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WHOSE ROOTS ARE THESE? LINKING ANATOMICALLY PRESERVED LIGNOPHYTE ROOTS AND STEMS FROM THE EARLY CARBONIFEROUS OF MONTAGNE NOIRE, FRANCE

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Premise of research. Despite their importance for understanding plant evolution and plant-environmental interactions through geological time, fossil roots have always received less attention than aerial parts. In the case of the lignophytes (i.e., progymnosperms and seed plants), the ability to form abundant secondary vascular tissues (secondary xylem and phloem) can, however, provide useful characters to compare isolated roots to stems from the same deposit to better understand the whole-plant structure and function of fossil plants.

Methodology. We studied five permineralized lignophyte roots with well-preserved secondary xylem, and in two cases some secondary phloem, from the Early Carboniferous Lydiennes Formation of the Montagne Noire, France, using classical thin sections.

Pivotal results. Analysis of the secondary vascular tissues of the roots allows us to distinguish three wood morphotypes that suggest affinities with at least three different types of stems previously reported in the Montagne Noire. One specimen is assigned to the arborescent seed plant *Eristophyton*; two are assigned to small, probably non-self-supporting seed plants belonging to either the Calamopityaceae or *Lyginopitys*; and two are assigned to the progymnosperms *Protopitys* or *Stauroxylon*.

Conclusions. This study illustrates how the affinities of isolated permineralized lignophyte roots can be narrowed down by comparing their wood anatomy with that of stems from the same deposit. The diversity of stem organization seen in the Montagne Noire deposit typically illustrates the morpho-anatomical diversification of the lignophytes' vegetative body in the Early Carboniferous. This study is a first step toward adding the underground organs to our understanding of this diversification.

Keywords: Carboniferous, roots, anatomy, France, gymnosperm, progymnosperm.

Introduction

Despite their importance for understanding plant evolution and plant-environment interactions through geological time, fossil roots have always received less consideration than aerial parts. An exception might be plants of the Devonian, when the increase in size and complexity of root systems is suspected to have significantly affected the formation of soils and the carbon cycle in general (e.g., Driese et al. 1997; Algeo et al. 2001; Raven and Edwards 2001; Beerling and Berner 2005; Simon et al. 2007; Morris et al. 2015). However, many of these studies are based on the analysis of paleosols and root casts or molds. While they provide important paleoecological information, they lack data on the anatomy and precise taxonomic affinities of the roots themselves. Even in fossil assemblages where plant remains are anatomically preserved, there have been few studies on root anatomy—whether in the Devonian or in more recent times. This is in part due to the much more uniform anatomical organization of roots compared with stems. The numerous variations in the anatomy of the primary vascular system that are highly significant in the systematic treatment of stems cannot be used in roots, which are characterized by a simple protostelic organization (Esau 1965; Beck 2005). Of course, leaf-trace anatomy and mode of production, another highly important systematic character in paleobotany, cannot be used in roots. As a result, isolated roots are often difficult to link to a definite taxon of stem, and our understanding of the diversity and evolution of root systems remains limited compared with what is known of the aerial systems.

In the case of the lignophytes (i.e., progymnosperms and seed plants; Kenrick and Crane 1997), the ability to produce abundant secondary vascular tissues (secondary xylem and phloem) with systematically significant anatomical characters can, however, provide useful information to compare isolated roots with stems from the same deposit. In this study, we use this approach to elucidate the affinities of roots with well-developed secondary vascular tissues from the Early Carboniferous of Montagne Noire. We identified anatomically preserved roots on the basis of the presence of a protostele and used secondary xylem char-

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acters classically used in the taxonomic treatment of stems and isolated pieces of wood (e.g., ray height and width, type of radial pitting of the tracheid walls) to investigate their affinities. Although there might be small differences between stem and root wood, it has been well established (e.g., Esau 1965; Patel 1965 and references therein) that they are quantitative rather than qualitative. Stem and root secondary vascular tissues are produced in continuity by the same cambium (e.g., Esau 1965, p. 530), and the quantitative differences can be linked to the distinct environmental conditions to which the aboveground and underground portions of the plant are subjected (e.g., Patel 1965 and references therein). Thus, while the occurrence, for example, of slightly larger tracheids or of more parenchyma in the root of a plant compared with its stem is possible, characters such as the type of pitting on the radial wall of tracheids are typically the same.

The Early Carboniferous (Tournaisian) Lydiennes Formation of Montagne Noire, France, is one of the oldest Carboniferous deposits to contain anatomically preserved plants (Scott et al. 1984), and numerous taxa have been described from this formation since the first descriptions by Schimper in 1870. Today, more than 30 taxa have been reported, representing lycopsids, sphenopsids, ferns, and lignophytes. Among lignophytes, about 10 taxa have been recognized on the basis of anatomically preserved stems. For the seed plants, these include several species of *Calamopitys* (Galtier et al. 1993; Galtier and Beck 1995), *Eristophyton feistii* (Decombeix et al. 2008), *Faironia difasciculata* (Decombeix et al. 2006), *Lyginopitys puechcapelensis* (Galtier 1970), *Stenomyelon bifasciculare* (Meyer-Berthaud 1984), *Triichnia meyenii* (Galtier and Beck 1992), and *Tristichia longii* (Galtier 1977). For the progymnosperms, these include *Protopitys* sp. (Decombeix et al. 2015) and possibly *Stauroxylon beckii* (Galtier 1970). Some of the taxa found in Montagne Noire, such as *Protopitys* or *Eristophyton*, could produce a large amount of wood with small rays and small tracheids. Large trunks are known for both genera in European and Australian localities (e.g., Goeppert 1845; Galtier and Scott 1990; Galtier et al. 1998; Galtier and Meyer-Berthaud 2006; Decombeix et al. 2011*b*). The Montagne Noire specimens of *Protopitys* and *Eristophyton*, which are smaller, are thus interpreted as representing the young distal portions of arborescent plants. Other genera, such as *Calamopitys*, produced a wood with a much higher proportion of parenchyma, large and high rays, and tracheids with a significantly larger diameter. Biomechanical analyses show that at least some species were not self-supporting and may have been lianescent (Rowe et al. 1993).

The diversity of habits and stem organizations seen in the Montagne Noire lignophytes illustrates the morpho-anatomical diversification of the lignophyte vegetative body in the Early Carboniferous (Decombeix et al. 2011*a*). This study is a first step toward adding the underground organs to our understanding of this diversification. Because the different groups of plants present in the deposit show a diversity of wood anatomies, it is possible to link isolated woody roots to stems from the same taxonomic group. The objectives are thus (1) to document in detail the anatomy of five woody roots from Montagne Noire, (2) to discuss their affinities with previously described stems from the same deposits, and (3) to put these results within the context of current knowledge about root evolution within Devonian-Carboniferous lignophytes.

Material and Methods

The Lydiennes Formation corresponds to sedimentary deposits in a shallow sea and consists of alternating beds of argilites and radiolarian cherts containing phosphatic nodules. Horizons containing plant fossils are considered middle Tournaisian in age (Tn2a–Tn2b) on the basis of conodonts (Galtier et al. 1988). The anatomically preserved plant fossils are found loose in the matrix or occasionally included in the nodules. Roots are rare, representing only 1%–2% of the permineralized flora versus 66% for stems, 27% for leaves, and 4%–5% for fructifications (Galtier et al. 1988). The specimens described in this study were collected in the locality of Coumiac. Other lignophyte taxa previously identified at this locality include specimens of *Calamopitys schweizerii* (Galtier et al. 1993), *Calamopitys eurameriana* (Galtier and Beck 1995), *Stenomyelon bifasciculare* (Meyer-Berthaud 1984), and *Triichnia meyenii* (Galtier and Beck 1992), as well as specimens assignable to *Calamopitys* cf. *embergeri*, *Lyginopitys* sp., and cf. *Eristophyton*. The five specimens used in this study were identified as possible roots by looking in the collections for woody axes in which all secondary xylem files seemed to come from a small central point, suggesting the presence of a protostele. The organic matter being partly replaced by minerals in most specimens, they were studied using classical thin sections (Hass and Rowe 1999).

Observation and photography were conducted with Sony XCD-U100CR digital cameras attached to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound microscope. Photographs were taken using either transmitted or reflected light depending on specimen color and preservation. Archimed software (Microvision Instruments) was used for the capture, and plates were composed with Adobe Photoshop CS5, version 12.0 (Adobe Systems). Transformations made to the images in Photoshop include cropping, rotation, and adjustment of brightness and contrast. Cell and tissue measurements were made with Archimed and with ImageJ, version 1.45 (Rasband 1997–2016). The specimens and corresponding slides are deposited in the AMAP Research Unit, Collections de Paléobotanique, Université de Montpellier, under the accession numbers MN710, MN711, MN916, MN964, and MN967.

Nomenclature and Terminology

The classification of lignophytes used in this article follows the nomenclature of Taylor et al. (2009), where progymnosperms and pteridosperms are recognized at the level of phylum (i.e., Progymnospermophyta and Pteridospermophyta). In the description of secondary xylem tracheids, "scalariform bordered pitting" is used to describe bordered pits that are uniseriate, transversely elongated, and contiguous. This is comparable to the "xenoxylean pitting" in the terminology used for Mesozoic woods (e.g., Philippe and Bamford 2008).

Descriptions

Variations in wood anatomy of the five specimens indicate that several different taxa are represented. For each specimen, we provide below a synthetic description of the primary and secondary xylem, traces to lateral roots, and/or secondary phloem when present. For easier reading, descriptions are ordered so

that specimens with similar types of wood follow each other regardless of specimen number. Figure 1 illustrates the size and general aspect of the five specimens as seen in transverse section.

MN710, cf. Eristophyton

The specimen is 50 mm long, 27 mm × 37 mm wide, decorticated, and preserved unevenly in cross section (fig. 1*A*). The central part is small (0.92 mm × 3 mm wide) and crushed so the shape and anatomy of the primary vascular structure could not be observed in detail (fig. 2*A*, 2*B*). A single type of thick-walled elements, presumably tracheids, is visible, suggesting that this central part is a protostele devoid of parenchyma, although we cannot entirely exclude that some parenchyma cells were initially present but not preserved. Primary tracheids range 22–90 μm in diameter. A group of small tracheids lining the inner edge of the secondary xylem may represent an exarch pole of protoxylem (fig. 2*C*).

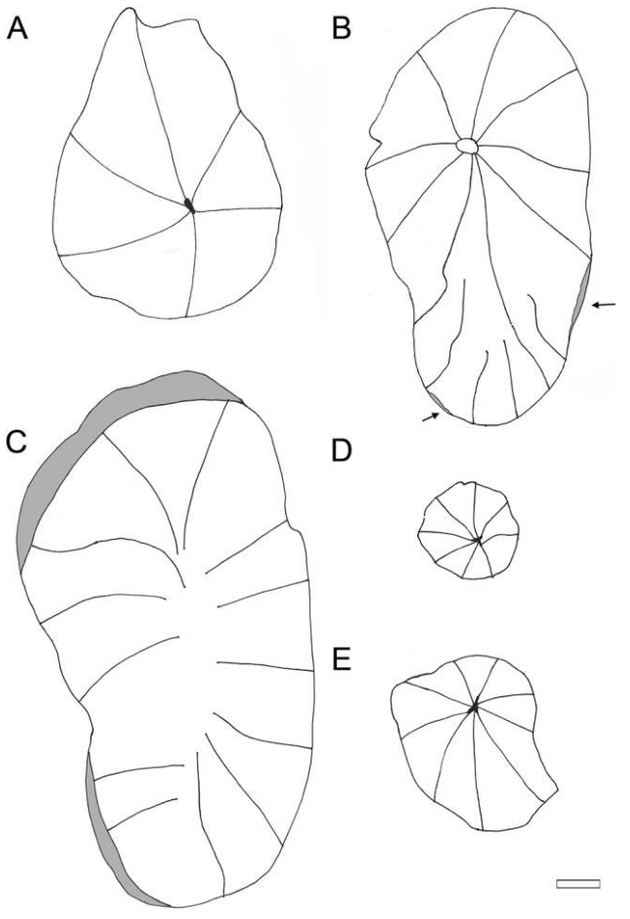


Fig. 1 General aspect of the five specimens in transverse section. *A*, MN710-CT1, cf. *Eristophyton*; *B*, MN711A-CT1, Calamopityaceae or *Lyginopitys*; *C*, MN964-CT1, Calamopityaceae or *Lyginopitys*; *D*, MN916-CT1, cf. *Protopitys* or *Stauroxylon*; *E*, MN967-CT1, cf. *Protopitys* or *Stauroxylon*. Gray areas on *B* (arrows) and *C* indicate preserved secondary phloem. Scale bar represents 5 mm.

The surrounding secondary xylem has a maximum thickness of 24 mm, indicating that the root had an original diameter of at least 50 mm. The wood lacks growth rings. Lateral root traces are not visible.

In transverse section, secondary xylem tracheids are rectangular to slightly rounded, with a diameter of 13–53 μm (mean: 29 μm; $n = 50$; fig. 2*D*, 2*E*). In at least one case, a tracheid much larger than the others (>70 μm) was observed (fig. 2*F*). There are frequent initiations of new tracheid files in some areas of the secondary xylem (fig. 2*D*). Rays separate 5–13 files of tracheids in transverse section (fig. 2*B*–2*D*). They are usually one to three cells in width. Some rare occurrences of rays up to five cells wide have also been observed (fig. 2*E*). Apart from a few rays that cross the entire wood, rays are relatively short, measuring between 300 μm and 4 mm in radial length (68% between 300 μm and 1 mm, 26% between 1 and 2 mm, and 6% between 2 and 4 mm; $n = 50$).

In tangential section, rays are short (fig. 2*G*). They range 90–530 μm in height and 20–51 μm in width (75% are between 100 and 400 μm high and less than 40 μm wide; $n = 20$). They comprise 2–22 cells in height (70% with 5–13 cells) and usually one to three cells in width (80% with two to three cells; fig. 3). All ray cells are thin walled and parenchymatous. Their size is variable, whether between rays or within a single ray (fig. 2*G*). Ray cells are 10–61 μm high and 10–30 μm wide. Eighty percent range 10–37 μm in height and 10–19 μm in width. They tend to be isodiametric when small and higher than wide otherwise. Some ray cells are very long, but their width rarely exceeds 30 μm. Transverse end walls in some elongated elements of the secondary xylem suggest the occurrence of vertical parenchyma (fig. 2*H*). High or wide cells with transverse walls associated with some rays may also represent axial parenchyma.

In radial section, tracheid walls bear 1–4 (generally 2) rows of bordered pits that are crowded, polygonal, and alternately arranged (fig. 2*I*, 2*J*). Radial pits are 9–13 μm in diameter ($n = 20$). Tracheid extremities can be enlarged (fig. 2*I*). As already observed in tangential section, rays are composed of cells of variable heights (fig. 2*J*). Cross-field pitting could not be observed.

MN964, Calamopityaceae or Lyginopitys

The axis is 200 mm in length and 70 mm × 35 mm in diameter (fig. 4*A*). Some preserved secondary phloem is present at the periphery (fig. 1*C*). In cross section, the central part of the axis is crushed and flattened (fig. 4*B*). A few preserved primary xylem cells range 34–80 μm in diameter.

The secondary xylem is up to 22 mm in thickness (fig. 4*C*). In transverse section, the tracheids are polygonal, rarely square or rectangular. They range 26–77 μm in diameter, with an average of 50 μm ($n = 50$). In radial section, the pitting of the tracheid walls consists of up to four rows of crowded circular bordered pits (fig. 4*D*, 4*E*). Pits are 6–15 μm in diameter, with an average of 9 μm ($n = 30$).

Rays separate one to seven files of tracheids in transverse section (fig. 4*C*) and are two to six cells wide (fig. 4*C*, 4*F*) in tangential section. Although the preservation does not allow the maximum ray height to be counted precisely in terms of cell number, we observed both small rays that are a few cells high (fig. 4*E*) and tall rays more than 1 mm in height (fig. 4*D*, 4*F*).

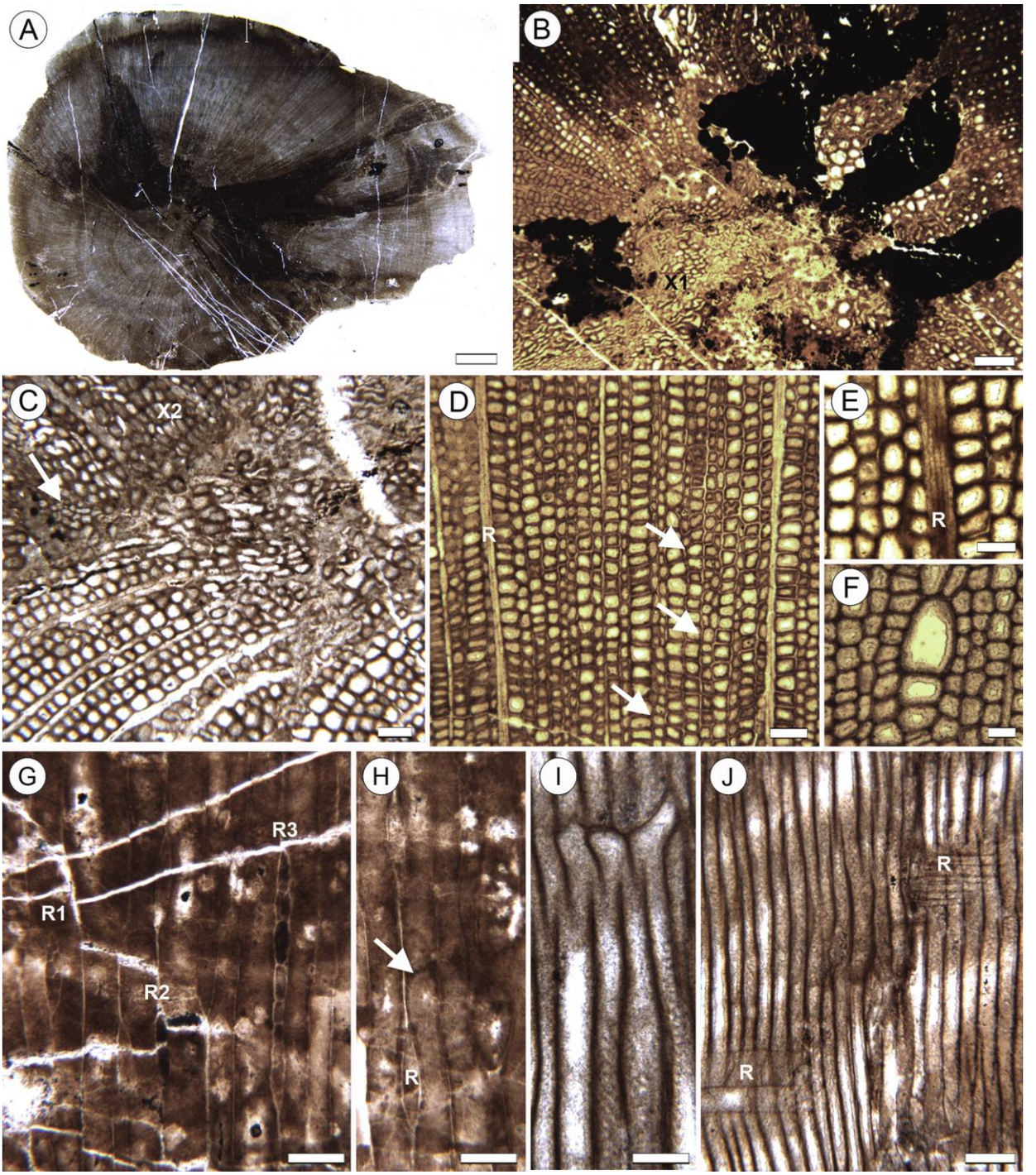


Fig. 2 MN710, cf. *Eristophyton*. *A*, General aspect of the axis in transverse section. Slide MN710-CT1. *B*, Center of the axis with crushed primary xylem (X1). Slide MN710-CT1. *C*, Detail of the center of the axis with a possible exarch primary xylem strand on the left (arrow). Slide MN710-CT1. *D*, Secondary xylem in transverse section showing one to three seriate rays (R). Note initiation of new files of tracheids (arrows). Slide MN710-CT1. *E*, Detail of a larger ray in transverse section. Slide MN710-CT1. *F*, Detail of an unusually large tracheid. Slide MN710-CT1. *G*, Tangential section of the secondary xylem with three rays of different sizes indicated: R1, biseriate ray four cells in height; R2, uniseriate rays two cells in height; and R3, partly biseriate ray 11 cells in height. Note the variable size of ray cells. Slide MN710-CL1. *H*, Tangential section showing a small ray (R), an elongated cell with a transverse wall (arrow) that might represent vertical parenchyma. Slide MN710-CL1. *I*, Radial section of tracheids with slightly enlarged extremities. Note multiseriate pitting. Slide MN710-CL2. *J*, Low rays and tracheid pitting in radial section. Note variable size of ray cells. Slide MN710-CL2. Scale bars represent 3 mm (*A*), 200 μm (*B*), 100 μm (*C, D, J*), and 50 μm (*E, F, H, I*). The center of the axis is toward the bottom of the photographs on all transverse sections except *D* (on the right) and toward the left on longitudinal sections.

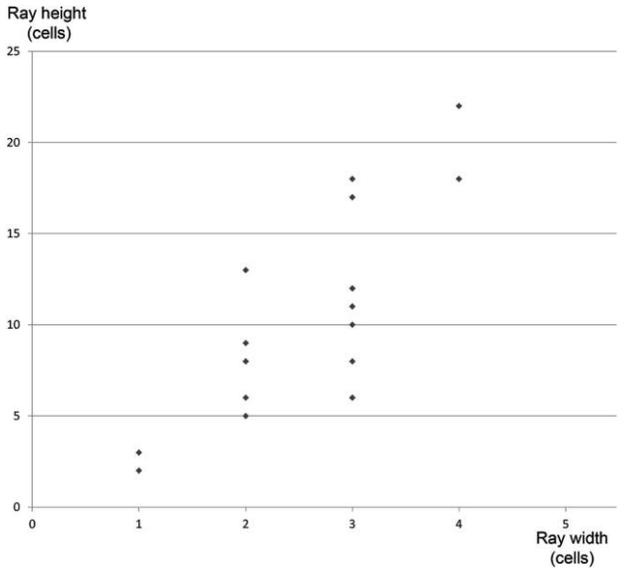


Fig. 3 Ray size in MN710, cf. *Eristophyton*. Each point represents a ray, with width and height in number of cells ($n = 20$).

The maximum thickness of preserved secondary phloem is 4 mm. The secondary phloem rays are the only well-preserved structures. They are all significantly enlarged and contain dark, thickened cells (fig. 4*G*, 4*H*).

MN711, Calamopityaceae or Lyginopitys

The specimen is 130 mm long and decorticated. It is slightly oval and measures 29 mm × 34 mm wide at one extremity. At this level, the wood is 16 mm thick, and a fragment of secondary phloem is preserved on the outside. At the other extremity, the specimen is 27 mm × 47 mm wide and shows what seems to be an asymmetrical production of wood (figs. 1*B*, 5*A*). The extra wood, however, is separated by a wide irregular zone of unpreserved elements. It may thus have been displaced during the fossilization of the specimen.

The central part of the axis is oval in cross section and measures 2.1 mm × 3.8 mm wide (fig. 5*B*). Its largest dimension is parallel to the direction of compression of the wood, suggesting that this shape is natural. The central part contains several types of cells (fig. 5*B*–5*D*). The most numerous ones consist of badly preserved elements measuring up to 85 μm wide. They may correspond to parenchymatous cells. The second type of elements is represented by large thick-walled sclereids that are isodiametric and measure up to 180 μm wide (fig. 5*C*). Finally, clusters of thick-walled cells arranged around very small elements are interpreted as primary xylem strands with a mesarch to exarch maturation (fig. 5*D*). In longitudinal section, some of the small cells show scalariform thickenings. Because of the shape and composition of the central part, it is possible that specimen MN711 does not represent a root. Its small stele diameter, however, indicates that it probably corresponds to the very basal portion of a stem, close to the stem-root transition.

The secondary xylem lacks growth rings. No vascular trace is visible within this tissue. In transverse section, tracheids are polygonal, more rarely rectangular (fig. 5*E*). They are large, 29–100 μm in tangential dimension, 39–156 μm radially, with a mean diameter of 72 μm ($n = 50$). Rays separate two to six files of tracheids and are variable in width, up to 10 cells wide. All rays are long and cross the entire wood.

In tangential section, rays are heterogeneous in size (fig. 5*F*). Some small rays are composed of a few cells. The other rays are up to 10 cells wide and can be more than 80 cells in height. Ray cells in multiseriate rays range 14–35 μm in width and 19–60 μm in height. They are usually larger in uniseriate portions of rays, where they measure up to 42 μm wide and 85 μm high. Vertical parenchyma consists of vertical rows of cells exceeding 100 μm in length (fig. 5*F*).

In radial section, the pitting of the tracheid walls consists of up to five rows of crowded, alternately arranged, bordered pits (fig. 5*G*). Pits are 7–14 μm in diameter ($n = 20$) and show oval apertures. Cross-field pitting could not be observed. Tracheid extremities in radial section are rounded to slightly expanded (fig. 5*G*). As in tangential section, ray size is conspicuously heterogeneous (fig. 5*H*).

The maximum thickness of the secondary phloem is a little less than 1 mm. In transverse section, the best-preserved elements are the phloem rays, which are in continuity with those of the secondary xylem and may enlarge significantly outward (fig. 5*I*). Phloem rays contain thick-walled dark cells that decrease in size radially and enlarge tangentially toward the outside. Rays enclose a complex tissue preserved in only a few areas (fig. 5*J*). This tissue consists of alternating tangential layers of two types: (1) one-cell-thick layers of large polygonal cells with a diameter comparable to that of the secondary xylem tracheids and (2) layers that are several cells in tangential thickness and contain poorly preserved, thin-walled, presumably parenchymatous cells (fig. 5*J*).

MN916, cf. Protopitys/Stauroxylon

This specimen is about 50 mm long. It is asymmetrical in transverse section and has a maximum diameter of 11.5 mm (figs. 1*D*, 6*A*). The central part contains a small triangular strand of primary xylem with an exarch maturation (fig. 6*B*). Metaxylem tracheids range 22–70 μm in diameter (mean: 39 μm; $n = 20$), whereas the protoxylem cells, located at the apices of the triangle, are 6–15 μm wide (mean: 9 μm; $n = 20$).

The surrounding ring of secondary xylem is about 5 mm thick and shows growth rings (fig. 6*A*). In the section where the asymmetry of the axis is more pronounced, the secondary xylem is 3.7 mm wide on one side and up to 6.7 mm on the other side (fig. 6*A*). Extraxylary tissues are 1.7–2.1 mm thick.

The secondary xylem tracheids are square to rectangular in transverse section. They range 12–148 μm in diameter, with smaller dimensions in the regions facing the protoxylem strands (fig. 6*B*, 6*C*). Analysis of the diameter range of tracheids in radial files shows that the 10–16 innermost tracheids show a rapid increase in both radial and tangential diameters. These measurements remain relatively stable for the next 20–30 tracheids except at at least two levels, when the radial diameter of one or two cells decreases sharply. These levels are interpreted as evidence of irregular growth rhythm. The outermost part of the wood makes a transition to the cambial zone. Rays separate 1–11 files of tracheids (fig. 6*B*, 6*C*). Rays departing from

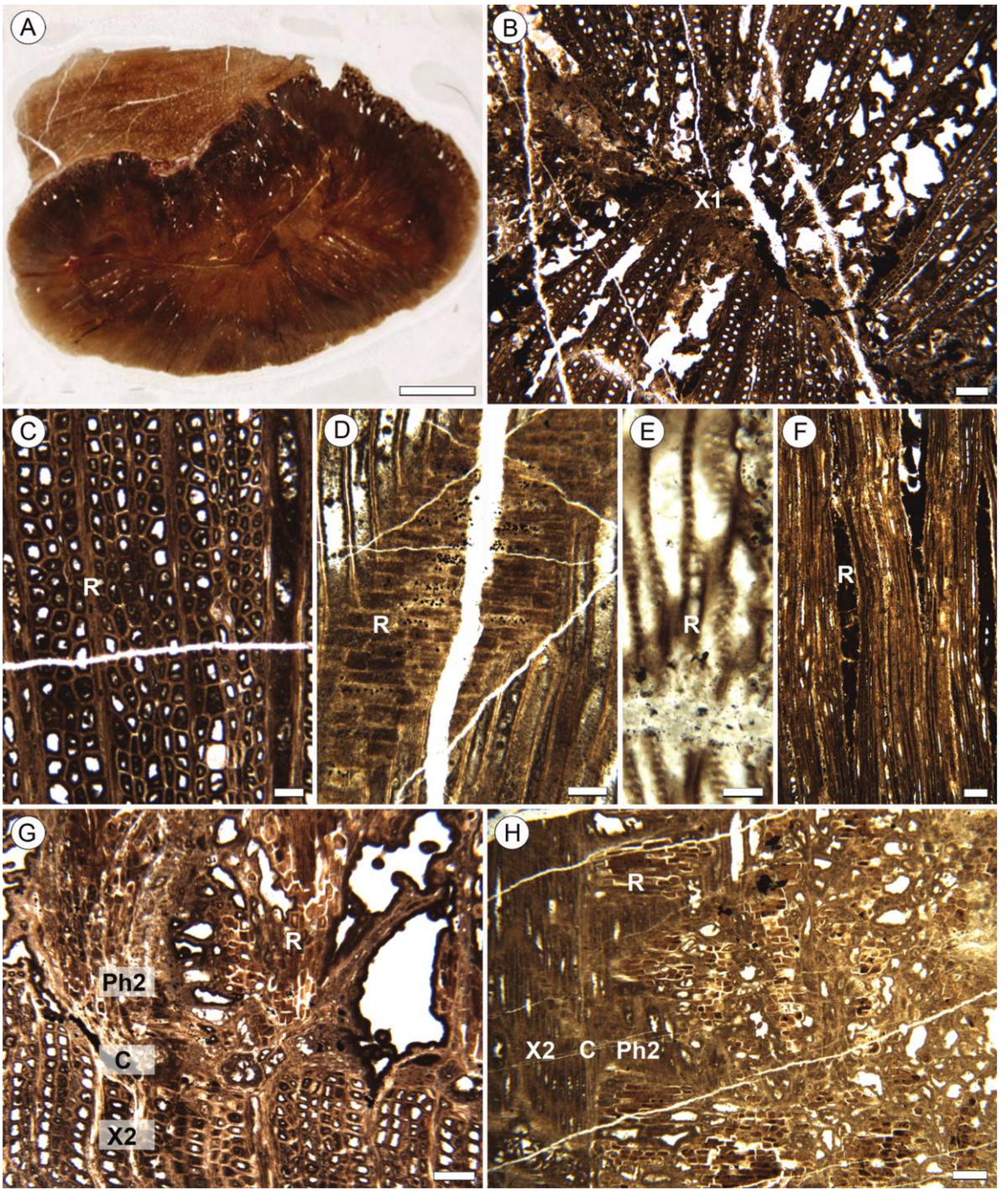


Fig. 4 MN964, Calamopityaceae or *Lyginopitys*. *A*, General aspect in transverse section. Slide MN964B-CT1. *B*, Center of the axis in transverse section showing the location of the stele. Slide MN964B-CT1. *C*, Wood in transverse section in the outer part of the axis. Slide MN964B-CT1. *D*, Radial section of the wood showing a typical very high ray (R). Slide MN964D$_1$-CL1. *E*, Longitudinal section showing multiseriate pitting on the radial wall of a tracheid and a small ray (R). Slide MN964D$_1$-CL1. *F*, Large rays (R) in tangential section. Slide MN964-CL3. *G*, Transverse section through the outer secondary xylem (X2), cambium zone (C), and secondary phloem (Ph2). Rays are enlarged in the phloem and contain thick-walled cells. Slide MN964A-CT1. *H*, Radial section through the outer secondary xylem (X2), cambium zone (C), and secondary phloem (Ph2). Note conspicuous rays (R) with thick-walled cells. Slide MN964D$_1$-CL1. Scale bars represent 1 cm (*A*), 200 μm (*B, F, G, H*), 100 μm (*C, D*), and 50 μm (*E*). The center of the axis is toward the bottom of the photographs on all transverse sections and toward the left on longitudinal sections.

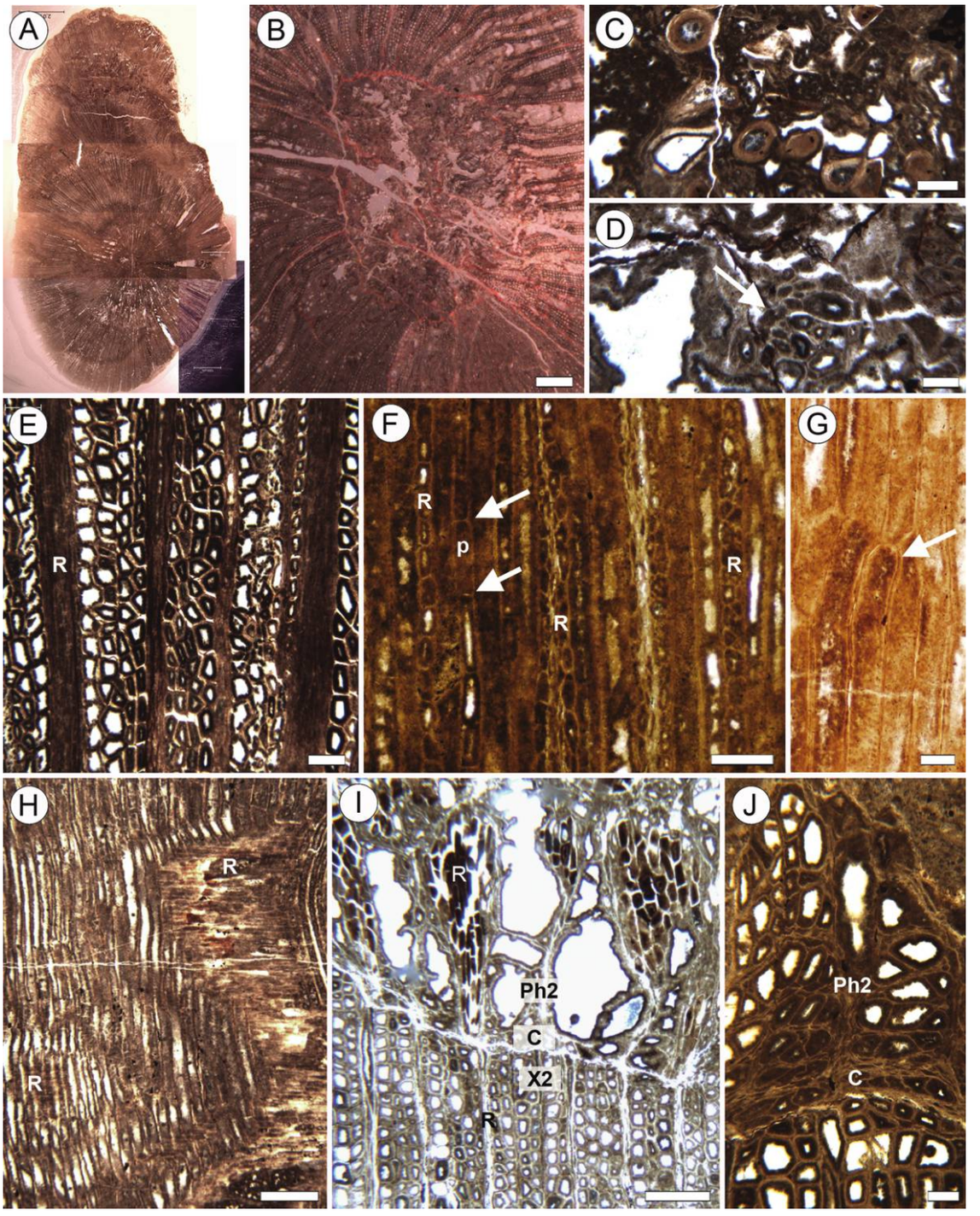


Fig. 5 MN711, Calamopityaceae or *Lyginopitys*. *A*, General aspect in transverse section. Slide MN711A-CT1. *B*, Center of the axis with crushed primary xylem (X1). Slide MN711A-CT1. *C*, Large thick-walled cells in the central part of the axis. Slide MN711A-CT1. *D*, Detail of primary xylem strand (arrow). Slide MN711A-CT1. *E*, Wood in transverse section showing polygonal tracheids and multiseriate rays. Slide MN711A-CT1. *F*, Tangential section of wood with uniseriate and multiseriate rays (R) and vertical parenchyma (p), indicated by the occurrence of horizontal transverse walls (arrows). Slide MN711-CL1. *G*, Radial section of wood with faint multiseriate pitting visible and tracheids with rounded ends. Slide MN711-CL2. *H*, Radial section of the wood showing a small ray (left) and a typical very high ray (right). Slide MN711-CL2. *I*, Transverse section of the outer part of the secondary xylem (X2), cambium (C), and secondary phloem (Ph2) displaying enlarged rays (R) with dark and thickened cells. Slide MN711A-CT1. *J*, Detail of a relatively well-preserved region of secondary phloem between two rays, showing alternating layers of thick-walled cells and crushed thin-walled cells close to the cambium (C). Slide MN711A-CT1. Scale bars represent 2 mm (*A*), 500 μm (*B*), 300 μm (*H*), 100 μm (*C, D, E, F, I*), and 50 μm (*G, J*). The center of the axis is toward the bottom of the photographs on all transverse sections and toward the left on longitudinal sections.

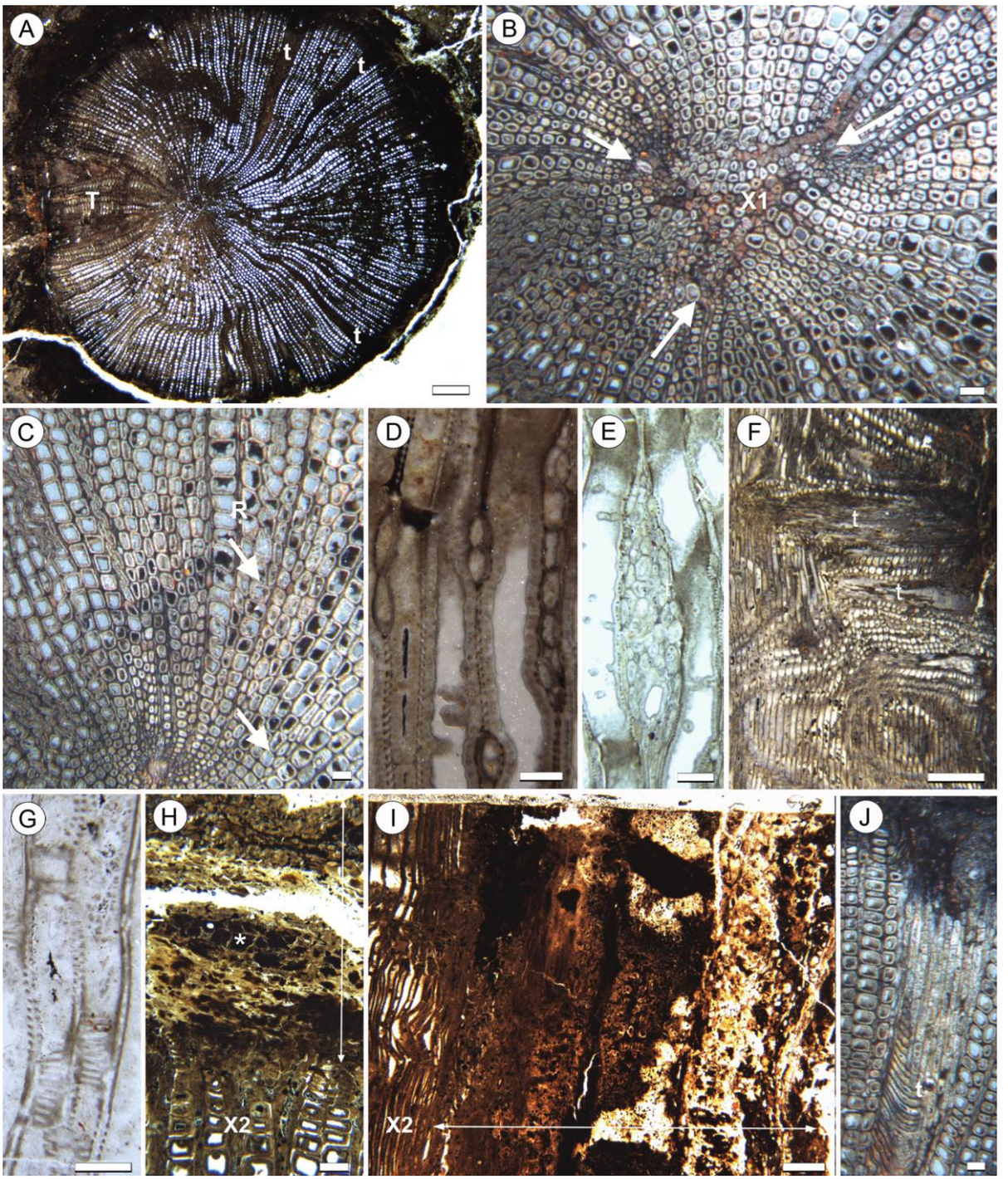


Fig. 6 MN916, cf. *Protopitys* or *Stauroxylon*. *A*, General aspect in transverse section. A large trace to a lateral (T) is visible on the left, and small ones (t) are visible on the upper right and lower right. Slide MN916C-CT4. *B*, Triradiate exarch protostele at the center of the axis (X1). Arrows indicate the location of the protoxylem strands. Slide MN916C-CT4. *C*, Transverse section of the secondary xylem in a region facing the protoxylem, at a level with no departing trace. Note the uniseriate rays (R) and the addition of new files of tracheids (arrows). Slide MN916C-CT4. *D*, Typical low, uniseriate to partly biseriate rays in tangential section. Slide MN916B-CL1. *E*, Unusual zone with large, irregular rays. Slide MN916B-CL1. *F*, Radial section showing traces to lateral organs (t), one just departing from the stele and the others in the outside part of the root. Slide MN916B-CL3. *G*, Scalariform bordered pits on the radial wall of the secondary xylem tracheids. Slide MN916B-CL3. *H*, Outer part of the wood (X2) and extraxylary tissues (double-headed arrow) in transverse section. Note the reduced tracheid diameter close to the putative cambial zone, crushed thin-walled cells, and a cluster of sclerified cells (asterisk). Slide MN916B-CT3. *I*, Radial section through the outermost secondary xylem (X2) and extraxylary tissues (double-headed arrow). Slide MN916B-CL3. *J*, Transverse section of the wood in the outer part of the axis showing a small trace (t). Slide MN916C-CT4. Scale bars represent 1 mm (*A, F*), 100 μm (*B, C, E, H, J*), 250 μm (*I*), and 50 μm (*D, G*). The center of the axis is toward the bottom of the photographs on all transverse sections and toward the left on longitudinal sections.

the inner border of the secondary xylem cross this tissue entirely. In tangential section, rays are uniseriate to triseriate (63% uniseriate, 20% biseriate, and 17% triseriate; $n = 30$) and about 1–12 cells high (37% are 1–4 cells high, 43% are 5–7 cells high, and 20% are 8–12 cells high; $n = 30$; figs. 6*D*, 7). Rays are wider and higher in the outermost part of the wood, close to the cambial zone. Some large rays are also embedding outgoing traces to lateral roots (fig. 6*A*, 6*E*, 6*F*). Ray cells are isodiametric to polygonal and higher than wide (mean dimension in tangential section: 33 μm; $n = 40$). In radial section, tracheid walls are characterized by a single row of scalariform-bordered pits (fig. 6*G*).

Extraxylary tissues are present but not well preserved, especially those occurring in the inner 500–800-μm-thick zone surrounding the secondary xylem and cambial zone (fig. 6*H*, 6*I*). They contain groups of elongated cells that are hardly identifiable and isodiametric parenchymatous cells measuring about 50–60 μm wide. In addition, clusters of sclereids 40–70 μm in diameter are scattered throughout this tissue (fig. 6*H*). The most external part of the axis consists of a 250-μm-thick band of tangentially flattened thin-walled cells, interpreted as a periderm, and remnants of a primary cortex composed of thin-walled polygonal cells measuring up to 55 μm in diameter.

Conspicuous, nonpermanent structures that cross the secondary xylem of the axis radially are interpreted as traces to lateral roots (fig. 6*A*, 6*F*, 6*J*). They appear either as large traces that occupy a whole sector of the axis (fig. 6*A*) or as smaller structures that superficially resemble an unusually large ray (fig. 6*A*, 6*J*). Even the smallest structures contain vascular tissues (fig. 6*F*, 6*J*) and are indeed traces to lateral organs. The traces are typically located in the areas facing the protoxylem strands, sometimes with two traces facing a single protoxylem strand (fig. 6*A*). Because secondary growth took place, it is not possible to know whether the lateral roots were produced from the pericycle and had an endogeneous origin.

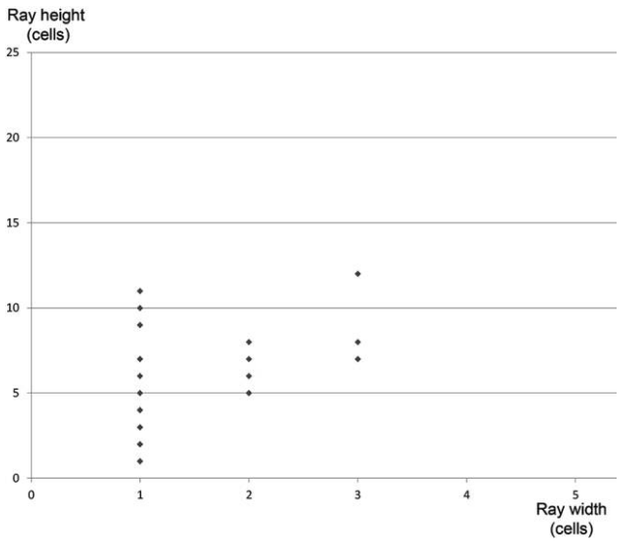


Fig. 7 Ray size in MN916, cf. *Protopitys* or *Stauroxylon*. Each point represents a ray, with width and height in number of cells ($n = 30$).

MN967, cf. Protopitys/Stauroxylon

This specimen is a decorticated axis about 20 mm in length with a maximum diameter of 21.5 mm (figs. 1*E*, 8*A*). In transverse section, the central part of the axis contains a triangular protostele that is partly crushed (fig. 8*B*). Remains of a lateral root still connected to the outer part of the axis are present at one extremity of the specimen (fig. 8*A*, 8*C*). Small traces to laterals are also present in the areas facing the protoxylem strands (fig. 8*D*). The smallest ones are detectable only by the disruption of the main axis secondary xylem (fig. 8*E*). The protostele is surrounded by a ring of secondary xylem up to 12 mm in thickness and devoid of any growth rings (fig. 8*A*).

In transverse section, the secondary xylem tracheids are square to rectangular, more rarely polygonal (fig. 8*F*). They have a diameter of 12–131 μm. Rays separate 1–11 files of tracheids (fig. 8*B*, 8*F*). Rays are long, and those departing from the inner part of the secondary xylem usually cross this tissue entirely. As in the previous specimen, some larger rays occur, but they seem to be related to the production of traces to laterals.

In tangential section, rays are 1–5 cells wide (40% uniseriate, 46% biseriate, and 14% 3–5 cells wide; $n = 50$) and 1–15 cells high (48% 1–4 cells, 34% 5–7 cells, and 18% 8–12 cells high; $n = 50$; figs. 8*G*, 9). Ray cells are isodiametric to polygonal and higher than wide (mean dimension in tangential section: 24 μm; $n = 40$). In radial section, tracheid walls are characterized by a single row of bordered scalariform pits (fig. 8*H*).

Discussion

Comparison with Lignophyte Stems from Montagne Noire

Based on their secondary xylem anatomy, especially their type of radial pitting and their ray size, three morphotaxa can be distinguished among the five root specimens.

Cf. Eristophyton *(specimen MN710).* In this wood type, tracheids bear one to three rows of crowded circular pits, and rays are one to three (rarely five) cells wide and 3–19 cells high. In the Montagne Noire deposit, this type of wood is found in *Eristophyton feistii* (Decombeix et al. 2008) and *Faironia difasciculata* (Decombeix et al. 2006). Both of these genera have been assigned to the informal group of the early arborescent seed ferns (Galtier and Meyer-Berthaud 2006). The group includes a variety of Early Carboniferous self-supporting seed plants characterized by a pycnoxylic wood. *Eristophyton feistii* and *F. difasciculata* are distinguished from one another by the character of their primary vascular structure and leaf-trace emission. The occasional occurrence in MN710 of tracheids with an enlarged extremity that appear much larger in cross section has been reported only in *E. feistii* (Decombeix et al. 2008), suggesting a closer affinity with this taxon.

We note that the largest rays observed in the root specimen MN710 are larger than what is known in *E. feistii* (five vs. three cells wide). However, this is a rare occurrence. It is also possible that rays were slightly larger in the roots than in the stems of this taxon. This is often the case in extant plants, in which the roots tend to contain a higher proportion of living cells in general and more ray cells than do the stems (Esau 1965). Given all the other similarities, we consider that MN710 most likely represents a root of *E. feistii*. While the holotype and

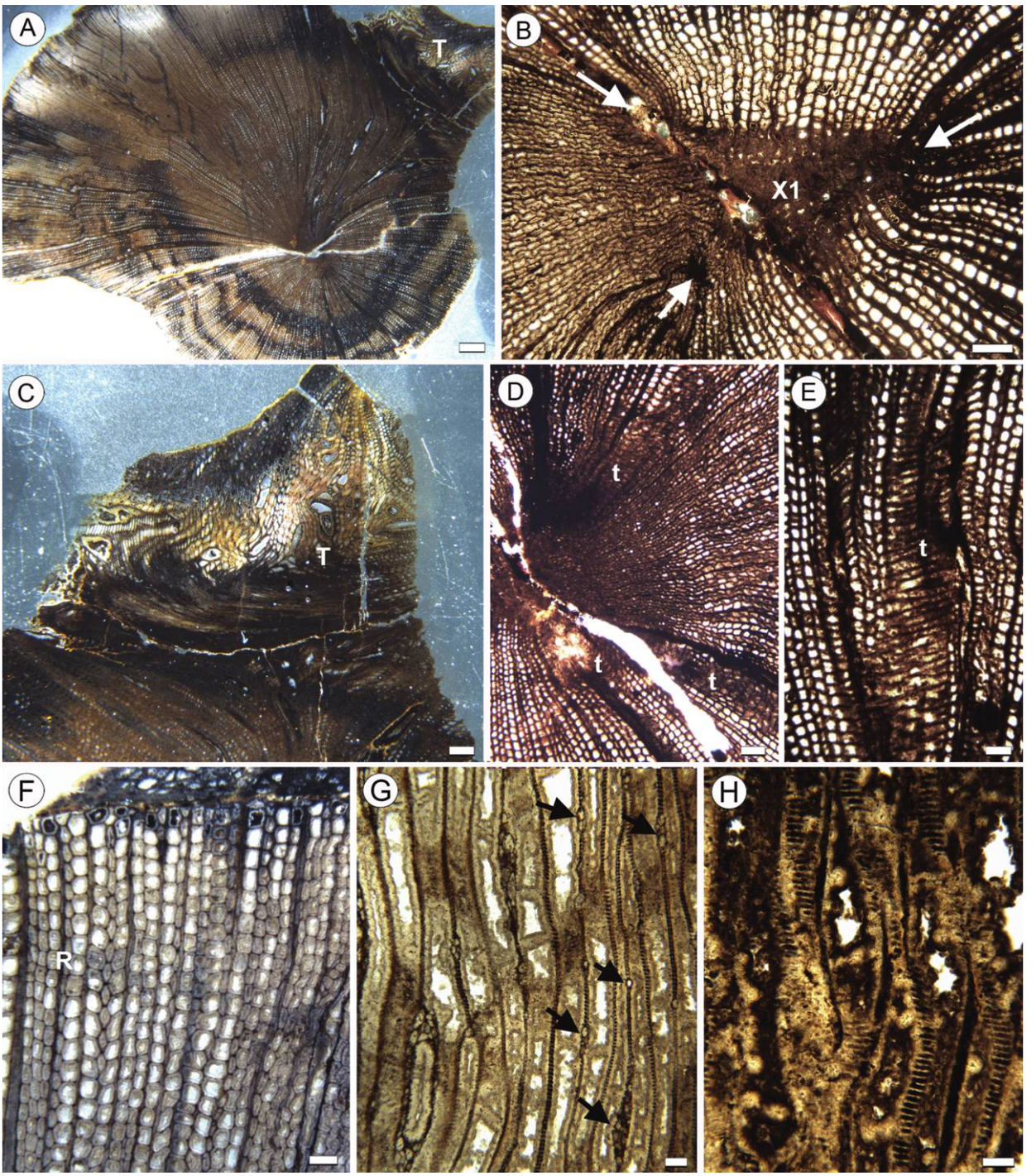


Fig. 8 MN967, cf. *Protopitys* or *Stauroxylon*. *A*, General aspect in transverse section. Part of a lateral is preserved in the upper right. Slide MN967-CT1. *B*, Center of the axis in transverse section showing a partly crushed triradiate protostele (X1). Arrows indicate the location of the protoxylem. Slide MN967-CT1. *C*, Detail of the lateral seen on *A* (T) still connected to the wood of the main axis (X2). Slide MN967-CT1. *D*, Center of the axis showing small traces (t) departing from the protostele. Slide MN967-CT2. *E*, Small trace to a lateral (t) visible only by the perturbation of the secondary xylem tracheid files in the main axis. Slide MN967-CT2. *F*, Transverse section of the wood in the outer part of the axis showing uniseriate to biseriate rays. Slide MN967-CT1. *G*, Tangential section showing typical very small rays and a few larger ones (arrows). Slide MN967-CL1. *H*, Scalariform bordered pits on the radial wall of the secondary xylem tracheids. Slide MN967-CL1. Scale bars represent 1 mm (*A*), 250 μm (*B*), 500 μm (*C*), 200 μm (*E, D*), 100 μm (*F*), and 50 μm (*G, H*). The center of the axis is toward the bottom of the photographs on all transverse sections and toward the left on longitudinal sections.

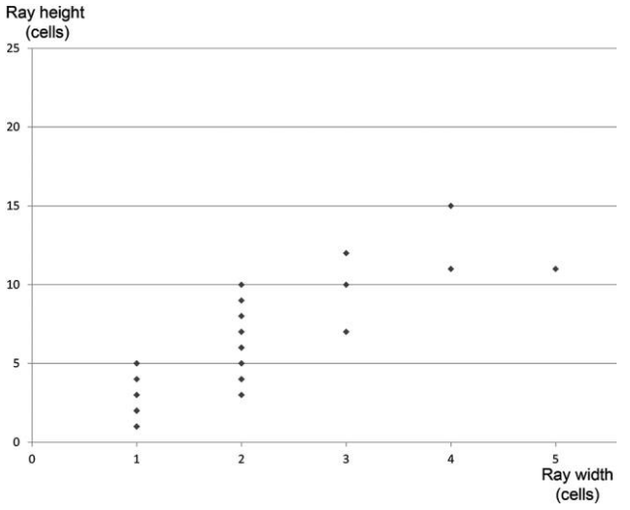


Fig. 9 Ray size in MN967, cf. *Protopitys* or *Stauroxylon*. Each point represents a ray, with width and height in number of cells ($n = 30$).

paratypes of *E. feistii* were collected in another locality of the Montagne Noire (St. Nazaire de Ladarez), several less well-preserved stems of this taxon have been collected in Coumiac (Decombeix et al. 2008).

Calamopityaceae or Lyginopitys *(specimens MN964 and MN711).* The wood of these specimens has tracheids with up to five rows of crowded circular pits on their radial walls and high multiseriate rays. Among the stem morphotaxa known in the Montagne Noire deposits, woods of this type belong to the Calamopityaceae (Meyer-Berthaud 1984; Galtier et al. 1988, 1993; Galtier and Beck 1992, 1995). The group is very well represented in the Montagne Noire, both in terms of relative abundance (42% of anatomically preserved specimens; Galtier et al. 1988) and in taxonomic diversity, with three genera present: *Calamopitys* (several species; Galtier et al. 1993; Galtier and Beck 1995), *Triichnia meyenii* (Galtier and Beck 1992), and *Stenomyelon bifasciculare* (Meyer-Berthaud 1984). The largest specimen from Montagne Noire is an axis of *Calamopitys* 600 mm long and 40 mm wide that bears eight petioles, each with a swollen base. Although there is no evidence of branching in that specimen, smaller stems can branch (Galtier and Holmes 1982). Galtier et al. (1993) suggested that, as in younger medullosan stems, the different taxa of Calamopityceae might have had slightly different habits. A non-self-supporting habit is documented for at least one species of *Calamopitys* (Rowe et al. 1993).

The different genera and species of Calamopityaceae can be separated by the organization of their primary xylem and their mode of leaf-trace emission. It is thus difficult to assign the new specimens MN964 and MN711 to a definite taxon based solely on their wood anatomy. The secondary xylem of the Calamopityaceae is generally only a few millimeters thick. The largest known specimen of *Calamopitys americana*, a taxon present in the Montagne Noire, has only a little more than 10 mm of wood (Galtier and Beck 1995). Secondary xylem tracheids range from 30 μm to slightly over 100 μm for all taxa of Calamopityaceae. Radial pitting is always multiseriate, with hexagonal to circular crowded pits in an alternate arrangement. *Stenomyelon bifasciculare* is the only taxon in which tangential pitting is present, not only locally but in all the wood (Meyer-Berthaud 1984), a difference with our new specimens.

Secondary xylem rays of Calamopityaceae are always multiseriate, up to 8–10 cells wide. In transverse section, rays separate 1–12 (generally 2–5) files of tracheids. They are also always very high. Among the Montagne Noire taxa, rays can reach 85 cells high in *S. bifasciculare* (Meyer-Berthaud 1984) and up to several hundreds of cells in *Triichnia* (Galtier and Beck 1992). Based on the heterogeneity of their ray size, specimens MN964 and MN711 are more similar to *Calamopitys schweitzeri* (Galtier et al. 1993) than any other Calamopityaceae from Montagne Noire. In this species, most rays are 30–90 cells high, but some very high (200–300 cells) or extremely low (3 cells) rays are also present.

In addition to the Calamopityaceae, another taxon from Montagne Noire, *Lyginopitys puechcapelensis* (Galtier 1970), possesses a wood that can be compared to MN964 and MN711. The stems of this monospecific genus of uncertain affinities differ significantly from those of the Calamopityaceae by the anatomy of their primary xylem and by the V- to W-shaped vascularization of their leaf bases, very distinct from the several discrete bundles present in the *Kalymma*-type petiole associated with the Calamopityaceae (e.g., Galtier 1988).

However, the wood of *Lyginopitys* is very similar to that of the Calamopityaceae. *Lyginopitys* stems typically produce 2–3 mm of secondary xylem, with tracheids ranging 30–70 μm in diameter. Rays separate one to eight files of tracheids in transverse section and are very high. They are multiseriate but "never very wide" according to Galtier (1970, p. 150). This character distinguishes them from our specimens.

Significantly enlarged rays are present in the secondary phloem of both the Calamopityaceae and *Lyginopitys* (Decombeix et al. 2014). Among Early Carboniferous seed plants, the presence of thick-walled cells in the phloem rays has been reported in only some (but not all) Calamopityaceae and in *Lyginopitys* (Galtier 1970; Galtier and Beck 1992; Galtier et al. 1993; Decombeix et al. 2014 and references therein). In *Calamopitys embergeri* and *C. schweitzeri*, the secondary phloem is composed of alternating layers of sieve cells and parenchyma, while in *Lyginopitys* there are also layers of fibers. Because of the lack of good preservation in longitudinal section, the presence of fibers in the secondary phloem of root specimens MN964 and MN711 is not clear.

To summarize, the secondary xylem and secondary phloem of MN711 and MN964 show significant similarities with those of the Calamopityaceae, especially the genera *Calamopitys* and *Triichnia*, and to a lesser extent with *Stenomyelon* (Calamopityaceae) and *Lyginopitys* (incertae sedis). Stems of all four genera have been previously reported from the locality of Coumiac. It is of course possible that the two root specimens MN711 and MN964, although they possess a comparable wood and secondary phloem anatomy, belong to two different taxa within this list.

Cf. Protopitys/Stauroxylon *(specimens MN916 and MN967).* The wood of these two specimens is characterized by secondary xylem tracheids with bordered scalariform radial pits and rays that are normally uniseriate to partly biseriate and only a few (<10) cells high. The occurrence of bordered scalariform pitting on the radial wall of secondary xylem tracheids is very rare

among the lignophytes. In the Early Carboniferous, it is documented in only two genera that are both present in the Montagne Noire deposits, *Protopitys* and *Stauroxylon*.

Protopitys is a genus of progymnosperms known in Europe and Australia (Decombeix et al. 2015). It is represented in the Montagne Noire by isolated pieces of wood a few centimeters in diameter and at least two stems, including one bearing a fertile organ. The radial pitting of the tracheids in those specimens ranges from uniseriate to biseriate circular pits to scalariform bordered pits. Rays are uniseriate to partly biseriate and are only a few cells in height, as is characteristic of the genus (Decombeix et al. 2015 and references therein). *Stauroxylon beckii* (Galtier 1970) is documented only in the Montagne Noire, although a possible compression/impression specimen has also been reported from contemporaneous deposits of Thuringia, Germany (Meyer-Berthaud and Rowe 1997). Stems of *Stauroxylon* are about 10 mm wide and characterized by a cruciform protostele with a central protoxylem strand, an anatomy highly reminiscent of the Aneurophytalean progymnosperms of the Devonian (Galtier 1970). The stems produce a small amount of secondary xylem composed of small uniseriate to biseriate parenchymatous rays and tracheids with scalariform pitting (Galtier 1970).

On the basis of the bordered scalariform radial pitting of their secondary xylem tracheids, root specimens MN916 and MN967 are strongly reminiscent of *Protopitys* and *Stauroxylon*. One difference is the occurrence of larger rays in some parts of the wood. However, in both specimens, it seems that these larger rays are associated with the emission of traces to lateral roots. The wood located between the protoxylem strands (interfascicular areas) shows rays that are uniseriate to biseriate only, which we interpret as the normal condition. While ray size might vary between roots and stems of the same taxon, there is no known evidence of such a different type of radial pitting in the wood of different organs. We thus consider this character as the most significant in terms of taxonomic affinities. In this context, MN916 and MN967 are interpreted as probably affiliated to the progymnosperms, either to *Protopitys* or to *Stauroxylon*.

Stems of *Protopitys* and of *Stauroxylon* from the Montagne Noire are small (Galtier 1970; Decombeix 2007; Decombeix et al. 2015). However, the presence of much larger specimens belonging to one or both genera is indicated by isolated pieces of wood with the typical scalariform pitting and small rays. Those reach over 5 cm in thickness, and the parallel course of the tracheid files indicates that they represent the outside part of larger trunks (Galtier 1970; Decombeix 2007).

Root Morpho-Anatomy in Devonian-Carboniferous Lignophytes

Based on their wood anatomy, the specimens from Montagne Noire can be assigned to three very different groups of lignophytes: (1) the arborescent seed plant *Eristophyton*; (2) smaller, lianescent to shrubby seed plants belonging to the Calamopityaceae or *Lyginopitys*; and (3) the progymnosperms *Protopitys* or *Stauroxylon*. What do these new specimens add to our knowledge of root morpho-anatomy among Devonian-Carboniferous lignophytes?

Progymnosperms. The oldest lignophytes, represented by the aneurophytalean progymnosperms, have been recently reconstructed as possessing long rhizomes that bore lateral branches and clusters of roots that were only a few millimeters wide (Stein et al. 2012). The exact anatomy and mode of branching of these roots remains unknown. Matten (1975) described an isolated diarch root that was 3.3 mm × 1.8 mm with a small amount of secondary xylem from Cairo, New York. He assigned this specimen to the Aneurophytales, but several other groups of plants are known from the Cairo locality, including Stenokoleales (Matten 1975), which are now known to be able to produce woody roots (Momont et al. 2016). There is to date no evidence of a well-developed root system in the Aneurophytales.

The underground structures of the archaeopteridalean progymnosperms have received much more attention. They represent the oldest-known deep and complex root system to date, and their development is thought to have impacted the carbon cycle at a global scale during the Late Devonian (e.g., Algeo et al. 2001; Morris et al. 2015 and references therein). Roots of *Archaeopteris*, recognizable by their typical *Callixylon* wood with groups of pits on the radial wall of tracheids, have been described on the basis of anatomical specimens up to 9 cm in diameter (Beck 1953; Snigirevskaya 1984; Meyer-Berthaud et al. 2013). These roots typically have a four-lobed protostele with two protoxylem poles in each lobe; however, there might have been more diversity in stele anatomy (Meyer-Berthaud et al. 2013, p. 378). *Archaeopteris* roots branch both by apical division and by the production of lateral roots of likely endogenous origin (Meyer-Berthaud et al. 2013). Last-order roots are narrow, short, and determinate; they can be produced by any other order of roots. Small and large lateral roots are arranged all around the supporting axis, in a number of rows corresponding to the number of lobes in the protostele. Overall, the morphology and anatomy of archaeopteridalean roots appear very similar to those of the seed plants. Among the Archaeopteridales, another taxon for which root morphology and anatomy has been documented is *Eddya sullivanensis*, described by Beck (1967) as a probable "sporeling" of *Archaeopteris*. *Eddya* is particularly interesting, because one specimen shows an attached root system, which Beck interpreted as having a main axis bearing lateral roots along its entire length. The distal parts of the laterals branch either dichotomously or pseudodichotomously. The transition zone between the stem and root is not anatomically preserved.

The roots of the third group of progymnosperms, the Early Carboniferous Protopityales, are very poorly known (Walton 1969; Decombeix et al. 2015), and this article is the most detailed description to date of roots assignable to this group. It is interesting to note that the two specimens from Montagne Noire with a *Protopitys*-type wood have a triangular protostele. We cannot, however, exclude the possibility that several protoxylem configurations were present in the root system, as this situation is known to occur in numerous extant and fossil root systems (e.g., Petry 1914; Wilcox 1962; Rothwell and Whiteside 1974; Neish et al. 1993), possibly including *Archaeopteris/Callixylon*, as mentioned above. In plants with variable protoxylem configuration, small roots typically tend to have fewer protoxylem strands than coarse roots, and proximal roots usually have more strands than distal ones (e.g., *Chamaecyparis*; Hishi and Takeda 2005). Both root specimens from Montagne Noire are small (ca. 10–20 mm in diameter), and it is indeed possible that they correspond to distal parts of the root system. Their distinctive wood anatomy in the areas facing the protoxylem strands, with the presence of significantly larger rays, has not been reported

previously in progymnosperm roots. Our evidence shows that these larger rays are linked to the production of lateral roots. It is possible that, in addition, the cambium produced a slightly different type of derivative in those fascicular areas, a phenomenon also common in roots (e.g., Philipson et al. 1971). Combined with field observation of *Protopitys* trunks in other localities (Decombeix et al. 2015), the new anatomical data from Montagne Noire presented here suggest that, like the Archaeopteridales, the Protopityales had a well-developed woody root system.

Seed plants. While the root system of the first seed plants of Late Devonian age, like *Elkinsia* (Serbet and Rothwell 1992), is unknown, there is some information on representative Carboniferous seed plants. Several stems assigned to the Lyginopteridaceae possess adventitious roots produced close to the nodes or in the leaf axils, such as *Trivena* (Dunn et al. 2003), *Schopfiastrum* (Stidd and Phillips 1973), *Microspermopteris* (Taylor and Stockey 1976), *Rhetinangium* (Gordon 1912), and *Laceya* (May and Matten 1983). Other descriptions of Lyginopteridaceae roots include axes associated with remains of *Lyginopteris* and *Heterangium*. Roots associated with *Lyginopteris* (*Kaloxylon hookeri*; Williamson 1887, 1894) have a protostele with three to eight protoxylem strands, whereas roots associated with *Heterangium* are diarch (Barnard 1962; Pigg et al. 1987). Secondary xylem is present in all cases, but the roots remain small (ca. 10 mm). Matten et al. (1984) also described small roots from the earliest Tournaisian of Ireland (Tn1a–Tn1b) that, on the basis of the associated flora, might belong to the Lyginopteridaceae. These roots (*Rhizoxylon ambiguum*) are 1–15 mm in diameter and have two to five protoxylem strands and a small amount of secondary xylem.

Among the Callistophytaceae, both adventitious roots and isolated roots are known in *Callistophyton* (Rothwell 1975, 1981). They have a maximum diameter of 12 mm, are diarch, and produce lateral roots in the areas opposite the two protoxylem strands. Both their secondary xylem and their secondary phloem are similar to those of the stems (Rothwell 1975; Russin 1981). Interestingly, Rothwell (1975, p. 183) reports "conspicuously large rays" in the areas facing the protoxylem strands. It is possible that, like in the Montagne Noire specimens assigned to *Protopitys*, these structures are linked to the production of lateral roots and/or a different cambial activity in those regions.

Small rootlets to woody roots over 20 mm in diameter are known in the Medullosaceae (Steidtmann 1944; Rothwell and Whiteside 1974 and references therein). They can have up to at least five protoxylem strands. The wood is comparable to that of the stems. In some species, the activity of the cambium is different in the fascicular areas, giving a stellate aspect to the wood.

The Calamopitaceae were a diversified group in the Early Carboniferous, but their root system is almost completely unknown. Meyer Berthaud and Stein (1995) report the production of adventitious rootlets occurring in groups proximal to the emission of leaf traces in stems of *Stenomyelon*. The two new axes from Montagne Noire described in this article represent the first documentation of large roots or basal parts that might belong to this group. However, as discussed above, we cannot be entirely sure whether the specimens belong to the Calamopitaceae or to *Lyginopitys*. Based on characters such as petiole anatomy, the latter might be closer to the Lyginopteridales (Galtier 1970). In any case, we note that, with its wood thickness of several centimeters, MN964 is larger than any known stem belonging to the Calamopitaceae or *Lyginopitys* and has a much more developed secondary xylem. This suggests that some of the small shrubby or non-self-supporting seed ferns of the Early Carboniferous possessed well-developed woody basal parts in addition to small adventitious roots.

The root system of the first arborescent seed ferns, an informal group containing about 10 genera of Early Carboniferous woody taxa (Galtier 1992; Galtier and Meyer-Berthaud 2006), is not very well known. In his review of *Pitus*, Gordon (1935) illustrated a root with a small amount of secondary growth possibly belonging to this genus. It is tetrarch, with "normally low, uniseriate rays except opposite the protoxylem poles where the rays are tall and multiseriate" (Matten et al. 1984, p. 313). Barnard (1962) later described two types of roots from the Early Carboniferous of Scotland that he compared to the arborescent seed ferns *Eristophyton* and *Bilignea*. *Amyelon bovius* is, according to Barnard, one of the most abundant plant remains at the locality of Oxroad Bay. These roots have a tetrarch protostele, a well-developed secondary xylem with growth rings, and lateral roots of endogenous origin arising in four rows at irregular vertical distance (Barnard 1962). Barnard tentatively compared *A. bovius* roots to cooccurring specimens of *Eristophyton* based on wood anatomy. He also created the species *Amyelon equivius* for a single root 4 cm in diameter from Horse Roads Bay (Scotland) and noted that its wood was identical to that of *Bilignea resinosa*. However, the root and stem are known from different localities and were thus kept as separate taxa (Barnard 1962). Specimen MN710 from Montagne Noire, which we relate to *E. feistii*, is a new example of an isolated root assignable to the Early Carboniferous arborescent seed ferns based on cooccurrence and details of wood anatomy.

Conclusions and Perspectives

The wood anatomy of silicified lignophyte roots from the Early Carboniferous (Tournaisian) of Montagne Noire, France, allows us to recognize three different morphotaxa. The roots correspond to three types of lignophytes with different affinities and habits: an arborescent pteridosperm, a smaller shrubby or climbing pteridosperm, and a progymnosperm. All these roots show relatively abundant secondary growth, which suggests that both the self-supporting and non-self-supporting plants had roots with a good potential for exploration and a significant underground biomass.

The Early Carboniferous was a time of diversification for the vegetative body of lignophytes. This can be seen from general characteristics, such as their habit, to more detailed points of their stem vascular anatomy, including their primary vascular system organization or secondary phloem anatomy (e.g., Galtier 1988; Galtier and Meyer-Berthaud 2006; Dunn 2006; Decombeix et al. 2011*a*, 2014). How their underground parts evolved, however, remains largely unknown. One would expect that the combination of the development of new habits and the colonization of a wide range of habitats made possible by the seed habit led to a diversification of the lignophyte root systems comparable to that of their aerial parts. More studies and whole-plant reconstructions are needed now to test this hypothesis.

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