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SPECIAL ISSUE—CELEBRATING WOMEN IN PALEOBOTANY

PERIDERM PRODUCTION IN THE MISSISSIPPIAN CLADOXYLOPSID *CLADOXYLON TAENIATUM* AND A REVIEW OF PERIDERM OCCURRENCE IN PALEOZOIC PLANTS

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Premise of research. Periderm is a protective secondary tissue that replaces the epidermis in stems and roots having secondary growth. The first periderm most commonly originates immediately below the epidermis, but in some species, it arises deeper in the stem, usually in the primary phloem. Periderm is a common feature of extant plants and has been reported in numerous fossil taxa. Here we investigate the presence of this tissue in a Carboniferous representative of the cladoxylopsids, an extinct group related to the ferns s.l.

Methodology. We describe anatomically preserved stems of *Cladoxylon taeniatum* with a well-preserved periderm from Tournaisian deposits in France and Germany. We also provide a short review of the current state of our knowledge on periderm production in Paleozoic plants, especially in relation to secondary vascular growth.

Pivotal results. The new specimens are 7–15 mm in diameter. They have a well-developed secondary xylem and a thin periderm that has a deep-seated origin in the innermost part of the cortex. This shows that *Cladoxylon* had the ability to accommodate secondary vascular growth with the production of a periderm that replaced the cortex and epidermis. *Cladoxylon taeniatum* is, to date, the only cladoxylopsid in which this feature is described, and it increases the diversity of anatomical strategies for secondary growth documented in the group. Changes in the nature and geometrical distribution of tissue between typical stems with a cortex and stems with a periderm suggest that *C. taeniatum* was non-self-supporting, a growth habit that also differs from that of most other older cladoxylopsids.

Conclusions. The new specimens increase the diversity of Paleozoic plants that produced both secondary vascular tissues and a periderm. Our review highlights the fact that anatomical homologies between the structures called "periderm" in these various taxa remain unclear; numerous questions about the origins of the periderm and the possible relation between secondary vascular growth and periderm production remain.

Keywords: paleobotany, Paleozoic, Carboniferous, anatomy, secondary growth.

Introduction

Periderm is the name given to the cork cambium (phellogen) and the tissues derived from its activity (phellem and phelloderm; Esau 1965). The periderm becomes the protective outer layer of the plant when the epidermis is damaged by being wounded or stretched out by the development of secondary vascular tissues inside the axis. The first periderm most commonly originates in a layer of cortical cells immediately below the epidermis, but in some species, it arises deeper in the stem, usually in the primary phloem; subsequent periderms can form repeatedly in successively deeper layers of the cortex or phloem (Evert 2006). Periderm is present in most extant gymnosperms and angiosperms undergoing significant secondary growth (Esau 1965). In other extant plants, periderm production has been reported in ferns belonging to the Ophioglossaceae, including *Botrychium* Sw., *Botrypus* Michx., *Helminthostachys* Kaulf., and *Ophioglossum* Linn. (e.g., Peterson 1971; Takahashi and Kato 1988). In the fossil record, the production of periderm is also documented in taxa that are now extinct or whose extant representatives do not produce periderm. The tree-size lycopsids of the Paleozoic, for example, produced a periderm that reached a thickness of several centimeters (e.g., Eggert 1961; D'Antonio and Boyce 2020; DiMichele and Bateman 2020) and has been interpreted as the main factor contributing to the stiffness of their trunks (Kisch 1913; Mosbrugger 1990). Among the sphenopsids, periderm occurs in some Paleozoic–Early Mesozoic representatives of the Equisetales, such as *Arthropitys* (Cichan and Taylor 1983), and in the extinct Sphenophyllales (e.g., Eggert and Gaunt 1973). A periderm is also present in rhizomes of the early fern *Zygopteris* (Scott 1912; Phillips and Galtier 2005). Finally, a periderm has been described in several representatives of the progymnosperms, the extinct grade of free-sporing plants that includes the sister group of the seed plants (e.g., Beck 1957; Stein and Beck 1983). Interestingly, all of these fossil taxa also had secondary vascular tissues resulting from the activity of a unifacial or bifacial cambium (Decombeix et al. 2019 and references therein).

The cladoxylopsids are an extinct group of plants known from the Middle Devonian to the Early Carboniferous. While often

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grouped with the ferns and/or sphenopsids, their relationships are far from fully understood, and they have a complex taxonomic history (e.g., Berry and Stein 2000; Cordi and Stein 2005; Rothwell and Nixon 2006; Meyer-Berthaud et al. 2007; Xue et al. 2010). In this article, we will use the term cladoxylopsid sensu Meyer-Berthaud et al. (2007), that is, including the Pseudosporochnales and a number of genera of uncertain affinities grouped under the name "nonpseudosporochnalean cladoxylopsids" and excluding the Iridopteridales. The cladoxylopsids include both large trees and smaller taxa (Taylor et al. 2009). Some genera, such as *Pietzschia*, had only primary tissues (e.g., Soria and Meyer-Berthaud 2004, 2005), while others, such as *Cladoxylon*, *Xenocladia*, or *Xinicaulis*, could produce secondary vascular tissues around each of the numerous vascular bundles that constitute their steles (e.g., Arnold 1952; Mustafa 1978; Xu et al. 2017). The outermost part of cladoxylopsid stems described in the literature is typically composed only of primary tissues or is missing.

The genus *Cladoxylon*, originally established by Unger (1856) for axes from Saalfeld, Germany, is one of the youngest representatives of the cladoxylopsids and occurs in Tournaisian–early Visean deposits in Europe (Richter and Unger 1856; Solms-Laubach 1896; Bertrand 1935; Long 1968, 1987; Galtier 1970; Scott et al. 1984; Scott and Galtier 1996) and possibly Australia (Galtier et al. 2007; A.-L. Decombeix, personal observation). Here we describe middle Tournaisian specimens of *Cladoxylon* from France and Germany that were initially reported by Soria and Galtier (2006) and Soria et al. (2006) and constitute the only known occurrence to date of periderm in the cladoxylopsids. We discuss their implications in the context of secondary growth and habit in the cladoxylopsids, and we provide a short review of periderm development in other Paleozoic plants in relation to secondary vascular growth.

Material and Methods

The specimens from France illustrated in this article were collected in the Lydiennes Formation of the Montagne Noire in the Hérault department. The Lydiennes Formation is composed of alternating beds of argillaceous rock and radiolarian cherts that contain phosphatic nodules. It was deposited in a shallow sea during the middle and early late Tournaisian (Feist et al. 2020 and references therein). Anatomically preserved plants occur both in the phosphatic nodules and in the surrounding matrix, mostly in the lower part of the formation, and are considered to be middle Tournaisian in age (Galtier et al. 1988). *Cladoxylon* represents about 10% of these anatomically preserved plants, with 48 specimens identified, and some of them are illustrated by Galtier (1970). Five of them are illustrated in this article. They were collected in the localities of Coumiac (MN400, MN876, MN958) and Puech de la Suque (MN904, MN925). In addition to the French specimens, we also illustrate here one specimen assigned to *Cladoxylon* from the middle Tournaisian of the (now closed) quarry of Kahlleite in Thuringia, Germany (KB4; see map and geological information in Terreaux De Félice et al. 2019).

Preparation of peel sections (Galtier and Phillips 1999) for specimens from the Montagne Noire and Kahlleite does not always yield very good results, and except for MN400, all the specimens were prepared as thin sections (Hass and Rowe 1999). Photographs in transmitted or reflected light were taken using digital cameras (Sony XCD-U100CR) attached to an Olympus SZX12 stereomicroscope and to an Olympus BX51 compound microscope. Images were captured using Archimed software (Microvision Instruments). Cell and tissue dimensions were measured using ImageJ version 1.51k (Rasband 1997–2018). Plates were prepared with Adobe Photoshop CS5 version 12.0 (Adobe Systems). All the specimens illustrated in this article have previously been included in preliminary studies on the ontogeny (Soria and Galtier 2006) and biomechanical properties (Soria et al. 2006) of *C. taeniatum* that included all known specimens from Montagne Noire and Kahlleite. The specimens, as well as corresponding slides and peel sections, are part of the Collections de Paléobotanique, Université de Montpellier, and are deposited in the Bot-Anique et Modélisation de l'Architecture des Plantes et des Végétations Research Unit. Additional fossils illustrated in figure 7 were all photographed by us.

Descriptions

Specimens with Only Cortex

Typical specimens of *Cladoxylon taeniatum* from Montagne Noire show a dissected stele with 9–12 xylem segments (i.e., composed of primary and secondary xylem) in a parenchymatous ground tissue that is often poorly preserved (figs. 1*A*, 1*B*, 2*A*–2*C*). The xylem segments can be radially elongated to almost circular in cross section (fig. 2*D*), with a more or less regular arrangement of elongated versus short segments (fig. 2*B*, 2*C*). The short segments are about 1 mm in diameter, the longest up to 3 mm. Rarely, two segments seem to anastomose to form a U- or V-shaped bundle (e.g., fig. 2*E*). Primary xylem tracheids range from 20 to 50 μm in diameter. Each xylem segment has one protoxylem strand located toward the periphery of the axis, typically with a peripheral loop (sensu Bertrand 1935; Leclercq 1970; figs. 2*F*, 2*G*, 3*D*). U- and V-shaped segments have two protoxylem strands, both located toward the periphery of the stem (fig. 2*E*). All specimens show some amount of secondary xylem composed of tracheids and small parenchymatous rays. The secondary xylem tracheids are square to rounded in cross section (fig. 2*D*, 2*E*). Their size is variable—including within the same vascular segment—but they typically range from 30 to 70 μm in diameter. In longitudinal section, the pitting of the tracheids ranges from scalariform to flattened bordered pits, with occasional occurrences of oval to circular bordered pits (fig. 3*B*). Rays are one or two cells high and one cell wide in tangential section. Secondary xylem development tends to be more important toward the inside of the stem, up to 15 layers of tracheids in thickness (e.g., fig. 2*C*, 2*E*). There is no evidence of secondary phloem, and the cambium is interpreted as unifacial. There are examples where a layer of tracheids with a smaller radial diameter is produced (e.g., fig. 2*E*), indicating a change in cambial activity. The cortex is about 2 mm thick and can be divided into three zones, but there is no clear delimitation between them. The innermost part is composed of thin-walled cells that are square to slightly higher than wide in longitudinal section (iC in figs. 2*F*, 3*A*). They are interpreted as parenchyma and are indistinguishable from the ground tissue surrounding the xylem segments. External to this is a zone composed of cells that are polygonal to rounded in cross section and that show a wide range of sizes (mC in fig. 2*F*, 2*G*). In longitudinal section, they are elongated, often with a larger

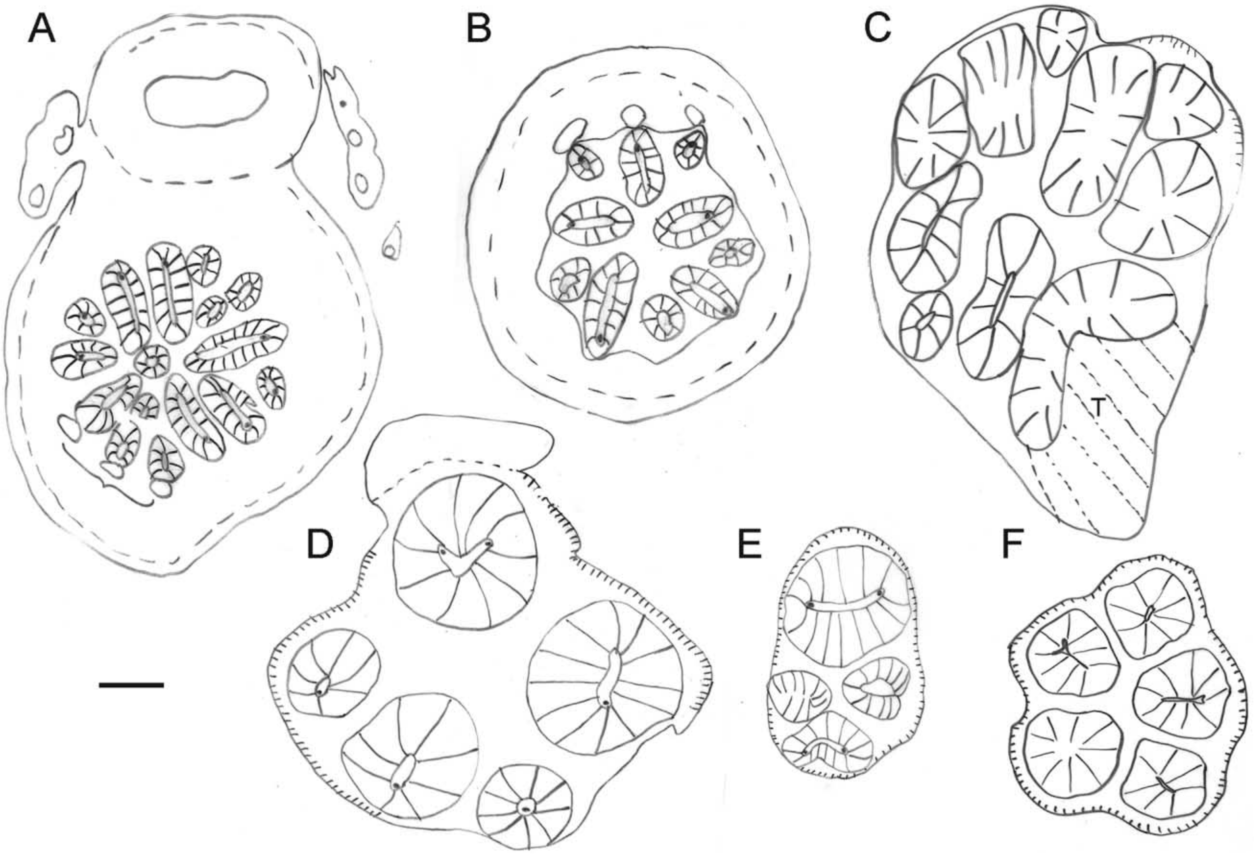

Fig. 1 Drawings of representative transverse sections of middle Tournaisian specimens of *Cladoxylon* at the same scale. *A–D* are from Montagne Noire, France, *E* is from Kahlleite, Thuringia, Germany (discussed in this article), and *F* is of the extant liana *Serjania* (Sapindaceae). *A*, MN925-A3S1. *B*, MN876. *C*, MN904-C2Si. *D*, MN400-DS01. *E*, KB4.4. *F*, *Serjania corrugata* (Sapindaceae), redrawn from Araújo and Costa (2006). The dashed lines in *A* and *B* indicate the outline of the outer cortex. The small dashes perpendicular to the periphery of the axes in *C–F* indicate the periderm. T = large woody trace to a lateral organ. Scale bar = 2 mm.

diameter in their median portion (mC in fig. 3*A*); this could explain the different diameters seen in cross section. These cells tend to have irregularly thickened walls and are interpreted as collenchyma. Finally, the most external part of the cortex (oC in figs. 2*F*, 2*G*, 3*A*) contains collenchyma cells but also groups of smaller cells with thicker walls that are much more elongated in longitudinal section (arrowhead in fig. 3*A*); these are interpreted as fibers.

Periderm Initiation

Some specimens from Montagne Noire, like the one illustrated in figure 2*C*, do not show a clearly recognizable periderm but have a dark layer of tangentially stretched cells in the inner part of the cortex surrounding the group of xylem segments (fig. 2*C*, 2*E*). This layer might represent the location of periderm initiation. Interestingly, the cells located between the groups of fibers in the outer part of the cortex in this specimen are also tangentially stretched (white arrowheads in fig. 2*G*), suggesting some deformation to accommodate the secondary vascular growth. In later developmental stages, specimens show a thicker, more conspicuous dark layer surrounding the xylem segments and clearly corresponding to the onset of a deep-seated periderm (fig. 3*C*, 3*D*).

Specimens with Periderm

Two specimens from Montagne Noire show a late developmental stage with good periderm development: specimens MN400 and MN904 (figs. 1*C*, 1*D*, 4*A*–4*C*). In MN904, the periderm is the preserved outermost tissue. In some sections of MN400, there are a few remnants of thin-walled cells of the cortex preserved right outside the periderm (arrowheads in fig. 4*C*). Both axes with periderm have secondary xylem that is 1–2 mm thick. They are, however, not much larger than the other specimens; the gain in thickness caused by secondary xylem development at this stage is in part compensated for by the loss of the thick cortex (fig. 1). The descriptions below focus on the best-preserved specimen, MN400.

MN400. MN400 is an axis ca. 5 cm in length, with a maximum diameter of 15 mm. It has five xylem segments of unequal size, the largest being 5.5 mm in diameter and the smallest 2 mm (figs. 1*D*, 4*B*, 4*C*). Protoxylem is located toward the external end of the xylem segment and typically shows a conspicuous peripheral loop (fig. 4*D*, 4*E*). In the smallest segments, metaxylem

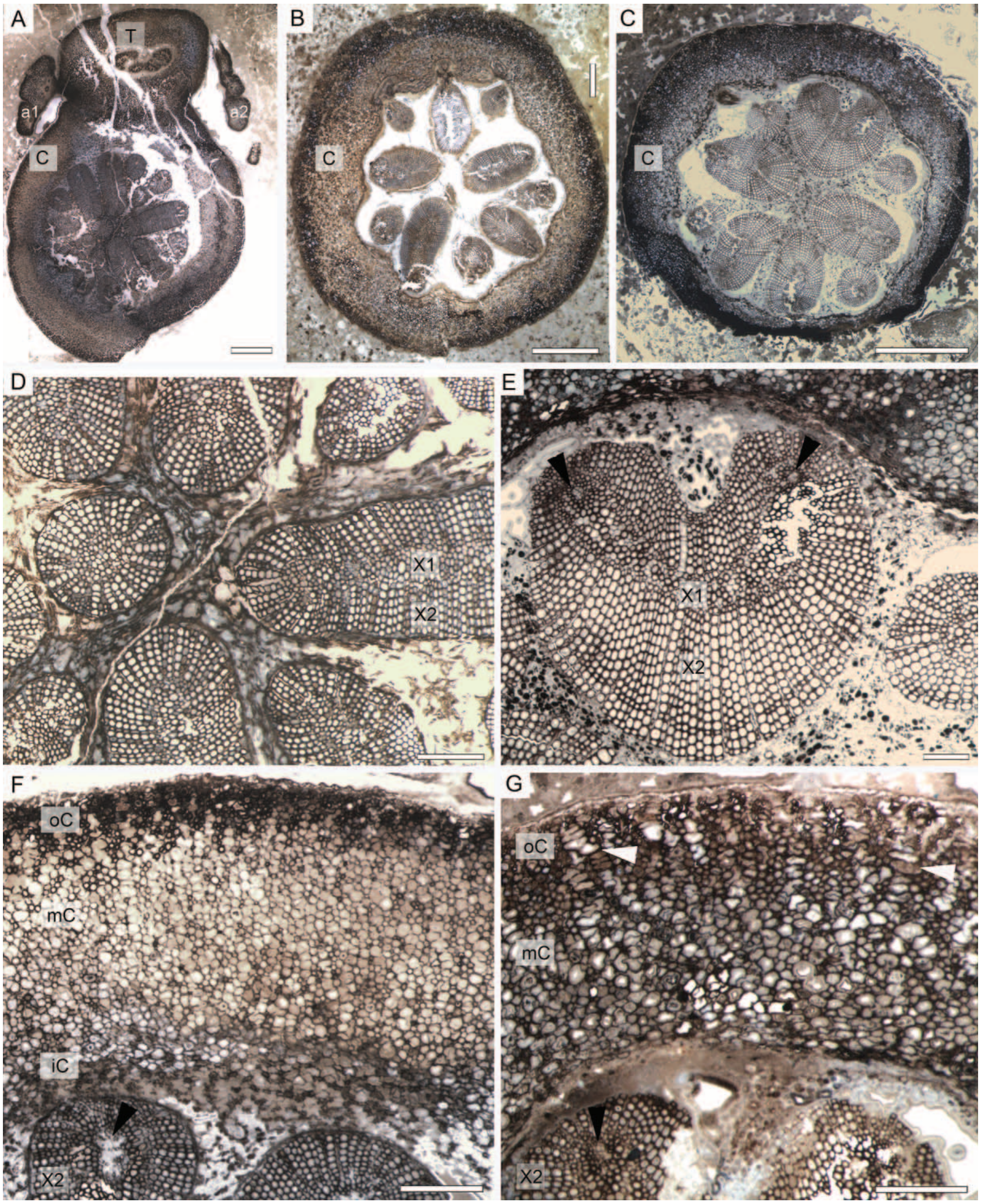

Fig. 2 Selected specimens of *Cladoxylon* with secondary vascular tissues and cortex from Montagne Noire, France. *A*, General view of a specimen with secondary vascular growth but with only (primary) cortical tissues (C). A departing lateral organ (T) and aphlebias (a1 and a2) are also visible in the upper third of the photo. Slide MN925-A3s1. *B*, General view of a specimen with secondary vascular tissues and cortex (C), showing the arrangement of small and large xylem segments. Slide MN876. *C*, General view of a specimen with secondary vascular tissues and cortex (C), showing a more developed secondary xylem and one V-shaped xylem segment. Slide MN958-As2. *D*, Detail of *A*, showing secondary xylem development (X2) around the vascular bundles (X1). Slide MN925-A3s1. *E*, Detail of *C*, showing secondary xylem development (X2) around the vascular bundles (X1). Note the presence of peripheral loops (arrowheads) and the mostly centripetal development of the secondary xylem. Slide MN958-As2. *F*, Detail of the cortex in *A*, showing remains of the ground tissue surrounding the xylem segments and the cortex. Three zones can be distinguished on the basis of gradual changes: an inner cortex (iC), a middle cortex (mC), and an outer cortex (oC), the latter containing groups of small thick-walled cells. The arrowhead indicates a peripheral loop. Slide MN925-A3s1. *G*, Detail of the specimen in C, showing the gradual change between the middle cortex (mC) and the outer cortex (oC). Note the presence of tangentially stretched cells between the small thick-walled cells of the outer cortex (white arrowheads). The black arrowhead indicates a peripheral loop. Slide MN958-B1i1. Scale bars = 2 mm (*A*–*C*), 500 μm (*D*, *F*, *G*), 250 μm (*E*).

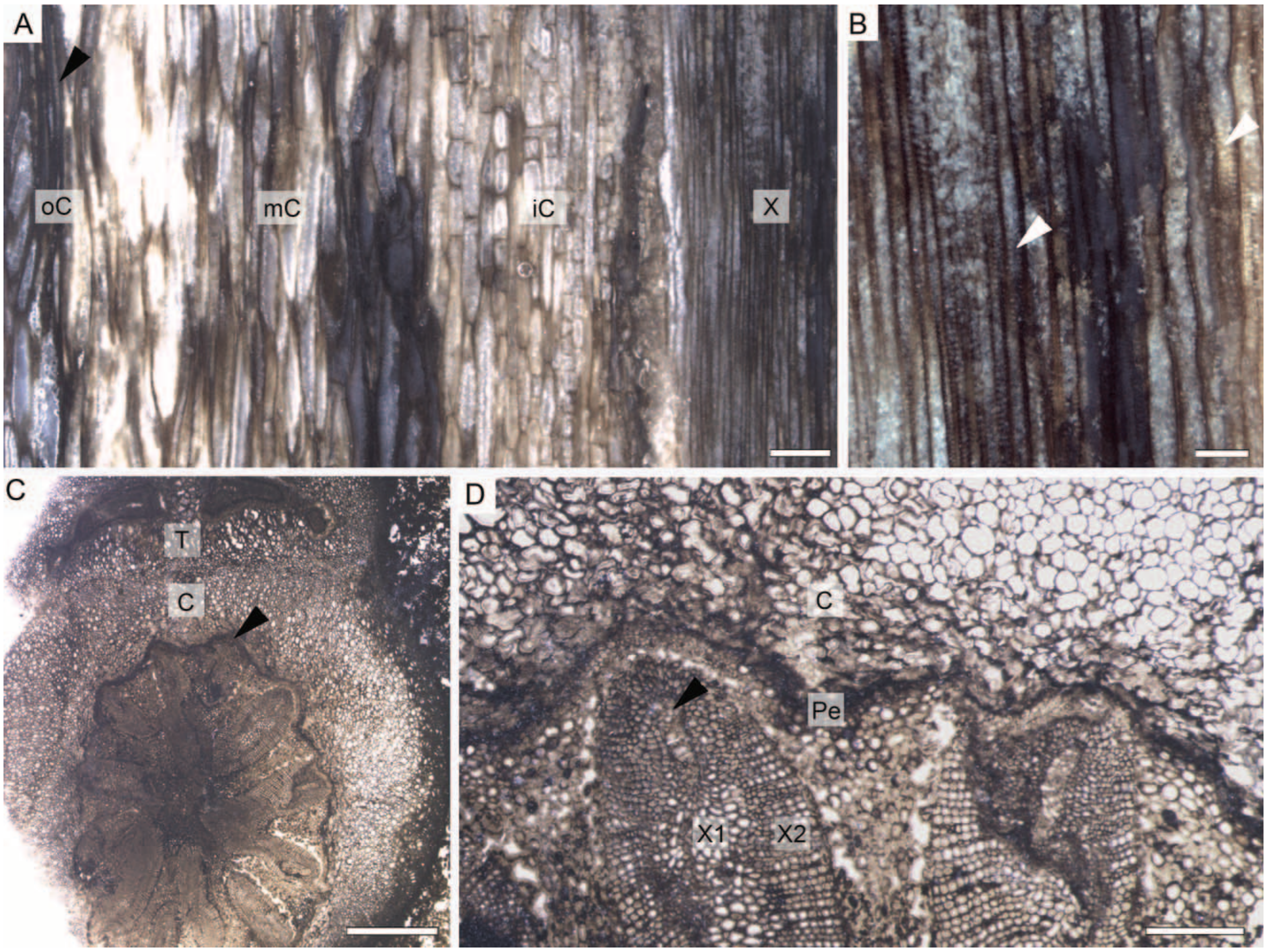

Fig. 3 Specimens of *Cladoxylon* from Montagne Noire, France. *A*, Longitudinal section through the specimen illustrated in figure 1*B*, showing the outermost part of the cortex (oC) with both large and smaller elongated cells (arrowhead); the middle part of the cortex (mC), composed mostly of collenchyma; an inner, mostly parenchymatous part of the cortex (iC); and a vascular bundle (X). Slide MN876-AL2. *B*, Detail of xylem tracheid ornamentation in radial section, with some tracheids bearing two rows of pits (arrowheads). Slide MN876-AL2. *C*, General view of a specimen, showing an early stage of periderm (arrowhead) development between the xylem segment and cortex (C). A trace to a lateral organ (T) is visible at the top. Slide MN953. *D*, Detail of *C*, showing the location and aspect of the periderm layer (Pe) between the cortex (C) and xylem segments with primary xylem (X1) and secondary xylem (X2). The arrowhead indicates an elongated peripheral loop. Slide MN953. Scale bars = 250 μm (*A*), 100 μm (*B*), 2 mm (*C*), 500 μm (*D*).

tracheids are up to 80 μm in diameter, comparable to those in the specimens with cortex described above. However, in some of the biggest xylem segments, the largest metaxylem tracheids can reach 100–110 μm in diameter (e.g., fig. 4*E*). Secondary xylem is up to 40 layers of cells in thickness, composed of tracheids that are comparable in size to those of specimens with cortex, that is, typically ranging from 30 to 80 μm in diameter. Parenchymatous rays are uniseriate and are often inconspicuous in cross section (fig. 4*D*, 4*E*). In longitudinal sections, the rays are uniseriate and a few cells high (fig. 4*F*). The radial walls of the tracheids bear elongated to oval pits (fig. 4*G*, 4*H*). There is no evidence of secondary phloem. A layer of large (up to ca. 100 μm) thin-walled cells that are polygonal in cross section is visible outside the secondary xylem in some parts of the specimen (white arrowheads in fig. 4*D*, 4*E*; fig. 5*A*). In longitudinal section, these cells are elongated (fig. 4*H*). They are interpreted as part of the primary phloem. The ground tissue surrounding the xylem segments is very compacted and distorted (figs. 4*D*, 5*A*–5*C*). The periderm occurs between this compressed zone and the remnants of the cortex (fig. 5*B*). It is typically 250–300 μm thick and is composed of dark thin-walled cells. Some better-preserved portions show the organization of the cells in radial files (e.g., Pe in fig. 5*C*). In one section, a zone of radially aligned cells just external to the phloem zone might represent the initiation of a second periderm layer (fig. 5*D*). It is, however, limited to one zone of the specimen and not the whole periphery. In longitudinal section, cells of the periderm are also poorly preserved (fig. 5*E*, 5*F*). They are short with thin walls, often have dark contents, and are clearly distinct from the cell types found in the cortex of ontogenetically younger specimens (fig. 3*A*).

MN904. MN904 is an axis with a diameter of 15 mm × 10 mm in its largest portion. Up to 10 xylem segments are visible in that stem, but the preservation is poor, and the general organization is obscured by the division of vascular segments and the initiation and departure of large woody traces to lateral organs (figs. 1*C*, 4*A*). All the segments have secondary xylem (fig. 6*A*–6*C*). A layer

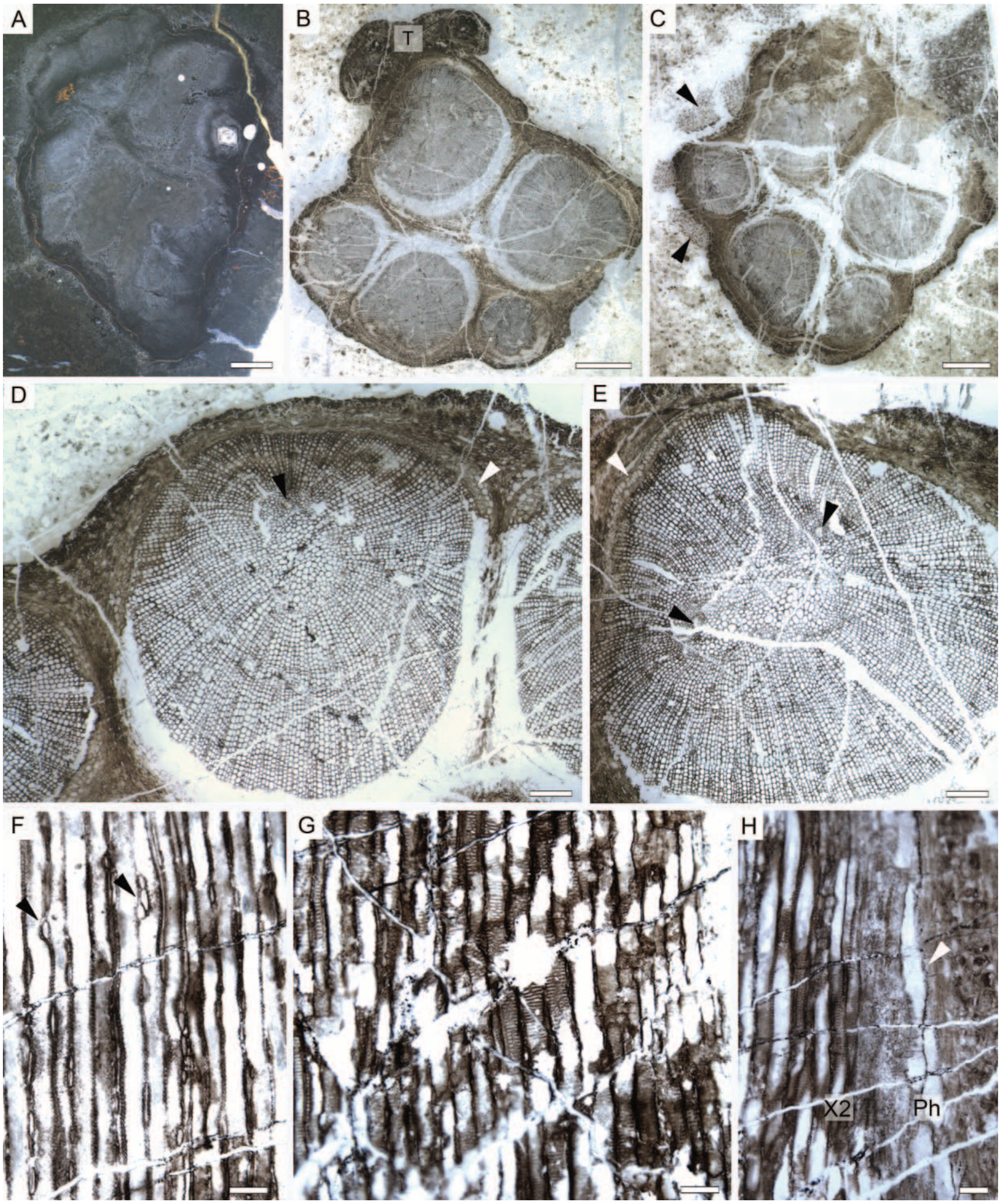

Fig. 4 *Cladoxylon* with periderm from Montagne Noire, France. *A*, General view of MN904 from Montagne Noire. See figure 1*C* for a drawing of this section. Slide MN904-C2Si. *B*, General view of MN400 from Montagne Noire, level with the departure of a lateral organ (T). At this level, the outermost tissue of the specimen is the periderm. Slide MN400-Ds01. *C*, General view of MN400 at a level where some cortical tissues external to the periderm (arrowheads) are preserved. Slide MN400-As02. *D*, Detail of a xylem segment from *B*, showing a single protoxylem strand (black arrowhead). Note the important centripetal development of secondary xylem and a layer of cells interpreted as primary phloem (white arrowhead). Slide MN400-Ds01. *E*, Detail of a xylem segment from *B*, showing two protoxylem strands (black arrowheads). Note the development of secondary xylem and a layer of cells interpreted as primary phloem (white arrowhead). Slide MN400-Ds01. *F*, Secondary xylem of one of the xylem segments in longitudinal section, showing small rays (arrowheads). Slide MN400-L6. *G*, Secondary xylem of another xylem segment seen in radial section, showing elongated to oval bordered pits. Slide MN400-L6 (focused stack of three images). *H*, Section through the outermost part of the secondary xylem (X2) and extraxylary tissues, including possible phloem (Ph) with a layer of large thin-walled cells (arrowhead) corresponding to the layer indicated in *D* and *E* and in figure 5*A*. Slide MN400-L12. Scale bars = 2 mm (*A*–*C*), 500 μm (*D*, *E*), 100 μm (*F*–*H*).

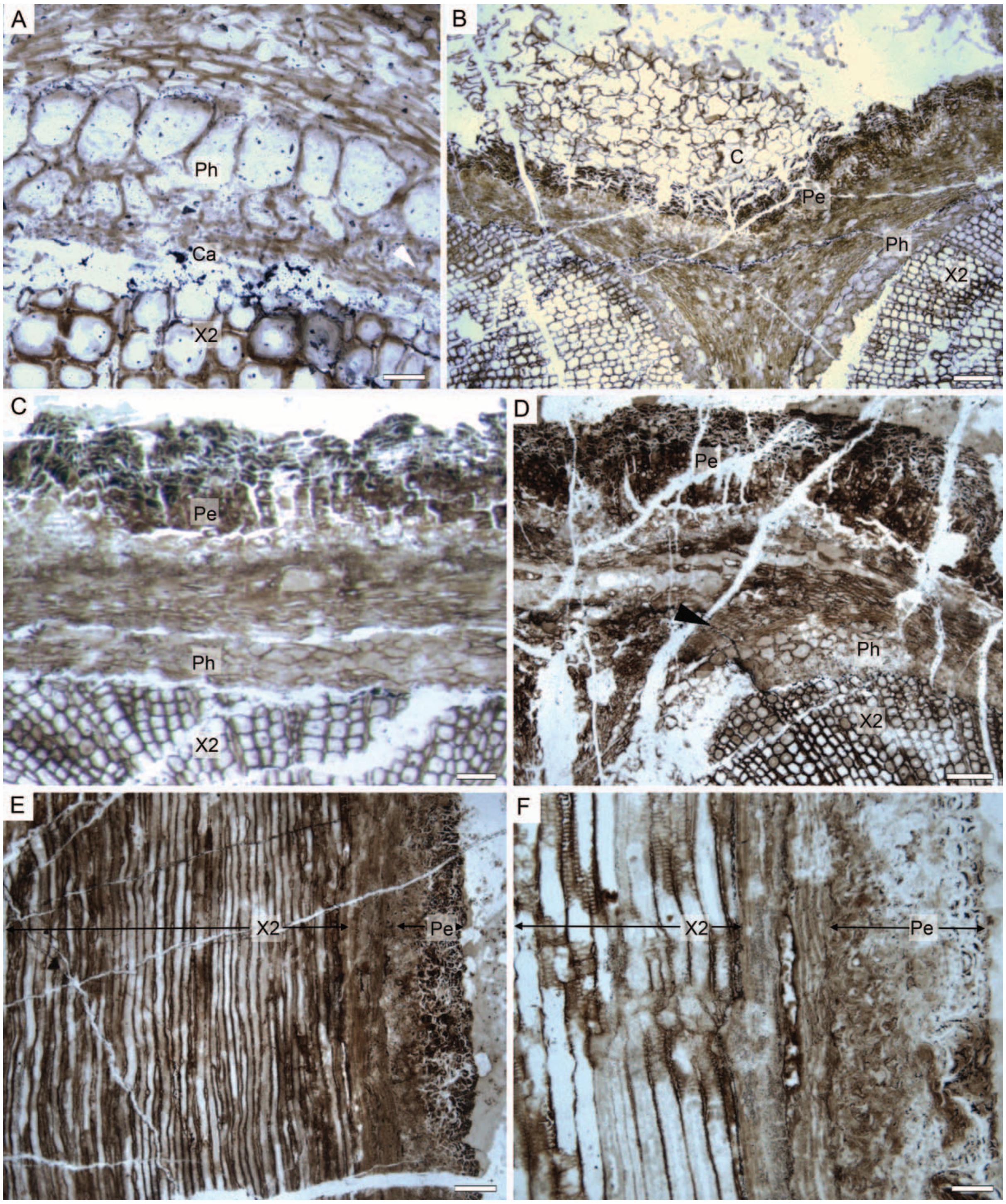

Fig. 5 *Cladoxylon* with periderm from Montagne Noire, France; detail of extraxylary tissues in MN400. *A*, Detail of the outermost part of the secondary xylem (X2), probable cambial zone (Ca), and primary phloem (Ph) with well-preserved large thin-walled cells corresponding to the ones in figure 4*H*. Slide MN400-As02 (focused stack of two photos). *B*, Outer part of the axis illustrated in figure 4C, showing the secondary xylem (X2), phloem (Ph) and ground tissue of two segments, the periderm (Pe) surrounding the axis, and remnants of the cortex (C). Slide MN400-As02 (focused stack of three photos). *C*, Close-up showing the secondary xylem (X2), phloem region (Ph), and periderm (Pe) with conspicuous radial files of cells. Slide MN400-As02. *D*, Transverse section at a level where a second layer of periderm seems to be produced between the phloem (Ph) and older periderm (Pe; arrowhead). X2 = secondary xylem. *E*, Tangential section showing the secondary xylem (X2) and periderm (Pe). Slide MN400-CLT7. *F*, Radial section showing the secondary xylem tracheids with elongated to oval bordered pits (X2) and the periderm (Pe). The tissues in between are poorly preserved but probably include some phloem. Slide MN400-CLT14. Scale bars = 50 μm (*A*), 250 μm (*B*, *D*, *E*), 100 μm (*C*, *F*).

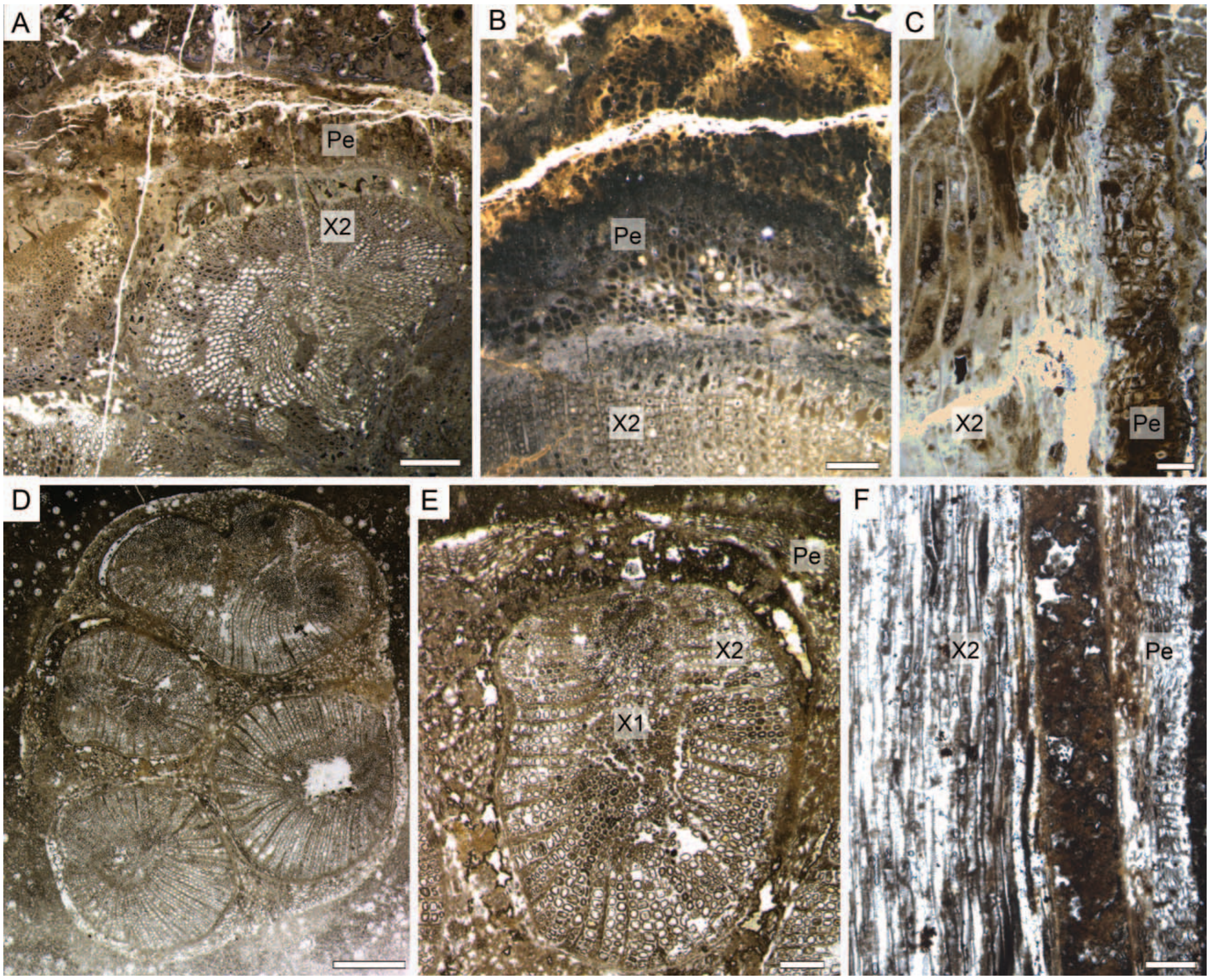

Fig. 6 Additional specimens of *Cladoxylon* with periderm. *A–C* (MN904) are from Montagne Noire, France, and *D–F* (KB4) are from Kahlleite, Thuringia, Germany. *A*, Transverse section of MN904, showing several xylem segments with secondary xylem (X2) and poorly preserved extraxylary tissues, including a periderm (Pe). Slide MN904-AT. *B*, Detail of the secondary xylem (X2) and a thick layer of periderm (Pe). Slide MN904-Bi4. *C*, Longitudinal section of a departing trace with secondary xylem (X2) and periderm (Pe). Slide MN904-Bi2. *D*, General view of KB4, showing four xylem segments with well-developed secondary xylem. Slide KB4-3s1. *E*, Detail of a transverse section, showing the primary xylem (X1), secondary xylem (X2), and extraxylary tissues, including the periderm (Pe). Slide KB4-2i1. *F*, Longitudinal section of KB4, showing the primary xylem (X1), secondary xylem (X2), and periderm (Pe). Slide KB4-CL. Scale bars = 500 μm (*A*), 250 mm (*B, C, E, F*), 1 mm (*D*).

of periderm is preserved in some portions of the specimen (fig. 6*A*, 6*B*), including in a woody trace that is departing perpendicularly to the stem and is seen in radial view (fig. 6*C*). It is composed of more or less isodiametric thin-walled cells that are 30–55 μm in diameter and that tend to be organized in radial files. The preserved periderm layer is typically about 500 μm thick (fig. 6*A*, 6*B*) but reaches 1 mm in a portion of the stem (fig. 6*B*).

Additional observation: KB4 from Kahlleite. KB4 is an axis that is 6 cm in length with a maximum diameter of 7 mm. It has four xylem segments of unequal size, the largest being 4 mm × 2.4 mm in diameter and the smallest being 2.3 mm × 1.7 mm in diameter (figs. 1*E*, 6*D*). Secondary xylem is up to 30 layers thick and is composed of tracheids that are 20–70 μm in diameter and uniseriate to partly biseriate parenchymatous rays (fig. 6*D*, 6*E*). There is no evidence of secondary phloem and no recognizable primary phloem. A periderm comparable to the one in the Montagne Noire specimens is present in the outer part of the stem (fig. 6*E*, 6*F*). It is about 250 μm thick. The best-preserved portions show that the cells are thin walled and slightly higher than they are wide in longitudinal section (fig. 6*F*).

Discussion

Affinities of the Stems with Periderm

Revisions of the Devonian species of *Cladoxylon* have resulted in the synonymy of *C. scoparium* from the Middle Devonian of

Germany with *Calamophyton primaevum* (Schweitzer and Giesen 1980; Fairon-Demaret and Berry 2000). The species *C. hueberi*, *C. onteorense*, and *C. dichotomum* (nom. nud. Hueber 1959 and 1960) from the Frasnian of New York have been assigned to *Pseudosporochnus hueberi* (Stein and Hueber 1989). Finally, *C. dawsonii*, also from the Frasnian of New York, was interpreted as an iridopteridalean and assigned to a new genus, *Rotoxylon*, by Cordi and Stein (2005). As a result, the genus *Cladoxylon* now includes only species from Mississippian deposits in Europe: *C. mirabile* (the type species), *C. radiatum*, *C. solmsii*, and *C. taeniatum* in middle Tournaisian deposits of Saalfeld, Germany (Solms-Laubach 1896; Bertrand 1935), and *C. waltonii* and *C. edromense* in late Tournaisian to early Visean localities in Scotland (Long 1968, 1987; Scott et al. 1984; Scott and Galtier 1996). *Cladoxylon taeniatum*, as revised by Bertrand (1935), includes specimens assigned to *C. dubium* by Unger (1856) and Solms-Laubach (1896). In addition, Early Carboniferous stems with numerous xylem segments assigned to *Steloxylon* and *Völkelia* (Solms-Laubach 1910) likely belong to *Cladoxylon* (see, e.g., Bertrand 1935, pp. 105, 111). A revision of the taxonomy and systematic relationships of *Cladoxylon* in light of branching and developmental information is needed but is beyond the scope of this article. The genus is not included in the phylogeny of Xue et al. (2010). In the Montagne Noire, Galtier (1970) recognized several morphotypes: *C. taeniatum*, *C. taeniatum* var. *dubium*, and *Cladoxylon* sp. The two specimens with periderm (fig. 1*C*, 1*D*) fall within the range of *C. taeniatum* as defined by Bertrand (1935). The specimen from Kahlleite (fig. 1*E*) shows a general organization comparable to that of the Montagne Noire specimens with periderm. However, some apparent anatomical differences—including in the mode of the production of traces to laterals—prevent us from assigning it with confidence to the same species before a better understanding of the ontogeny and taxonomy of *Cladoxylon* is available.

Growth Habit of C. taeniatum

A biomechanical analysis conducted by Soria et al. (2006) on 40 specimens—including the ones presented here—showed that *C. taeniatum* was a non-self-supporting plant. Interestingly, secondary growth changes the properties of the stems in two ways (fig. 1*A*–1*E*). The first event is the development of secondary xylem. While this tissue represents a small portion of the stem in cross section in the younger stages, it is the most abundant in older stages, such as MN400. This secondary xylem is a relatively tough tissue formed by tracheids that have a small diameter and thick walls and a minor proportion of small parenchymatous rays. The major mechanical event during ontogeny, however, is the change in the periphery of the axis from a thick and fibrous cortex to a narrow periderm composed of thin-walled cells. This change is not compensated for mechanically by the development of the secondary xylem and results in a significant loss of stem stiffness in the older stages (Soria et al. 2006). Such a change to more flexible older axes during development is typical of lianas, suggesting that these specimens of *C. taeniatum* might have had a creeping or climbing habit. A similar ontogeny and habit have, for example, been suggested for the Devonian progymnosperm *Tetraxylopteris schmidtii* (Speck and Rowe 2003). Among extant plants, old stems of lianas with a size and distribution of tissues quite comparable to that of the specimens of *Cladoxylon* with periderm can be found, for example, in the genus *Serjania* Mill. (Sapindaceae; fig. 1*F*), in which there are typically a few distinct vascular cylinders (e.g., Fisher and Ewers 1991; Araújo and Costa 2006; Angyalossy et al. 2015; and references in these articles). In these extant lianas, the presence of several cylinders of vascular tissues surrounded by softer deformable tissues results in a “cable-like structure” that improves flexibility and resistance to injury in the old parts of the stem (Fisher and Ewers 1991; Putz and Holbrook 1991). Additional information on the geometry of lateral organs in *C. taeniatum* (type, diameter relative to that of the stem, angle of insertion, deciduousness, internode length, etc.) is now needed to reconstruct the plant completely. The presence of decorticated specimens of *C. taeniatum* reaching 3.5 cm × 2.5 cm in diameter at Saalfeld (fig. 1 in Bertrand 1935) and 3 cm × 2 cm at the Montagne Noire (MN911; Soria and Galtier 2006) suggests that this species could reach a larger diameter than the specimens with preserved periderm illustrated in this article. It is important to note that the development and habit of *C. taeniatum* might not be representative of the genus as a whole. *Cladoxylon radiatum*, for example, can reach 1.5 cm × 2.5 cm in diameter (e.g., fig. 64 in Bertrand 1935) but is characterized by the almost complete absence of secondary vascular tissue; its growth habit might thus have differed from that of *C. taeniatum*.

Comparison with Other Cladoxylopsids with Secondary Growth

The new specimens illustrated here show that some cladoxylopsids could have grown beyond the size of their primary body by producing a deep-seated periderm that replaced the cortex and epidermis as secondary vascular tissues developed. In addition to *Cladoxylon*, several geologically older cladoxylopsid genera produced secondary vascular tissues. The Late Devonian *Polypetalophyton wufengensis* (Hilton et al. 2003) shows numerous anatomical similarities, including the number of xylem segments and primary xylem anatomy, to *C. taeniatum*. *Polypetalophyton wufengensis* also produced a small number of radially aligned tracheids with elongated to circular bordered pits on their radial walls. No cellular details of putative rays are visible in the illustrated cross sections. However, at least one ray is visible in a radial section (fig. 8*H* in Hilton al. 2003), supporting the fact that *Polypetalophyton* did produce secondary xylem—and not aligned metaxylem. Cortical tissues of *Polypetalophyton* are unknown, and the largest stems are less than 1 cm in diameter. Larger Devonian cladoxylopsids with secondary growth include *Duisbergia* (Kraüsel and Weyland 1938; Mustafa 1978) and *Xenocladia* (Arnold 1952; Lemoigne and Iurina 1983; Meyer-Berthaud et al. 2004) from the Middle Devonian and *Xinicaulis* (Xu et al. 2017) from the Late Devonian. A specimen of *Xenocladia* was interpreted by Arnold (1952) as having originally been about 10 cm in diameter, although only 5 cm of it is preserved. *Duisbergia mirabilis*, as reinterpreted by Giesen and Berry (2013) as the trunk of *C. primaevum*, can reach 20–25 cm in diameter. The largest example to date of a cladoxylopsid with secondary vascular tissues is a 70-cm-wide trunk of *Xinicaulis* (Xu et al. 2017).

Compared with other vascular plants, secondary vascular growth in the cladoxylopsids remained relatively limited in terms of the amount produced around each primary xylem strand, from less than 1 mm in *Metacladophyton* to about 10 mm in the specimens of *Xinicaulis* illustrated by Xu et al. (2017). However, because of the presence of numerous segments, the total amount of secondary xylem produced in a stem can be important in terms of cross-sectional area. While it surely increased hydraulic conduction (Cascales-Miñana et al. 2019), the mechanical role of this wood remains to be quantified, as it was largely dependent on its geometrical distribution in the stem (Mosbrugger 1990; Niklas 1992). To date, no periderm has been reported in these large woody cladoxylopsids. In *Xenocladia*, Lemoigne and Iurina (1983) describe the outer part of the specimen as a multicellular layer of sclerenchyma that forms indentations between the external xylem segments, a conformation typical of a cortex (i.e., primary tissues). The *Duisbergia*/*Calamophyton* stems illustrated by Mustafa (1978) do not show evidence of secondary tissues in the cortex, but the one stem with well-developed secondary xylem is decorticated (pl. 14, fig. 2 of Mustafa 1978). In *Xinicaulis*, only primary tissues have been described around the xylem segments (Xu et al. 2017).

A first hypothesis for the lack of periderm in cladoxylopsids with secondary vascular growth is that since many specimens are decorticated, a periderm was indeed produced but has not been preserved in the axes known to date. A second hypothesis, however, is that no periderm was produced, either because secondary vascular growth was not important enough to warrant it or because the cortex of the plant kept pace by cell divisions, which led to a certain amount of diffuse unorganized growth. If secondary vascular growth remained limited, it could theoretically have been accommodated within the primary body of the plant. Such a situation is seen in some Early Carboniferous species of the seed plant *Calamopitys* in which there is no periderm formation despite the production of some secondary xylem and secondary phloem (Hotton and Stein 1994; Masselter et al. 2009). Alternatively, if secondary growth could develop beyond what the cortex of cladoxylopsids could accommodate, the stems would have had either to develop a periderm or to keep pace by frequent diffuse divisions in the cortex. Among extant plants, the latter strategy is observed both in some monocotyledons with secondary growth and in some dicotyledonous trees (Evert 2006). It can be accompanied by divisions of the epidermis cells, and as a result, some taxa retain their epidermis for a much longer time than others (Evert 2006). For example, the xerophytic "palos verdes" species of *Parkinsonia* (syn. *Cercidium*, Fabaceae) of the southwestern United States and Mexico retain their epidermis for a long time; periderm is developed only in the roots and the older trunks (e.g., Scott 1935; Gibson 1983). The hypothesis that secondary vascular growth was accommodated by diffuse cell proliferation in the ground tissue and cortex is what has been suggested for *Xinicaulis* by Xu et al. (2017). No detailed mechanism for the increase in the width of the cortex was proposed for *Calamophyton* (Giesen and Berry 2013) or other woody taxa. The specimens of *C. taeniatum* illustrated in this article show that some cladoxylopsids had the ability to produce a periderm to accommodate the production of secondary vascular tissues and replace the cortex as a protection against biotic and abiotic stress. This strategy, with the presence of both secondary vascular tissues and periderm, is very similar to that found in many lignophytes, and, as in that group, it is not necessarily associated with a self-supporting growth habit. New specimens and detailed anatomical studies of cladoxylopsids are still needed to better understand the full range of growth strategies and habits that occurred in the group.

Periderm in Other Devonian–Carboniferous Plants

The evolution of the periderm has received less attention than that of secondary vascular growth, probably in part because fossil plant stems are often decorticated. Tomescu and Groover (2019) advocated for an approach combining studies of extant and fossil plants to understand the evolution of secondary vascular growth and noted that a comparable approach could be applied to the evolution of the periderm. Like secondary vascular tissues, periderm evolved early (at least by the Middle Devonian; Banks 1981) and in a diversity of plant groups, including extinct taxa and taxa that do not have secondary growth today. Interestingly, studies of extant seed plants show that the phellogen and vascular cambium tissues share many regulatory components (e.g., Campilho et al. 2020), raising questions about the possible influence of one of these meristems on the activity of the other. The oldest evidence of periderm formation was described by Banks (1981) in a specimen of cf. *Psilophyton* from the Emsian of Gaspé, Canada. In this specimen, there are no secondary vascular tissues. The periderm is very localized and is interpreted as a result of wound repair and not part of normal development. On the basis of observations of the periderm in *Tetraxylopteris* and *Triloboxylon*, Rowe and Speck (2004, p. 309) suggested that periderm could indeed result from a "co-option where an original wound repair mechanism possibly related to phytophagy was later modified and deployed as an integral developmental system linked to growth of the bifacial vascular cambium." In the following section, we review current knowledge of periderm formation in Paleozoic plants and how it correlates with secondary vascular growth.

Lycopsids. The tree-size lepidodendralean lycopsids of the Paleozoic and early Mesozoic are an example of growth with no extant equivalent. The group was characterized by a relatively small amount of secondary vascular tissues produced by a unifacial cambium (e.g., Cichan 1985*a*). Vascular tissues formed a small central cylinder surrounded by a wide periderm (fig. 7*A*) in which the presence of well-defined layers corresponding to the phellogen and its derivative was variable between taxa. Compared with that of other extant and fossil plants, the periderm of these lycopsid trees was extremely thick, up to 15 cm, according to Arnold (1940). In extant seed plants, the periderm is always significantly thinner, and species with thick bark actually possess a rhytidome, that is, successive layers of periderm alternating with the remains of old secondary phloem (Esau 1965; fig. 7*F*). Some specimens of fossil lycopsids show periderm development at levels of the stem where there is no secondary vascular growth (e.g., Renault 1896; Kisch 1913; Eggert 1961). The exact nature of the lycopsid periderm and possible differences from that of extant seed plants have been discussed by several authors. Walton (1935), for example, suggested that the so-called periderm of *Lepidophloios* was actually more similar to the primary thickening meristem of extant monocotyledons than to a phellogen and resulting secondary tissues. Beck (1958) identified several successive meristematic layers in the cortex of *Levicaulis*. Eggert (1961) studied numerous specimens of Late Carboniferous branches and trunks of *Lepidodendron* and *Lepidophloios*. He concluded that these secondary tissues were not produced by a single

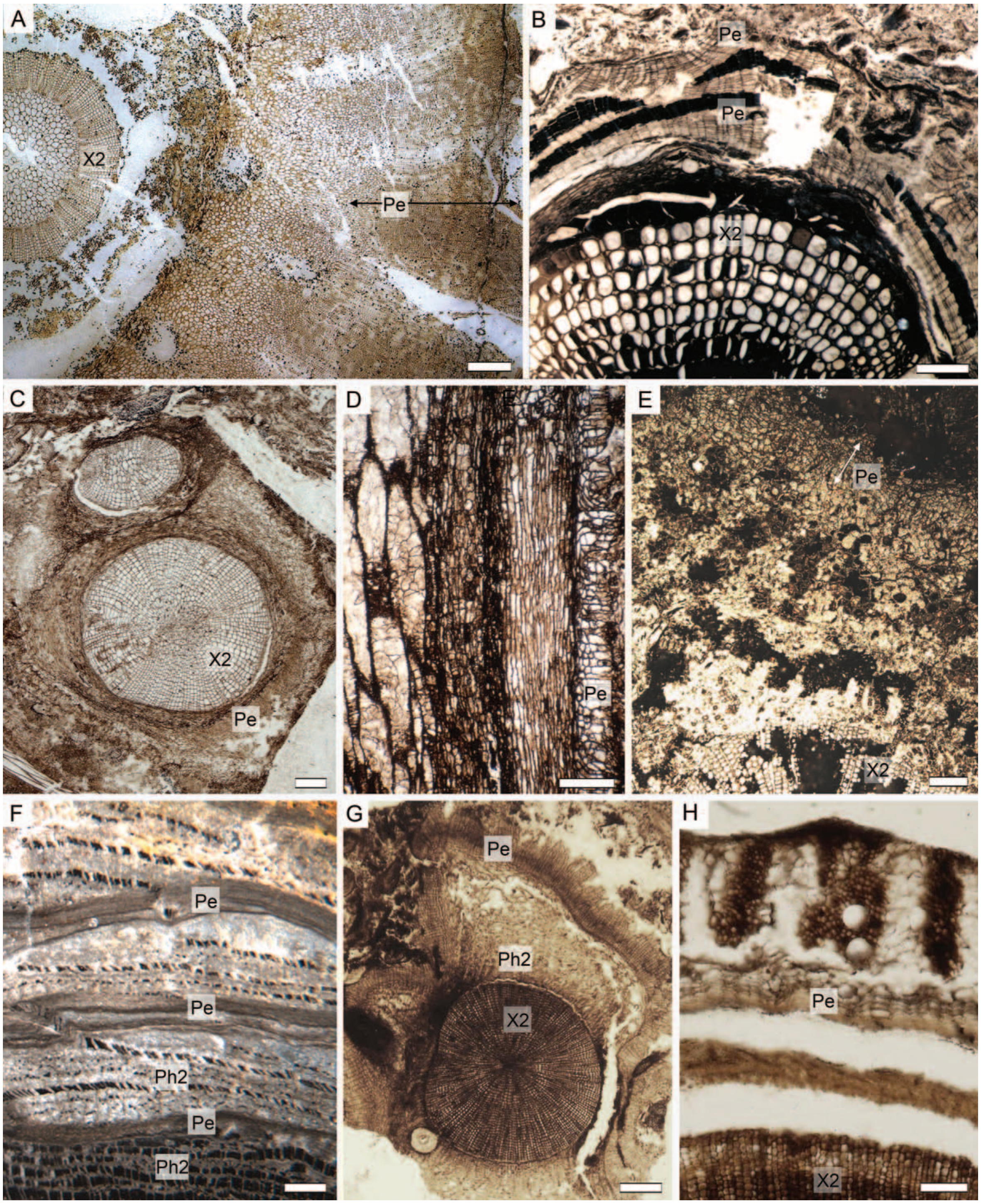

Fig. 7 Periderm in selected Paleozoic plants. *A*, Transverse section of a Pennsylvanian lycopsid stem in a coal ball from Illinois, showing a thick layer of periderm (Pe; teaching collection, peel donated by T. Philips). *B*, Transverse section of a Permian stem of *Sphenophyllum* from Autun, France, showing several layers of periderm (Pe; Collection Roche, box D, Muséum d'Histoire Naturelle, Autun). *C*, Transverse section of a Carboniferous *Zygopteris* stem and petiole from Cross Mountain, Tennessee, with abundant periderm (Pe; slide UI 36148BTOP-239; Phillips and Galtier 2005). *D*, Longitudinal section of a Carboniferous *Etapteris* (Zygopteridales) petiole from Cross Mountain with well-preserved periderm (Pe; slide UI 36148BTOP-1; Phillips and Galtier 2005). *E*, Transverse section of a Middle Devonian stem of *Triloboxylon* (Aneurophytales) from Spring Creek, New York, showing a layer of periderm (Pe) in the cortex (specimen 23284, slide LD-2-13c; Stein and Beck 1983). *F*, Transverse section of a Mississippian lignophyte trunk with rhytidome bark, showing alternating layers of periderm (Pe) and secondary phloem (Ph2; slide USNM553730-H-CT2; Decombeix 2013). *G*, Transverse section of a Carboniferous Cordaites root with abundant periderm (Pe; slide 323, Collection Roche, box 15, Muséum National d'Histoire Naturelle [MNHN], Paris). *H*, Transverse section of a Carboniferous Cordaites stem, showing an early stage of periderm (Pe) development (slide 964, Collection Renault, box 43, MNHN, Paris). X2 = secondary xylem. Scale bars = 1 mm (*A*, *C*, *F*, *G*), 500 μm (*B*), 250 μm (*D*, *E*), 200 μm (*H*).

meristematic layer (i.e., a phellogen) but resulted from "continued division of cells at several depths in the outer cortex and leaf base zone" (Eggert 1961, p. 77). Further work has shown that different periderm anatomies actually occurred among lycopsid trees (Bateman et al. 1992 and references therein). Some have no distinct phellem and phelloderm, while the distinction is conspicuous in others (e.g., *Diaphorodendron* and *Synchysidendron*; DiMichele and Bateman 1992). While further discussion is outside the scope of this short review, it is interesting to note that the structure called a periderm in the arborescent lycopsids could vary greatly in anatomy (and likely in function) among different genera.

Sphenopsids. Unlike extant *Equisetum*, several extinct genera of Equisetales produced a significant amount of wood. Some early authors supposed that given this large amount of wood (>10 cm thick), the lack of periderm in most tree-size Equisetales was only the result of decortication, but others, like Agashe (1964), concluded that they produced only a very small amount of periderm. Small (1 cm maximum) stems of *Arthropitys deltoides* studied by Cichan and Taylor (1983) have a few millimeters of wood and conspicuous successive layers of periderm. The species was interpreted by these authors as a liana or herbaceous plant based on its small diameter. A periderm was also reported in Permian stems of *Arthropitys junlianensis* (Wang et al. 2003) and in roots attached to *Arthropitys* trunks (Rößler et al. 2014). Most other known fossil Equisetales with secondary growth are decorticated, and little is known about the presence of a periderm or the anatomy of their extraxylary tissues in general (Taylor et al. 2009).

The extinct Sphenophyllales were small scrambling or climbing understory plants with stems ≤2 cm in diameter (Baxter 1948) that produced a small amount of secondary vascular tissues. Late Carboniferous and Permian specimens of *Sphenophyllum* show a well-developed periderm in the stems and roots, with distinct layers equivalent to the phellogen, phelloderm, and phellem (e.g., Renault 1873; Eggert and Gaunt 1973; Cichan 1985*b*; Taylor et al. 2009). In old stems, the periderm can have a banded aspect (fig. 7*B*), which was first interpreted as evidence for successive periderms ("scale bark" of Williamson) but more likely results from the activity of a single persistent phellogen (Eggert and Gaunt 1973). Young stems of *Sphenophyllum* sometimes display a conspicuous periderm before the development of any secondary vascular tissue at the same level. There is to date no evidence of a periderm in Early Carboniferous specimens of *Sphenophyllum* (Terreaux De Félice et al. 2019) or in Late Devonian representatives of the group such as *Rotafolia* or *Hamatophyton* (Wang et al. 2006*a*, 2006*b*), all of which had the ability to produce a small amount (<1 mm) of secondary vascular tissues.

Paleozoic ferns (sensu Phillips and Galtier 2005). The Zygopteridales are an extinct group of late Paleozoic ferns. Among them, *Zygopteris* produced a small amount of secondary xylem, likely from the activity of a unifacial cambium (Dennis 1974; Phillips and Galtier 2005). A conspicuous periderm is also present in the stems, petiole bases (fig. 7*C*, 7*D*), and roots of this genus (Scott 1912; Phillips and Galtier 2005). *Zygopteris* was a small plant with a partly buried rhizome bearing erect fronds. It was adapted to water-stressed, high light intensity environments, and it has been suggested that its development of secondary vascular tissues was linked to water transport (Phillips and Galtier 2005). In the Late Devonian Rhacophytales, another group of early ferns (sensu Phillips and Galtier 2005), secondary xylem up to about 1 mm in thickness was reported in *Rhacophyton ceratangium* (Dittrich et al. 1983), but there is no evidence of a periderm.

Lignophytes. The aneurophytalean progymnosperms are to date the oldest group in which the presence of a periderm is well documented, with good examples in Frasnian (Late Devonian) specimens of *Proteokalon*, *Triloboxylon* (fig. 7*E*), and *Tetraxylopteris* (Beck 1957; Scheckler and Banks 1971; Stein and Beck 1983). Scheckler and Banks (1974) suggested that the periderm of *Triloboxylon* had a structure comparable to that of extant seed plants, with distinct phellogen, phellem, and phelloderm. This has, however, been disputed by Stein and Beck (1983), who interpreted the periderm of this taxon as extensive but without distinct layers. A biomechanical analysis of *Tetraxylopteris* (Rowe et al. 1993) indicates that secondary growth (vascular and cortical) in this taxon did not provide increased support and did not lead to a self-supporting growth form, a situation that can be compared to that of *C. taeniatum*.

Archaeopteridalean progymnosperms were the first large woody trees, producing trunks of up to at least 1 m in diameter (e.g., Arnold 1930). While secondary phloem is well preserved in a few specimens (Arnold 1930; Decombeix and Meyer-Berthaud 2013), no evidence of a periderm has been observed to date, even in axes with several centimeters of wood. This suggests that if a periderm was present, it did not originate deep in the secondary phloem. The extraxylary tissues of the protopityalean progymnosperms, a Mississippian group that also includes large trees up to 1 m in diameter, are not well known (Decombeix et al. 2015 and references therein).

Among early seed plants of Late Devonian age, there is no evidence of periderm development in *Elkinsia* (Serbet and Rothwell 1992) or *Laceya* (May and Matten 1983). These two genera, however, have a small amount of secondary vascular growth (<1 mm). It is only in the Mississippian that periderm production is documented in seed plants, with the oldest examples dating from the Tournaisian. Some specimens show evidence of a single periderm layer; in others, successive periderm layers form the oldest known rhytidomes (fig. 7*F*; Galtier and Scott 1991; Decombeix 2013; Decombeix et al. 2014). Some groups like the Calamopityales had limited secondary growth and apparently did not produce a periderm (Hotton and Stein 1994; Masselter et al. 2009). A periderm is documented in several younger groups of Carboniferous seed plants, including the Medullosales, Lyginopteridales, Callistophytales, and Cordaitales (fig. 7*G*, 7*H*; Taylor et al. 2009).

Conclusions

1. We report and illustrate the production of periderm in early Mississippian axes of *Cladoxylon taeniatum*, the only cladoxylopsid in which this tissue has been documented to date.

2. The presence of secondary vascular growth and periderm combined with a non-self-supporting habit adds to the diversity of anatomies and growth strategies encountered in a group that is mostly known for its arborescent Devonian representatives.

3. Periderm has been described in many taxa of vascular plants in the Devonian and Carboniferous, but anatomical homologies remain unclear, and the number of evolutionary origins of the periderm remains unknown.

4. Although there are shared regulatory components between the cambium and phellogen of extant seed plants, secondary vascular growth and periderm development are not always correlated. Devonian–Carboniferous taxa that produced a periderm typically also had the ability to produce secondary vascular tissues, but the opposite does not appear to be always true.

5. Periderm development in fossil plants, like secondary vascular growth, likely did not evolve initially in relation to mechanical support.

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