AN EARLY ORIGIN OF SECONDARY GROWTH: *FRANHUEBERIA GERRIENNEI* GEN. ET SP. NOV. FROM THE LOWER DEVONIAN OF GASPÉ (QUEBEC, CANADA)[1]

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- *Premise of the Study:* Secondary xylem (wood) produced by a vascular cambium supports increased plant size and underpins the most successful model of arborescence among tracheophytes. Woody plants established the extensive forest ecosystems that dramatically changed the Earth's biosphere. Secondary growth evolved in several lineages in the Devonian, but only two occurrences have been reported previously from the Early Devonian. The evolutionary history and phylogeny of wood production are poorly understood, and Early Devonian plants are key to illuminating them.

- *Methods:* A fossil plant preserved anatomically by cellular permineralization in the Lower Devonian (Emsian, ca. 400–395 million years old) Battery Point Formation of Gaspé Bay (Quebec, Canada) is described using the cellulose acetate peel technique.

- *Key Results:* The plant, *Franhueberia gerriennei* Hoffman et Tomescu gen. et sp. nov., is a basal euphyllophyte with a centrarch protostele and metaxylem tracheids with circular and oval to scalariform bordered multiaperturate pits (P-type tracheids). The outer layers of xylem, consisting of larger-diameter P-type tracheids, exhibit the features diagnostic of secondary xylem: radial files of tracheids, multiplicative divisions, and a combination of axial and radial components.

- *Conclusions: Franhueberia* is one of the three oldest euphyllophytes exhibiting secondary growth documented in the Early Devonian. Within the euphyllophyte clade, these plants represent basal lineages that predate the evolution of stem-leaf-root organography and indicate that underlying mechanisms for secondary growth became part of the euphyllophyte developmental toolkit very early in the clade's evolution.

Key words: Canada; Devonian; Emsian; euphyllophytes; fossil; *Franhueberia*; multiplicative division; secondary growth; wood.

Secondary growth, the production of tissues from lateral meristems or cambia, results in an increase in girth of the plant body. In seed plants, a bifacial vascular cambium contributes secondary xylem (wood) toward the interior, and secondary phloem toward the exterior, of stems and roots. Secondary tissues can be recognized using a series of anatomical criteria listed in all major plant anatomy textbooks and applied in paleobotanical studies (e.g., Cichan and Taylor, 1982, 1990; Gerrienne et al., 2011): (1) radially aligned files of cells (as seen in cross sections); (2) multiplicative divisions in secondary xylem—anticlinal divisions of cambial initials that generate new radial files of cells; (3) combination of axially and radially oriented components (e.g., conducting cells and rays).

The plant world provides exceptions to each of the three criteria. In *Botrychium*, Rothwell and Karrfalt (2008) showed that radial files of tracheids, traditionally interpreted as secondary xylem, are produced in primary growth by patterned divisions of procambial cells. The vascular cambium may not undergo multiplicative divisions in all plants; in the extinct sphenopsid *Sphenophyllum*, absence of multiplicative divisions limited secondary growth to a girth at which outermost secondary xylem tracheids reached a maximum viable diameter (Cichan and Taylor, 1982). Finally, some plants produce rayless wood (e.g., species of *Viola* and *Lysimachia*; Carlquist, 1974). These exceptions show that none of the criteria, taken separately, provides unequivocal evidence for growth derived from a vascular cambium. However, their concurrent application is a reliable means of recognition of secondary vascular tissues.

The oldest occurrences of secondary growth have been reported from the Lower Devonian (late Pragian–Emsian, ca. 409–394 million years ago; Cohen et al., 2012) of France and Canada (Gerrienne et al., 2011) and comprise two different plants of euphyllophyte affinities that have not yet received a taxonomic treatment. The plants exhibit secondary xylem with narrow tracheids and probably uniseriate rays. They are younger than the lycophyte-euphyllophyte split and the origin of leaves in the lycophytes (*Baragwanathia*, Late Silurian; Rickards, 2000; Gensel, 2008), and are coeval with the earliest euphyllophytes exhibiting departures from simple organography (*Eophyllophyton*; Hao and Beck, 1993).

Prior to this discovery, secondary growth from a vascular cambium had been documented in Middle Devonian (as old as the late Eifelian, ca. 391–388 million years ago; Mustafa, 1975, 1980; Beck and Stein, 1993) or younger representatives of isoetalean lycopsids and several euphyllophyte lineages: cladoxylopsids, stenokolealeans, rhacophytaleans, zygopterids, sphenopsids, and lignophytes (a clade defined by the presence

of a bifacial vascular cambium and which includes the progymnosperms and seed plants; Cichan and Taylor, 1990; Rothwell and Serbet, 1994; Rothwell et al., 2008; Table 1 and Fig. 1).

Here, we describe an anatomically preserved fossil plant from Emsian (ca. 402–394 million years old) rocks of the Battery Point Formation, in Quebec (Canada). The plant, *Franhueberia gerriennei* Hoffman et Tomescu gen. et sp. nov., displays secondary growth; it is different anatomically from all major euphyllophyte lineages and is similar to, but not identical with, *Psilophyton* and the two euphyllophytes described by Gerrienne et al. (2011). *Franhueberia* is ≥6 million years younger than one of Gerrienne et al.'s plants (the Châteaupanne euphyllophyte) and coeval with the other one (the New Brunswick plant); these three plants represent the only known occurrences of secondary vascular tissues in the Early Devonian.

MATERIALS AND METHODS

The fossil described here is preserved by calcareous cellular permineralization in a cobble collected by Dr. Francis M. Hueber (Smithsonian Institution–NMNH) in 1965 from an exposure of the Battery Point Formation on the south shore of Gaspé Bay, in the vicinity of Douglastown, Quebec, Canada. The cobble contains abundant specimens assignable to *Psilophyton dawsonii*. Exposures of the Battery Point Formation yielding *Psilophyton* cobbles are located between Douglastown and Seal Cove (Banks and Colthart, 1993). The age of Battery Point Formation deposits ranges between early Emsian at Tar Point (East of Seal Cove) and late Emsian at Douglastown (McGregor, 1977). Therefore, the age of the fossil described here is mid- to late Emsian, ca. 402–394 million years old (Cohen et al., 2012). The rocks represent sediments deposited in braided fluvial to coastal environments (Cant and Walker, 1976; Griffing et al., 2000).

Anatomical sections were obtained using the cellulose acetate peel technique (Joy et al., 1956), and the specimen description is based on examination of serial sections. Microscope slides were prepared with Eukitt (O. Kindler, Freiburg, Germany) mounting medium. Images were captured using a Nikon Coolpix 8800VR digital camera mounted on a Nikon E400 compound microscope and processed using Adobe (San Jose, California, USA) Photoshop 5.0. Cobble slabs, acetate peels, and slides are housed in the U.S. National Museum of Natural History–Smithsonian Institution (USNM no. 558725, field specimen no. FMH 65-6/B21).

SYSTEMATICS

Subdivision—Euphyllophytina Kenrick and Crane 1997

Genus—*Franhueberia* Hoffman and Tomescu gen. nov.

Generic diagnosis—Small axis with centrarch protostele and secondary tissues produced by a vascular cambium. Metaxylem tracheids with circular to oval bordered pits; secondary xylem tracheids with multiaperturate scalariform bordered pits. Rays uniseriate.

Etymology—*Franhueberia* is named for Francis Hueber, Smithsonian Institution–NMNH, USA, who collected the specimen, in recognition of his contribution to the understanding of Devonian floras.

Type species—*Franhueberia gerriennei* Hoffman and Tomescu sp. nov.

Specific diagnosis—Axis xylem ca. 1.9 mm in diameter. Protostele ca. 0.5 mm in diameter. Protoxylem tracheids 8 μm

TABLE 1. Age and selected anatomical characters of the oldest representatives of lineages that had evolved secondary vascular tissues by the end of the Devonian.

|	Age/first occurrence	Lineage	Primary xylem maturation	Pitting of metaxylem tracheids	Pitting of secondary xylem tracheids	Rays	References
Franhueberia	Mid-Emsian	Basal euphyllophyte	Centrarch	Circular bordered pits to oval and scalariform multiaperturate bordered pits (P-type)	Multiaperturate scalariform bordered pits (P-type)	Frequent, uniseriate	Present study
Psilophyton	Emsian	Basal euphyllophyte	Centrarch	Multiaperturate scalariform bordered pits (P-type)	—	Absent	Banks et al., 1975; Hartman and Banks, 1980; Trant and Gensel, 1985
Châteaupanne euphyllophyte	Late Pragian–earliest Emsian	Basal euphyllophyte	Centrarch	(Multiaperturate?) scalariform bordered pits	Multiaperturate scalariform bordered pits (P-type)	Variable	Gerrienne et al., 2011
New Brunswick euphyllophyte	Emsian	Basal euphyllophyte	Centrarch	?	Multiaperturate scalariform bordered pits (P-type)	Uniseriate?	Gerrienne et al., 2011
Xenocladia	Late Eifelian	Cladoxylopsid	Mesarch	Scalariform to multiseriate alternate bordered pits	Multiseriate alternate bordered pits	Rare, uniseriate or absent	Arnold 1940, 1952; Lemoigne and Iurina, 1983; Meyer-Berthaud et al., 2004
Rellimia, Aneurophyton, Actinoxylon	Late Eifelian–Frasnian	Progymno-sperms	Mesarch	Scalariform–reticulate and oval to circular multiseriate, alternate bordered pits	Circular multiseriate alternate bordered pits	Narrow, uniseriate to multiseriate	Schweitzer and Matten 1982; Dannenhoffer and Bonamo, 1989, 2003; Dannenhoffer et al., 2007
Crossia	Late Eifelian	Stenokoleales	Mesarch	Scalariform–fimbriate, scalariform–reticulate, and oval to circular multiseriate bordered pits	Not documented	Uniseriate?	Beck and Stein, 1993
Rhacophyton	Famennian	Rhacophytales	Mesarch	Scalariform bordered pits	Scalariform to reticulate bordered pits	Uniseriate	Dittrich et al., 1983
Rotafolia	Famennian	Sphenopsid	Exarch	Scalariform and circular bordered pits	Scalariform bordered pits	Rare; uniseriate?	Wang et al., 2005, 2006
Phytokneme	Frasnian	Lycopsid	Exarch	Scalariform	Scalariform	?	Andrews et al., 1971
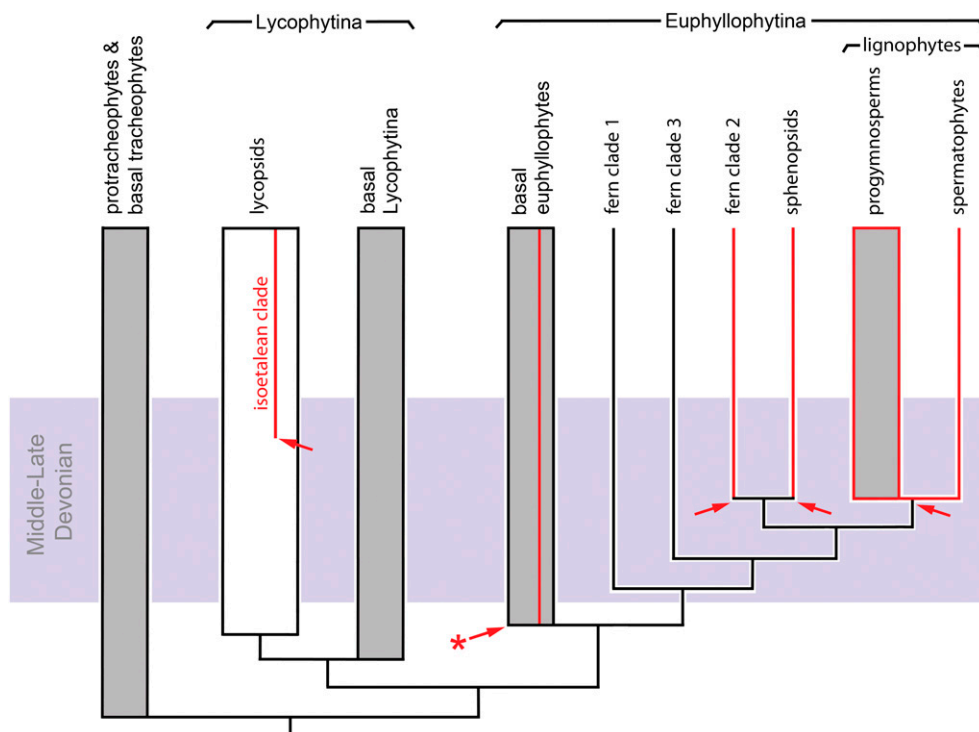
Fig. 1.   Vascular plant phylogeny and occurrences of secondary vascular tissues (tree based on Kenrick and Crane, 1997; Rothwell, 1999). Gray rectangles represent paraphyletic grades. Fern clades 1–3 as defined by Rothwell (1999): (1) Stauropteridales; (2) Zygopteridales + cladoxylopsids; and (3) living and extinct Filicales and Hydropteridales. Lineages with secondary vascular tissues arrowed, in red: the isoetalean clade (nested within the lycopsids); fern clade 2 with up to three distinct lineages (not shown) exhibiting secondary vascular tissues (cladoxylopsids, Zygopteridales, and Rhacophytales); sphenopsids; lignophytes; and basal euphyllophytes (asterisk), which now include three distinct plants with evidence for secondary xylem—two described by Gerrienne et al. (2011) and *Franhueberia* described here.

in diameter. Metaxylem tracheids 7–15 µm in diameter. Pitting round to oval, bordered, 4.4–6.6 µm in diameter. Secondary xylem tracheids rectangular in cross section, 8.4–28.5 µm wide tangentially, 21.6–40.8 µm radially; scalariform bordered pits on tangential and radial tracheid walls, width same as that of tracheids, height 3.4–9.6 µm, separated by horizontal thickenings 1.4–3.4 µm across. Pit membranes with multiple apertures ca. 3 µm diameter, in one or two rows. Rays frequent, narrow (9–12 µm) and 90 µm to >150 µm tall.

Etymology—The species is named for Philippe Gerrienne, University of Liège, Belgium, in recognition of his numerous

and continued contributions to characterization of Early Devonian plant diversity.

Holotype hic designatus—Specimen in cobble USNM no. 558725 (field specimen no. F. M. Hueber 65-6/B21), slab E; specimen peeled entirely—peel numbers Eb 1–230, E(2)s 1–130; microscope slides mounted from numbers Eb 21, Eb 28–150, E(2)s 1–76.

Locality—South shore of Gaspé Bay, in the vicinity of Douglastown, Quebec, Canada.

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Fig. 2.   *Franhueberia gerriennei* gen. et sp. nov. (USNM 558725). (A) Transverse section of axis; primary xylem at center, surrounded by secondary xylem. Slide B21 E_b no. 106. Scale = 300 µm. (B) Radial longitudinal section; primary xylem at center (arrows); asterisk indicates same position as in C. Slide B21 E(2)_s no. 42A. Scale = 100 µm. (C) Detail of B (asterisk indicates same position as in B). Primary xylem longitudinal section; protoxylem tracheid with annular-helical thickening (at left, next to asterisk) and metaxylem tracheids with circular and oval bordered pits. Note tracheids with continuous secondary wall lining interrupted by sparse pitting (right of protoxylem tracheid); oval pits with two apertures per membrane close to the upward tapering end of a metaxylem tracheid (arrowhead); and metaxylem tracheid with scalariform multiaperturate pits (right). Scale = 40 µm. (D) Transverse section; primary xylem at center, with no particular patterning of tracheids (and with taphonomically induced compression and fracturing) surrounded by secondary xylem exhibiting radial patterning of tracheids. Note inner ends of xylem rays (some indicated by arrowheads). Slide B21 E_b no. 85. Scale = 100 µm. (E) Transverse section; transition from primary xylem (right; note varied tracheid diameters) to secondary xylem (left); approximate position of transition marked by arrowheads. Slide B21 E_b no. 138. Scale = 40 µm. (F) Longitudinal section; metaxylem tracheids with circular to oblique-oval bordered pits (some with double apertures—upper and lower right). Note tracheid with continuous secondary wall lining interrupted by sparse pitting (center). Slide B21 E(2)_s no. 42A. Scale = 30 µm. (G) Longitudinal section; metaxylem tracheids with circular, oblique, and scalariform bordered pits. Slide B21 E(2)_s no. 40A. Scale = 30 µm. (H) Transverse section; multiplicative divisions (arrowheads). Slide B21 E_b no. 107. Scale = 30 µm.
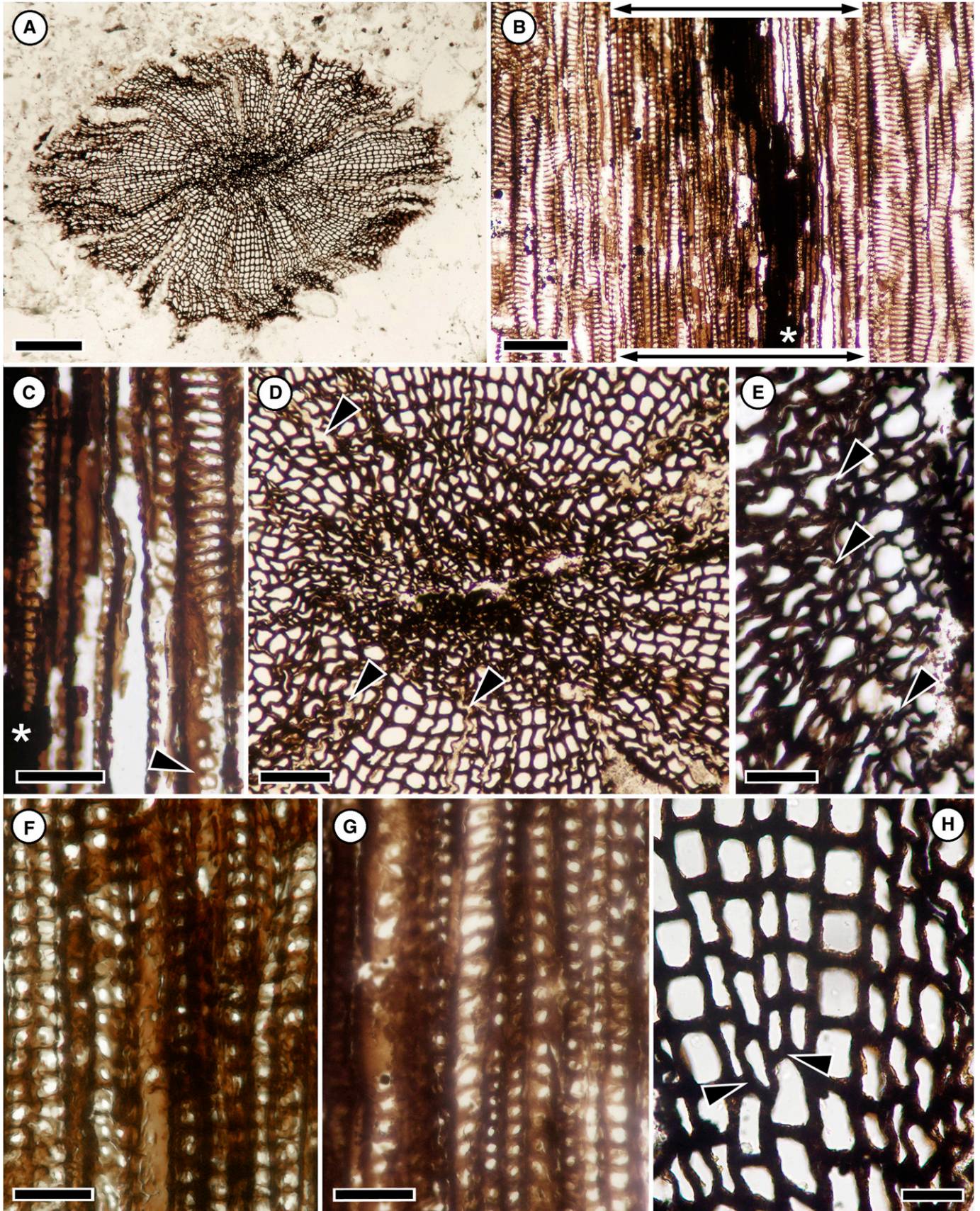
Stratigraphic position and age—Battery Point Formation, mid- to late Emsian, ca. 402–394 million years ago.

DESCRIPTION

The *Franhueberia* axis preserves only the central cylinder of xylem and lacks extraxylary tissues. It can be traced for ≥27 mm of length; the two ends are broken, and one is split by a fissure in the rock. The axis is oval in cross section because of lateral compression, with a large diameter of 1.9 mm and a small diameter of 1.2 mm (Fig. 2A).

The central primary xylem is protostelic and 0.5 mm in diameter (Fig. 2A, D). The pattern of primary xylem maturation is somewhat obscured by compressive disturbance of tissues at the center of the axis. Centrarch primary xylem maturation is nevertheless indicated by the combination of (1) absence of a consistent pattern of distribution of narrow tracheids (potential protoxylem) around the primary xylem periphery in cross sections; (2) absence of protoxylem tracheids (i.e., narrow, with annular or helical thickenings) at the primary–secondary xylem boundary, in the series of longitudinal sections examined, which runs through the entire axis; (3) presence of a dense central area, most readily interpreted as very narrow tracheids collapsed because of compression, and of tracheids with helical secondary wall thickenings, as narrow as 8 μm, positioned centrally in the primary xylem (Fig. 2B, C). Some cross sections exhibit areas of well-preserved metaxylem, which consists of tracheids of variable diameter (7–15 μm; Fig. 2D, E). In longitudinal sections, metaxylem tracheids (Fig. 2C, F, G) feature round to oval bordered pits 4.4–6.6 μm in diameter, which can sometimes have two apertures in their membrane. Some metaxylem tracheids exhibit portions characterized by continuous secondary wall lining, which separates areas of sparse pitting (Fig. 2C, F). Metaxylem tracheids close to the periphery of the stele have scalariform bordered pits with multiaperturate pit membranes (corresponding to the P-type tracheids of Kenrick and Crane, 1997) like those seen in the secondary xylem tracheids, albeit narrower.

The boundary between primary and secondary xylem is conspicuous in the distribution of tracheid diameters, which are narrower in the primary xylem and wider in the secondary xylem (Fig. 3A). Additionally, in cross sections, the boundary is marked by a transition from smaller, thinner-walled, rounder tracheids to larger, rectangular tracheids (Fig. 2D, E). In longitudinal sections we see a transition between the characteristically of the larger-diameter secondary xylem tracheids, through a few narrower tracheids with multiaperturate scalariform bordered pits (peripheral metaxylem), to oval bordered pits of the primary xylem (Fig. 2B).

The secondary xylem of the specimen is ≤0.7 mm thick, and comprises radial files ≤25 tracheids long. The outer margin of secondary xylem, which is also the outer margin of the specimen, is poorly preserved (Figs. 2A and 4C, D). Secondary xylem tracheids are rectangular in cross section (Fig. 2D, H), ≥670 μm long, and were produced by a nonstoried cambium (Fig. 4A, B). Tracheids are 19.5 μm wide (range: 8.4–28.5 μm, $n = 45$) tangentially, and 29.5 μm (range: 21.6–40.8 μm, $n = 38$) radially.

Pitting of the secondary xylem tracheids, occurring along both radial and tangential walls, consists of scalariform bordered pits with multiaperturate pit membranes (P-type) (Figs. 4A, B and 5A). The scalariform pits span the width of tracheids and are 6.9 μm high (3.4–9.6 μm, $n = 20$), separated by hori-zontal wall thickenings that are 2.6 μm wide (1.4–3.4 μm, $n = 19$). Within the membranes of scalariform pits, apertures form one to two horizontal files ≤10 apertures long. Apertures in the pit membranes are circular to oval and measure ≤5 μm in diameter (usually ca. 3 μm in diameter). The scalariform pits transition to narrower scalariform and oval to circular bordered pits at the tapered ends of tracheids (Fig. 5A).

Multiplicative divisions in the secondary xylem (Fig. 2H) are present, as close as 3 cells and as far as 16 cells from the primary xylem (Fig. 3B). The number of multiplicative divisions observed in single cross sections is 10–15 (i.e., 3.8–5.7/mm^2 secondary xylem cross section at a 0.95-mm axis radius; Fig. 4C).

Rays are numerous but the walls of ray cells are not preserved (Figs. 4D and 5B, C). They are distorted to different degrees by taphonomic agents, and in cross sections their distal ends are flared. Where they are least distorted, their sides are parallel and they have widths of 9–12 μm (Fig. 5B, C). In tangential longitudinal sections, rays are identified as narrow, tall spindle-shaped spaces that are bordered by tracheids and show secondary thickenings only on the tracheid side (Fig. 5E–I). The shortest rays identified are ca. 90 μm tall, and some are >150 μm tall. Between 14 and 20 rays can be counted in individual cross sections (Fig. 4D). Their inner ends are located 1 to 14 cells from the primary xylem cylinder (Fig. 3C).

DISCUSSION

Franhueberia is an Early Devonian (mid- to late Emsian) plant that exhibits all the characters of secondary growth: radially aligned tracheid files, multiplicative divisions, and presence of axial and radial tissue components. *Franhueberia* is known only by its xylem—the extraxylary tissues of the axis described here were probably separated from the xylem cylinder during transport and deposition. Taphonomic factors are also responsible for the mode of preservation of the rays. Rays are more readily distorted than tracheids because of their parenchymatous nature and thin cell walls. The latter were degraded prior to fossilization, which provided planes of weakness along which the axis tissues were fractured during lateral compression of the specimen. The narrowness of rays in cross sections nevertheless suggests that they were uniseriate. Anatomically, the rays of *Franhueberia* appear to be similar to conifer rays, such as those of extant *Pinus* (compare Fig. 5C, D); although the latter have undergone no preservational deformation, they show the same thin, undulating walls punctuated by constrictions induced by periclinal tracheid walls.

Compared to the two Early Devonian euphyllophytes described by Gerrienne et al. (2011), *Franhueberia* is coeval with the New Brunswick plant (late Emsian) and ≥6 million years younger than the Châteaupanne plant (late Pragian–earliest Emsian). The two plants reported by Gerrienne et al. and *Franhueberia* are, thus far, the only records of secondary growth in the Early Devonian. As the oldest examples of secondary growth, they may hold the key to understanding the phylogeny and evolution of the woody habit. In this context, it is important to assess the taxonomic affinities of *Franhueberia*.

Franhueberia *and the phylogeny of early vascular plants*— The oldest vascular plant fossils are ca. 428 million years old (*Cooksonia*, mid-Silurian, Homerian; Edwards and Davies, 1976; Edwards and Feehan, 1980; Edwards et al., 1992). Reports of *Baragwanathia*, a crown-group lycophyte, in the late Silurian
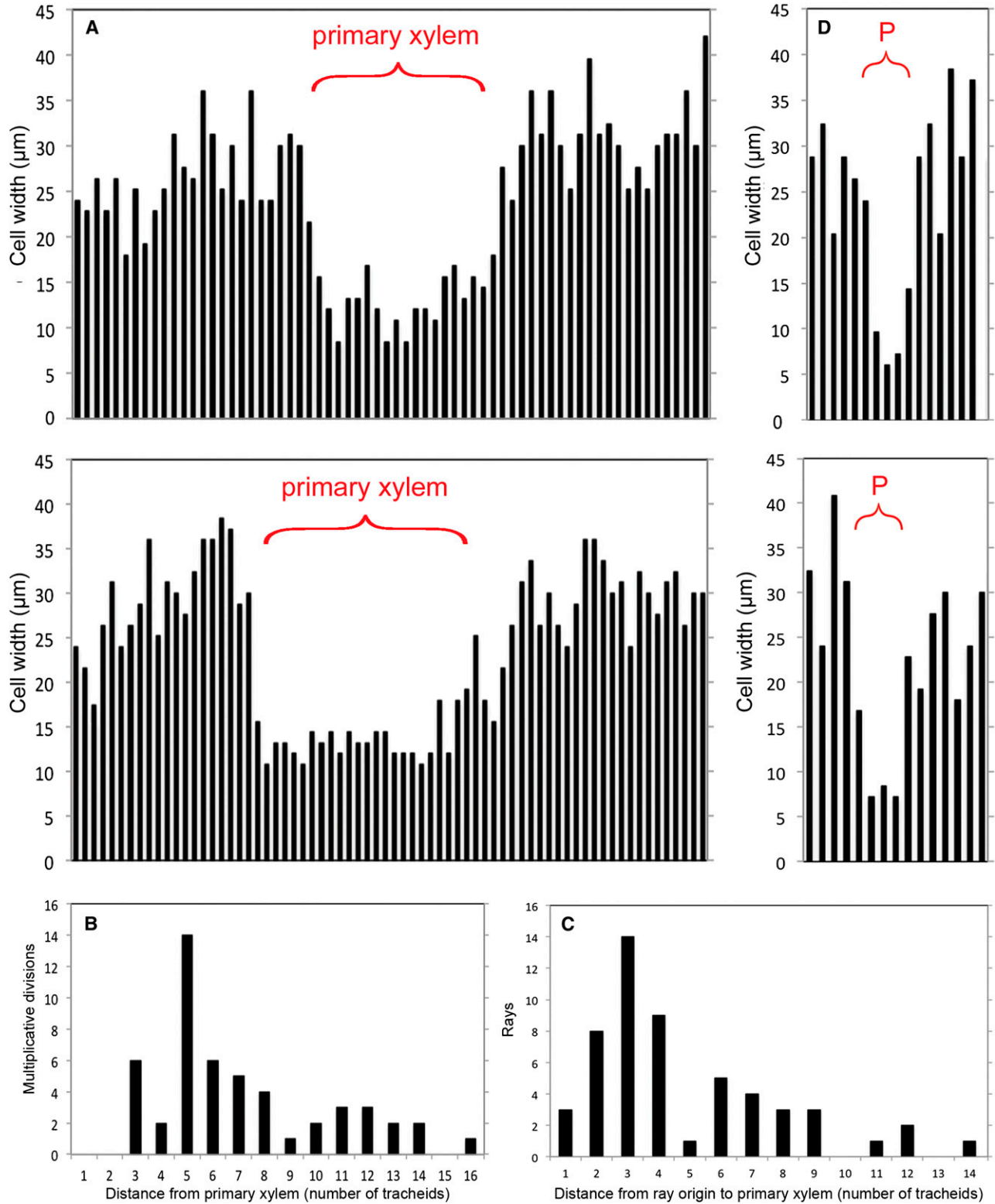
Fig. 3. Descriptive morphometrics of *Franhueberia gerriennei* gen. et sp. nov. and comparison with *Psilophyton dawsonii* Banks et al. (1975). (A) Two transverse transects recording individual tracheid diameters at two levels across the center of the *Franhueberia* axis; note sharp transitions between primary xylem (center) and secondary xylem (left and right). (B) *Franhueberia* frequency of multiplicative divisions (*n* = 51) as a function of distance from the primary xylem (measured in number of secondary xylem tracheids). (C) *Franhueberia* frequency of ray origins (*n* = 54) as a function of distance from the primary xylem (measured in number of secondary xylem tracheids). (D) Two transverse transects recording individual primary xylem tracheid diameters at two levels across the center of a *Psilophyton dawsonii* axis (P = protoxylem, at center); the metaxylem tracheids of *Psilophyton* have diameters comparable to those of *Franhueberia* secondary xylem tracheids and twice as large as those of *Franhueberia* metaxylem tracheids.

(Gorstian; Rickards, 2000) imply that the euphyllophyte–lycophyte split is prelate Silurian and that the lycopsid radiation started before the Devonian (Gensel, 2008; Wellman et al., 2009). Thus, derived lycophytes coexisted through the Early Devonian with plants characterized by simple organography (undifferentiated, photosynthetic, branched sporangium-bearing axes) that are classified into three main groups (Fig. 1): (1) a grade of protracheophytes and basal tracheophytes paraphyletic to the major divide between the Lycophytina and the Euphyllophytina; (2) a paraphyletic grade (basal Lycophytina) at the base of the lycopsids; and (3) a paraphyletic grade of basal euphyllophytes.

Lycophytes are characterized by exarch (to marginally mesarch) primary xylem maturation, whereas basal euphyllophyte axes and stems exhibit centrarch (or mesarch) primary xylem (Table 1). *Franhueberia*, with centrarch primary xylem, fits among basal euphyllophytes, like the Châteaupanne and New Brunswick plants (Gerrienne et al., 2011). Because the phylogeny of basal euphyllophytes is poorly understood, these Early Devonian taxa cannot be assigned to any of the major lineages recognized in the Middle Devonian and thereafter. They predate the earliest examples of secondary growth in major euphyllophyte lineages—late Eifelian cladoxylopsids (*Xenocladia*; Mustafa, 1980), stenokolealeans (*Crossia*; Beck and Stein, 1993), and progymnosperms (*Rellimia*, *Aneurophyton*; Mustafa, 1975; Schweitzer and Matten, 1982; Gerrienne et al., 2010).

Franhueberia *compared with Middle and Late Devonian plants*—Of the Middle Devonian plants exhibiting secondary growth, *Franhueberia* compares most favorably in overall cross-sectional anatomy with the smaller vascular segments of the cladoxylopsid *Xenocladia* (e.g., Meyer-Berthaud et al., 2004). Cladoxylopsids are polystelic, and the larger vascular segments have mesarch primary xylem, but smaller ones can appear to be centrarch. Given the structure of cladoxylopsid axes, their vascular segments can become separated taphonomically and preserved separately. Could *Franhueberia* be an isolated vascular segment detached from a cladoxylopsid axis? If so, it would be the oldest known cladoxylopsid. However, *Franhueberia* is distinctly different from cladoxylopsids by the secondary-wall thickening patterns of tracheids in the primary and secondary xylem (Table 1).

All Middle to Late Devonian euphyllophytes have metaxylem characterized by scalariform to oval and circular bordered pits, and secondary xylem with scalariform and/or oval to circular (multiseriate, alternate) bordered pits. The lycopsids (*Phytokneme*) have scalariform tracheids in the metaxylem and secondary xylem. In contrast to all these, the metaxylem of *Franhueberia* consists principally of tracheids with circular and oval bordered pits, although some (at the periphery of the stele) have scalariform bordered pits with multiaperturate membranes (P-type). The latter type of pitting also characterizes the secondary xylem tracheids. Only the scalariform-fimbrilate tracheids described in the metaxylem of the stenokolealean *Crossia* (Beck and Stein, 1993) are somewhat similar to the multiaperturate scalariform bordered pits of *Franhueberia*. However, in *Crossia* the end-member of the developmental series of metaxylem tracheid pitting consists of multiseriate round to elliptical bordered pits with horizontal slit-shaped apertures. Additionally, the axes of *Crossia* have mesarch protosteles with characteristic protoxylem parenchyma strands (Beck and Stein, 1993).

Franhueberia *compared with basal euphyllophytes*—Among euphyllophytes, the only plants that share *Franhueberia*'s

scalariform bordered pits with multiaperturate membranes represent basal lineages—*Psilophyton* and the Châteaupanne and New Brunswick euphyllophytes (Table 1). However, *Psilophyton* has scalariform bordered pits with multiple apertures in the metaxylem (Banks et al., 1975; Trant and Gensel, 1985), whereas in *Franhueberia* this type of pitting is seen in the secondary xylem and only in peripheral metaxylem tracheids. Nevertheless, both plants have centrarch steles and P-type tracheids; these shared characters, along with presence in *Psilophyton dawsonii* Banks et al. (1975) of radially aligned xylem reminiscent of secondary growth, beg the question: could *Franhueberia* be a larger *P. dawsonii* axis?

Two lines of evidence indicate that this is not the case. First, the zone of radially aligned tracheids of *P. dawsonii* is not extensive and does not exhibit the two other defining characters of secondary growth, which makes its origin from a vascular cambium unlikely. Second, *Franhueberia* is distinctly different from *P. dawsonii* in the size distribution of primary xylem tracheids (compare Fig. 3A and D). Most *P. dawsonii* metaxylem tracheids are ≥20 μm (66%; $n = 45$), ≥25 μm (47%), or ≥30 μm (29%) in diameter, whereas those of *Franhueberia* are much smaller, very few exceeding 15 μm diameter; tracheid diameters similar to those of *P. dawsonii* metaxylem are reached only in the secondary xylem of *Franhueberia*.

An axis assigned to *P. crenulatum* Doran (1980) from the Emsian (Lower Devonian) of New Brunswick exhibits radially aligned tracheids that are reported to have circular and scalariform bordered pits and seem to conform to the P-type. Since (i) the axis was obtained by bulk acid maceration of rock samples, (ii) it is decorticated and (iii) it was not found in connection with any *P. crenulatum* specimen, its identity with the latter species cannot be proved. By the same token, if the Gaspé cobble containing *Franhueberia* were macerated, the single *Franhueberia* axis would be found among a multitude of fertile and sterile *P. dawsonii* axes and potentially identified as *P. dawsonii*. Doran's axis has a significantly higher amount of radially aligned xylem than any of Banks et al.'s (1975) *P. dawsonii* specimens. In this respect, it is not unlike *Franhueberia*. However, Doran reports a lack of rays and, overall, the dearth of descriptive information available on that specimen precludes conclusive comparison.

Another question to be addressed is how does *Franhueberia* compare to the basal euphyllophytes reported by Gerrienne et al. (2011) (Table 1)? The New Brunswick plant, which is the same age as *Franhueberia*, is similar in the P-type tracheid pitting and the relatively large primary xylem cylinder. Additionally, the New Brunswick plant has relatively numerous rays which seem to act as planes of taphonomic separation for sectors of tracheid files, like in *Franhueberia*, albeit less markedly. However, the New Brunswick plant is different from *Franhueberia* in the elongate-elliptical cross-sectional shape of its primary xylem, and the protoxylem which forms a long central band.

Franhueberia is closely comparable to the Châteaupanne plant (which is ≥6 million years older), so could *Franhueberia* be a larger specimen of that plant? The taphonomic distortion of the *Franhueberia* axis, on the one hand, and the comparatively small amount of secondary tissue of the Châteaupanne specimen, on the other hand, make direct comparisons between the two plants difficult. Although both the Châteaupanne euphyllophyte and *Franhueberia* have a primary xylem cylinder much narrower than that of *Psilophyton*, the primary xylem of the Châteaupanne euphyllophyte is about half the size of that of *Franhueberia*. Perhaps the most important feature that distinguishes

the two plants is ray anatomy. *Franhueberia* exhibits numerous, regularly distributed and consistently shaped narrow rays that originate within just a few tracheids from the primary–secondary xylem boundary, whereas the Châteaupanne plant has few conspicuous rays; the structures identified as rays in the Châteaupanne plant are very diverse in dimensions, shape, and extent.

In conclusion, *Franhueberia* cannot be classified into any of the crown-group euphyllophyte lineages known starting in the Middle Devonian. Although the presence of multiplicative divisions has been interpreted as indicating lignophyte affiliations for the Châteaupanne and New Brunswick plants (Gerrienne et al., 2011), this anatomical feature is not limited to lignophytes (e.g., the polystelic cladoxylopsid, cf. *Xenocladia*, described by Meyer-Berthaud et al. [2004] from the Frasnian of Morocco; see their fig. 4d). *Franhueberia* predates the Middle Devonian euphyllophytes that exhibit secondary growth. Although anatomy indicates euphyllophyte affinities, *Franhueberia* is also different from Early Devonian euphyllophytes—*Psilophyton* and the two euphyllophytes described by Gerrienne et al. (2011). Taken together, these justify erection of a new genus of basal euphyllophytes.

The evolution of secondary growth—Although secondary vascular tissues are thought to have evolved independently in lycophytes and several euphyllophyte lineages (Cichan and Taylor, 1990; Rothwell et al., 2008; Boyce, 2010), the evolution of secondary growth is incompletely understood. Difficulties arise from a lack of resolution of phylogenetic relationships between major vascular plant lineages (Rothwell and Nixon, 2006). This is due in part to the lack of phylogenetic resolution within the basal plexus of Late Silurian–Early Devonian vascular plants, as well as to a gap in understanding of evolutionary relationships between basal paraphyletic groups with simple organography (protracheophytes and basal tracheophytes, basal lycophytes, basal euphyllophytes; Fig. 1), and the groups derived from them, which had evolved stem-leaf-root organography by the Middle Devonian.

Rothwell et al. (2008) showed that the same mechanism involving polar auxin flow in secondary vascular tissue production is shared by widely divergent lineages—lycopsids, sphenopsids, and lignophytes. They also pointed out that it is unclear whether this regulatory mechanism evolved independently in the different lineages or was inherited from a common ancestor. The Châteaupanne plant (Gerrienne et al., 2011) pushed the origin of secondary vascular tissues at least as far back in time as the Pragian–Emsian boundary (ca. 408 million years ago). With two other basal euphyllophytes producing secondary xylem in the Emsian—the New Brunswick euphyllophyte (Gerrienne et al., 2011) and *Franhueberia*—it is now clear that secondary tissue production predates the origin of major lineages and of stem-leaf-root organography within the clade, and that mechanisms for secondary growth became part of the developmental toolkit very early in the evolutionary history of euphyllophytes.
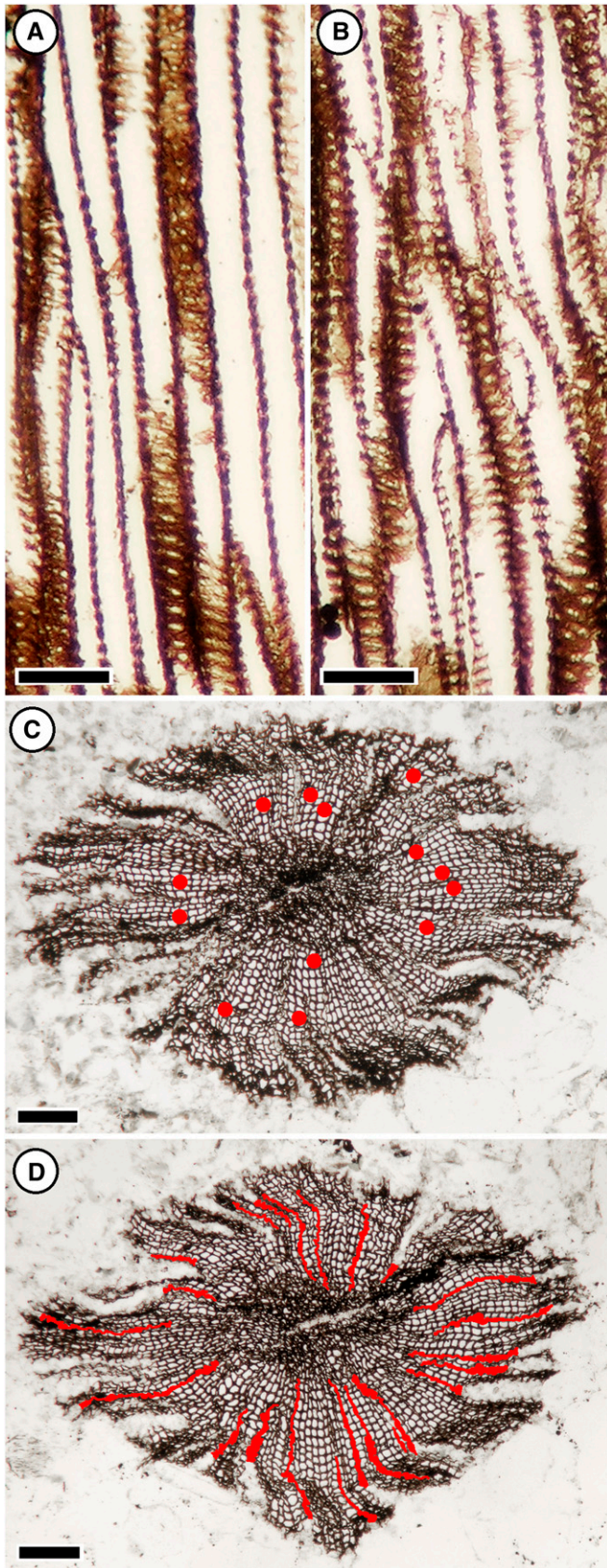
Fig. 4.   *Franhueberia gerriennei* gen. et sp. nov. (USNM 558725). (A, B) Tangential longitudinal sections; secondary xylem tracheids with gradually tapering ends (showing transition from scalariform to oval and circular bordered pits) and indicative of nonstoried cambium. Slide B21 E(2)$_s$ no. 76A. Scale = 50 μm. (C) Transverse section; locations of multiplicative divisions indicated by red dots. Slide B21 E$_b$ no. 85. Scale = 200 μm. (D) Transverse section; xylem rays traced in red. Slide B21 E$_b$ no. 128. Scale = 200 μm.
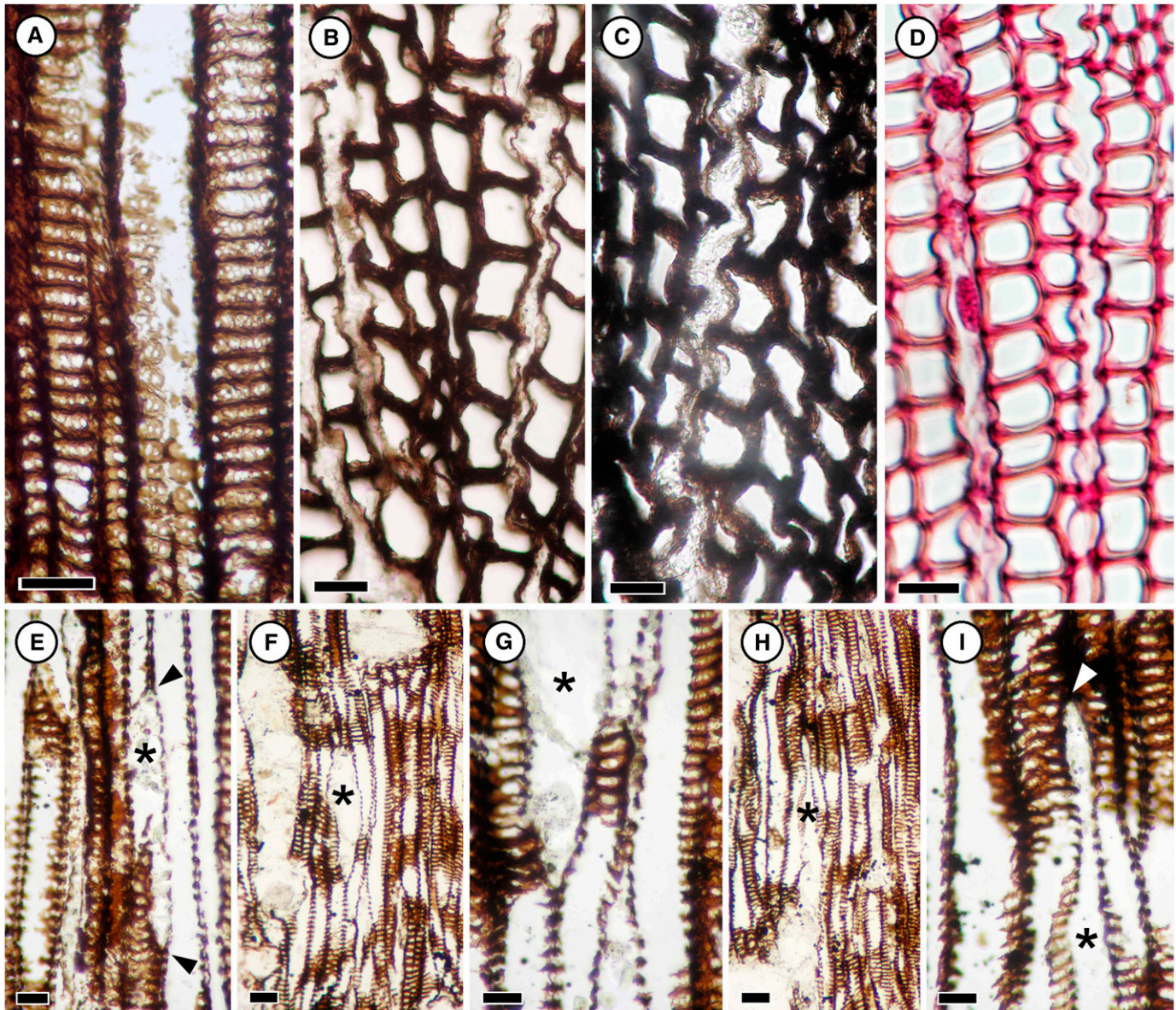
Fig. 5. *Franhueberia gerriennei* gen. et sp. nov. (USNM 558725). (A) Longitudinal section; secondary xylem tracheids with P-type pitting (scalariform bordered pits with multiaperturate membranes); note the oval-scalariform to round bordered pits on the tapered tracheid end at the lower left. Slide B21 E(2)$_s$ no. 42A. Scale = 20 µm. (B, C) Transverse sections; secondary xylem with xylem ray details. Slides B21 E$_b$ nos. 138 and 41. Scale = 20 µm. (D) Extant *Pinus* stem, transverse section of secondary xylem with xylem ray details. Note close similarity with *Franhueberia* in the thin, undulating ray walls punctuated by constrictions due to periclinal tracheid walls. Scale = 15 µm. (E–I) Rays (marked by asterisks) in tangential longitudinal sections. (E) Upper and lower end of ray indicated by arrowheads; note single tracheid walls (ray cell walls not preserved) bordering the ray, compared to double tracheid walls (walls of adjacent tracheids) above and below ray and elsewhere. Slide B21 E(2)$_s$ no. 26A. Scale = 20 µm. (F) Short ray; larger vertical space at left of figure may be a distorted ray. Slide B21 E(2)$_s$ no. 20A. Scale = 50 µm. (G) Detail of lower end of ray in F. Scale = 20 µm. (H) Ray with conspicuous upper end and disrupted lower portion. Slide B21 E(2)$_s$ no. 20A. Scale = 50 µm. (I) Detail of upper end (at arrowhead) of ray in H. Scale = 20 µm.

Conversely, these earliest occurrences of secondary growth in the euphyllophyte clade are ≥15 million years younger than the major divergence of the Lycophytina and Euphyllophytina (the oldest lycophytes, ≥426 million years old, are reported from Ludlow rocks of Australia and Canada; Kotyk et al., 2002; Gensel, 2008). Consequently, although lycopsids and euphyllophytes share a mechanism for secondary vascular tissue production (Rothwell et al., 2008), the question still remains whether that mechanism was inherited from a common tracheophyte ancestor.

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