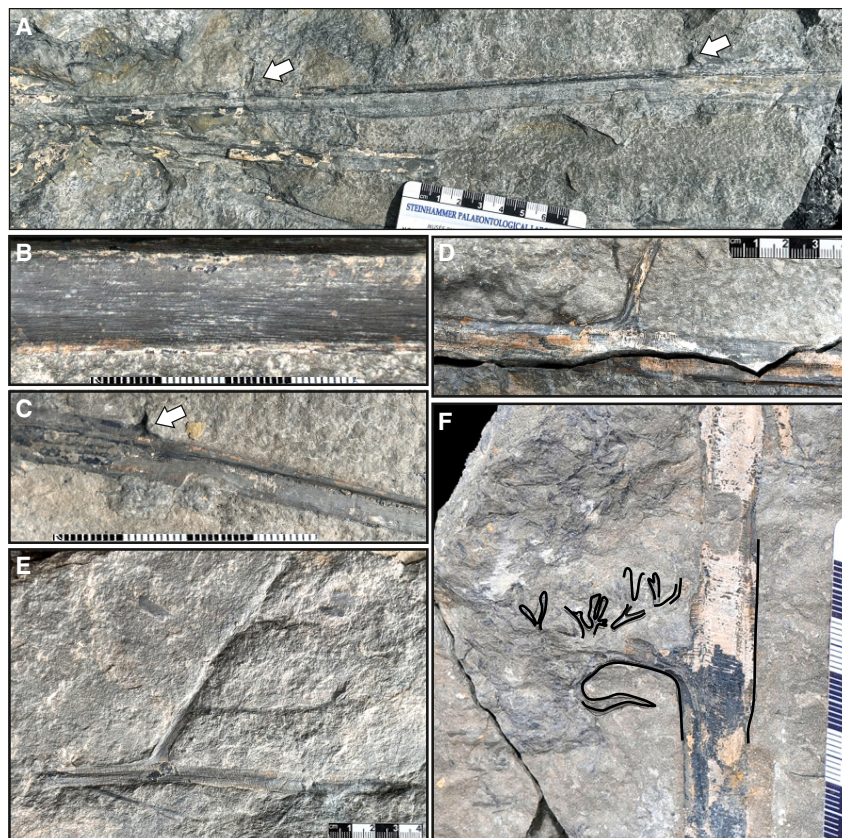


Figure 5. Evidence of compound leaves and pinnules. NBM 22403/2

(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 Cladoxylales⁴⁹ (Figure 7). Individual trees in mixed-age, monodominant stands⁴⁸ 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 forest⁵⁰ 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 rootstocks² 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 m². 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 mixed² or gallery forests.⁵² Although Late Devonian systematic diversity was relatively high compared with older assemblages, groundcover 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 it⁵³ (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

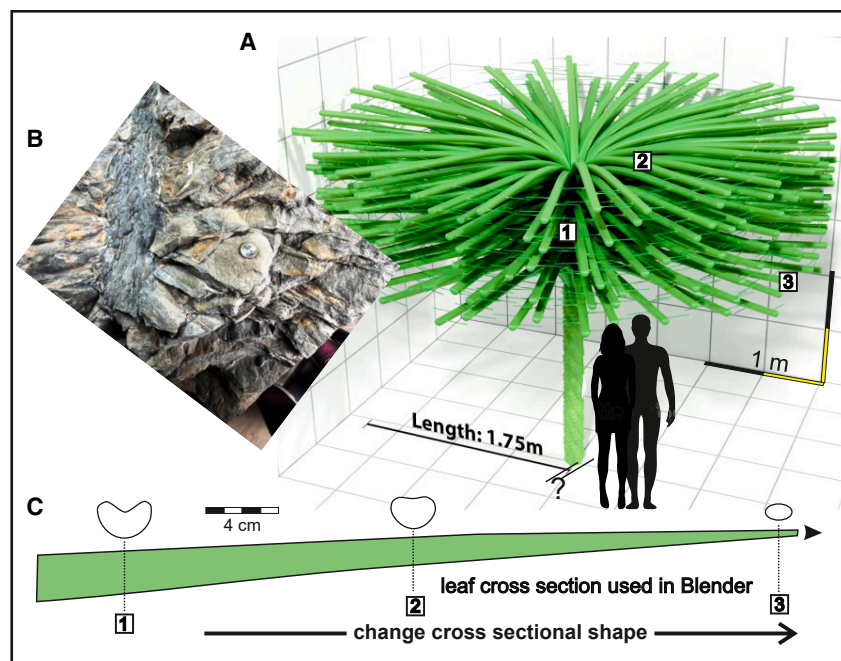


Figure 6. *Sanfordiacaulis densifolia* reconstruction

(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).

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-

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 wetlands⁵⁷ 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 subsidence⁹ 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 pattern⁵⁹ (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). Marattialeans (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

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 CO₂ 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

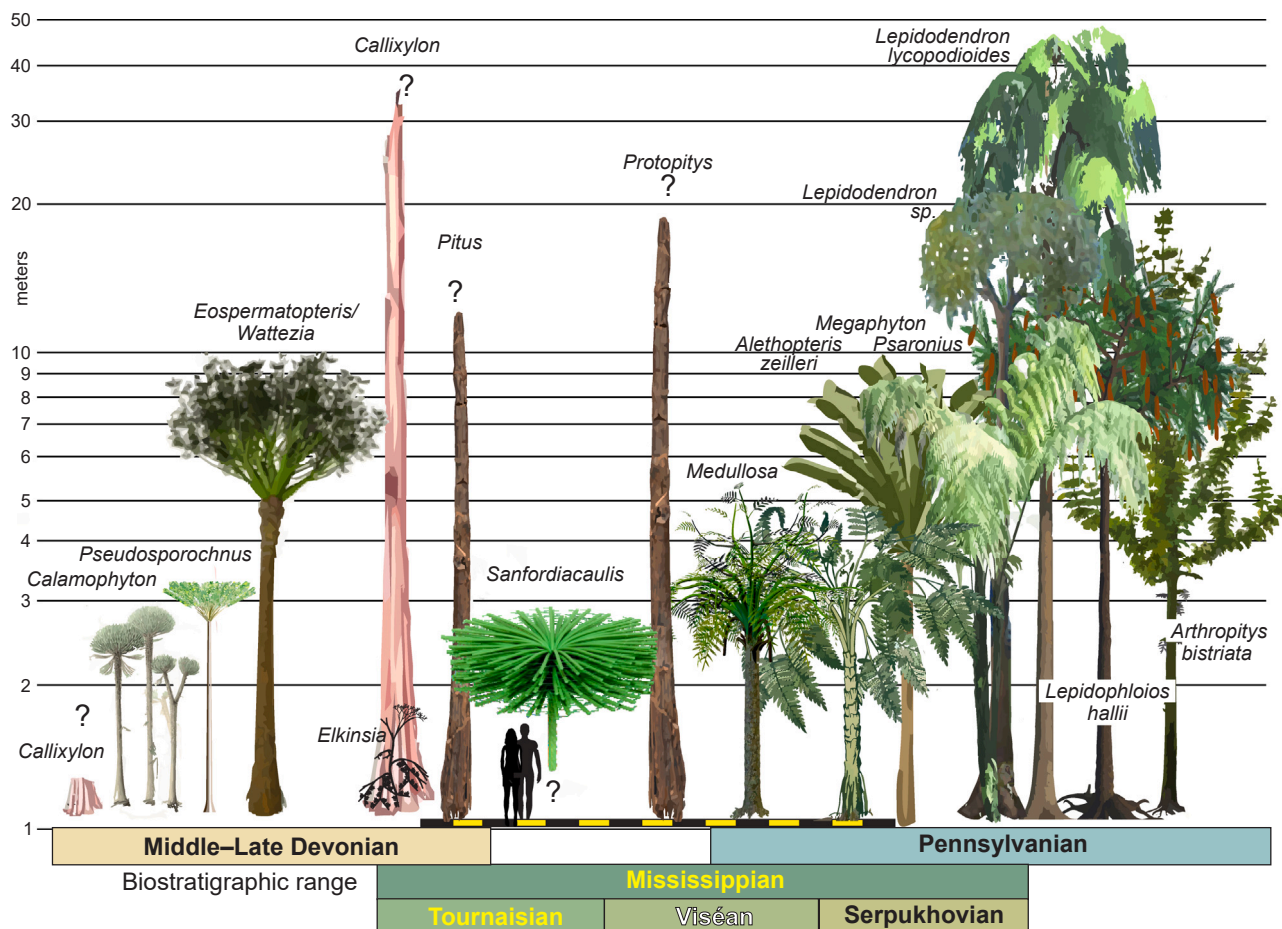


Figure 7. Actual and reconstructed tree heights and biostratigraphic ranges of Middle Devonian to Pennsylvanian trees

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/Wattezia*¹; Progymnosperms: *Callixylon*,^{2,28,29} *Pitus*,³⁰ and *Prototypis*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; log₁₀ 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 *Oxroa-dia 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 m³. 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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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.01.011>.

ACKNOWLEDGMENTS

We thank Laurie Sanford for quarry access fossil transport to NBM; J. Curtis, Colby College '24, for early models; A. Graham (NBM) for additional

images; and A. MacRae, Saint Mary's University, Halifax, for field assistance and palynological discussions. This study was funded by RAP Bursary 60576 (O.A.K.), NSERC 547631 (M.R.S.), George Frederick Matthew Fellowship (M.R.S. and O.A.K.), G.F. Matthew Fellowship (P.G.G.), NSF EAR 1828359 (I.J.G. and R.A.G.), the Geological Surveys Branch-New Brunswick Department of Natural Resources and Energy Development (S. Allard and K. Thorne), and HMRC R&D tax credit SME scheme (D.M.).

AUTHOR CONTRIBUTIONS

Conceptualization, M.R.S., O.A.K., R.A.G., I.J.G., and P.G.G.; investigation, M.R.S., O.A.K., S.J.H., A.F.P., P.G.G., R.A.G., I.J.G., D.M., and T.S.; writing, R.A.G., P.G.G., and I.J.G.; contributions from all authors; review & editing, all authors; funding acquisition, M.R.S., O.A.K., P.G.G., R.A.G., and I.J.G.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: July 17, 2023

Revised: October 31, 2023

Accepted: January 3, 2024

Published: February 2, 2024

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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 soft-sediment 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 wavy and has a pointed cusped 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. cabottii*, *S. galearis*, *Vallatisporites vallatus*, *Verrucosporites nitidus*, and *Waltzisporea polita*. A fairly diverse accessory assemblage includes *Acanthotriletes hacquebardii*, *Claytonispora distincta*, *Claytonispora rarisetosa*, *Crassisporea 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 *Crassisporea 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 hystichosus*? (22SAN-06) and a comparison record of *Schopfites cf. augustus* (22SAN-08). Occurrences of *Claytonispora distincta* along with *Crassisporea 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 *Verrucosporites nitidus* indicates correlation with the late Tournaisian *Spelaeotriletes pretiosus*-*Raistrickia clavata* (PC) Biozone of Higgs et al.⁸⁹ The records of *Crassisporea 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 Biozone⁸⁹ 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 Chaloner⁹⁶ 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 to 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.