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Lyginopteris royalii sp. nov. from the Upper Mississippian of North America

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Abstract

A new species of the seed fern *Lyginopteris* is described from a nodule in Upper Mississippian (middle Chesterian-Namurian A) shales of the Fayetteville Formation in northwestern Arkansas. The pyritized stem is 29 cm long and slightly compressed, with a diameter of about 11 × 5 mm, and shows seven diverging leaf bases. The primary xylem of the specimen is eustelic. Foliar bundles extend through five internodes before entering the rachis bases; they do not divide along their trajectory through the stem. Phyllotaxis of the specimen approaches 2/5. Longitudinally oriented sclerenchyma strands accompany the diverging foliar vascular bundles adaxially in the cortex, and are incorporated in the outer cortex above the level of foliar rachis divergence. In contrast to previously described *Lyginopteris* species, this species lacks capitate epidermal glands. A *Lyginopteris* type rachis with a paired vascular bundle is preserved in the same nodule. Coprolites probably produced by oribatid mites are present in different tissues of the stem. The study of the leaf trace divergence necessitated the use of a deformation model to help reconstruct the original position of the cauline bundles in the compressed stele. This occurrence of *Lyginopteris* confirms earlier reports of the genus from North America and emphasizes that it was not restricted to Western Europe.

Keywords: deformation; *Lyginopteris*; Mississippian; North America; pteridosperm

1. Introduction

The genus *Lyginopteris* is well known from the Carboniferous coal-ball floras of Europe, where its stratigraphic range covers the Visean V3 (middle) — Westphalian A interval (Galtier, 1997), roughly centered on the Mississippian–Pennsylvanian boundary. *Lyginopteris* played an important role in both the development of whole-plant reconstructions and the definition of the pteridosperm concept (Stewart and Rothwell, 1993). This was accomplished by inferring organic connection between stems of *Lyginopteris oldhamia* and *Lagenostoma lomaxi* cupulate ovules based on the similarity of the epidermal capitate glands borne by both form genera (now morphogenera). On the basis of this connection Oliver and Scott (1904) initiated whole-plant reconstructions of coal-ball plants and described the pteridosperms as a group of extinct seed plants.

Although wide spread in the Carboniferous deposits of Europe, *Lyginopteris* had no reported fossil record in North America until 1991. Its potential presence was nevertheless presumed, based on the finds of form genera assigned to lyginopterids. Pfefferkorn and Gillespie (1982) reported foliage that they assigned to *Lyginopteris hoeninghausi*, *L.*

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fragilis and *L. bermudensiformis* from the Bluestone (Namurian A), Pocahontas and New River Formations (Namurian B) of West Virginia and Virginia. The three species refer exclusively to compressed foliar remains; however, the genus *Lyginopteris* defines either anatomically preserved stems (with or without leaves) or the whole plant, whereas compression–impression foliage fossils like those produced by *Lyginopteris* conform to the form genus *Sphenopteris* (e.g. *Sphenopteris hoeninghausi*). Microsporangia assigned to *Crossotheca* and *Feraxotheca*, that also may have been produced by *Lyginopteris*, were described from the Middle Pennsylvanian Mazon Creek coal-ball flora of Illinois (Arnold and Steidtmann, 1937) and from the lower Middle Pennsylvanian Lewis Creek coal-ball flora of Kentucky (Millay and Taylor, 1977), respectively. The Upper Mississippian Fayetteville Formation of Arkansas, the same formation that yielded the specimen described in this paper, produced lagenostomalean cupulate ovules (Taylor and Eggert, 1967a), frond rachises assigned to *Lyginorachis* (personal observation, G.M.), and the pollen organ of lyginopterid affinities, *Telangiopsis* (Eggert and Taylor, 1971). Read and Campbell (1939) gave a very short description of a new *Lyginorachis* species from the Lower Mississippian New Albany Shale of Indiana and Kentucky. Putative pteridosperm axes exhibiting a surface *Dictyoxylon*-type network pattern characteristic of *Lyginopteris*, are reported by Lacey and Eggert (1964) from the Chester Series of southern Illinois.

The first reported occurrence of anatomically preserved *Lyginopteris* in North America was in coal-balls from Alabama (Winston and Phillips, 1991). The age of those deposits is uncertain, being interpreted as Namurian C-Westphalian A based on the micro and macroflora. That brief description of the *Lyginopteris* specimens mentions paired leaf traces. *Lagenostoma* ovules and lyginopterid foliage bearing capitate glands were also reported at the locality, but those specimens were not described.

There is at least one early citation of a possible *Lyginodendron* stem in a floral list from the Stephanian coal-ball floras of Illinois (Noé, 1924). However, there is no further documentation of that specimen. Until the description of the Alabama coal-ball flora by Winston and Phillips (1991), no North American coal-ball flora was known to be older than the Westphalian A/B boundary, which is younger than the known range of all *Lyginopteris* species.

The flora of the Fayetteville Formation of Arkansas represents one of the most diverse anatomically preserved Mississippian assemblages worldwide. In an early study, White (1937) described a fossil flora of casts and impressions from the Wedington Sandstone, a member of the Fayetteville Formation representing deltaic deposits. Eggert and Taylor (1971) described the genus *Telangiopsis* from a shale sequence within the Wedington Sandstone. The first record of plant fossils from the dark shales that form most of the Fayetteville Formation was given by Mapes (1966), who describes a lycopsid branching system. Taylor and Eggert (1967a) provided the first account on the diversity of the flora in the shales. In two following papers (Taylor and Eggert, 1967b, 1968) they described a pteridosperm ovule and a lycopsid cone. Mapes and Schabilion (1976) also reported pteridosperm ovules and lepidodendralean remains. More recently, Serlin et al. (1979) described a calamite axis. Mapes and Rothwell (1980) and Mapes (1985) described pteridosperm stems.

Summarizing these finds, aside from the flora of the Wedington Sandstone, plants attributed to four groups are known to date from the Fayetteville Formation: lycopsids, ferns, calamitales and seed ferns. The ferns include *Etapteris* and *Ankyropteris*. The lycopsid remains are assignable to *Lepidodendron*/*Lepidophloios*, *Lepidocarpon* and *Lepidostrobus*. Calamitales are represented by *Archaeocalamites*/*Calamites*. The pteridosperms are the most diverse group, including *Heterangium*, *Rhetinangium*, *Megaloxylon*, *Myeloxylon*, *Medullosa*, *Quaestora*, *Lyginorachis*, as well as *Pachytesta*, *Rhynchosperma* and lagenostomalean cupulate ovules.

In the current study we describe a new species of *Lyginopteris* from the Fayetteville Formation.

2. Occurrence, material and methods

The *Lyginopteris royalii* specimen is preserved in a nodule (M1664) collected on the bank of White River, northeast of the community of Durham, Washington County, Arkansas (see locality M-26 of Mapes, 1979). The nodule was collected from the unnamed lower

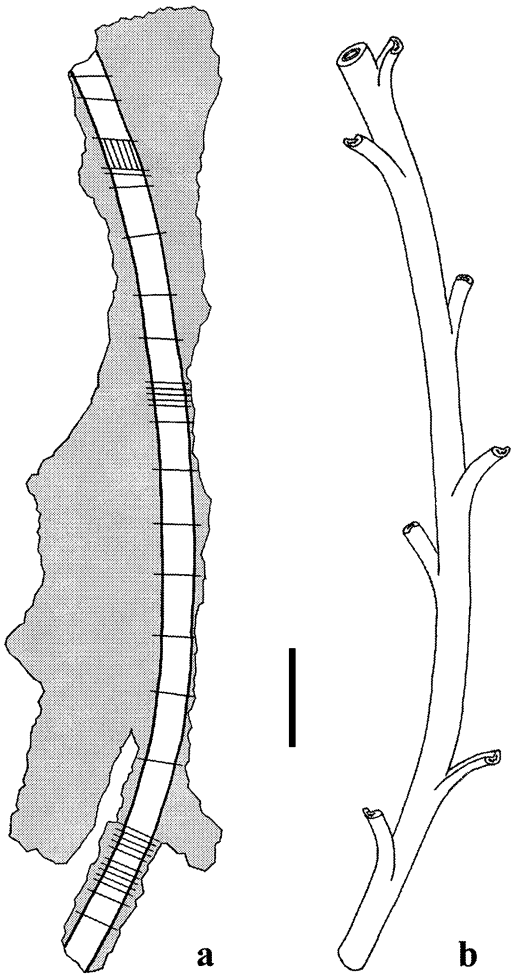


Fig. 1. (a) Diagram of nodule M1664 showing the position of the *Lyginopteris royalii* stem and of the sections cut for studying it; (b) Reconstruction of the *Lyginopteris royalii* stem showing positions of frond divergences; bar = 3 cm.

shale member of the Fayetteville Formation, which is middle Chesterian in age (equivalent to the E_1 or Pendleian stage of the Namurian A in Western Europe — Saunders, 1973). At Durham, Arkansas the lower shale member is a black, pyritic, organic-rich shale that represents an outer shelf marine deposit (Hanford and Manger, 1993).

The lower shale member has yielded numerous concretions (Zangerl et al., 1969). One of the concretion types mentioned but not described by those authors is phosphate with lesser amounts of pyrite. According to R. Mapes (personal communication, 2000) such concretions sometimes contain plant fossils and commonly contain vertebrate debris, invertebrate shells (especially ammonoid cephalopods) and coprolites as nuclei. The ammonoids, which serve as the main basis for dating the strata, dominate the invertebrate fauna in the shale and in the phosphate concretions. The fossiliferous concretions sometimes occur as isolated individuals, although most are recovered within distinct concentration zones in the shale, where they show no preferential orientation. The plant-bearing phosphate concretions are usually elongated revealing approximately the shapes of the plant material included.

Most of the sediment comprising the Fayetteville Formation was probably produced by erosion of highlands to the north of the Durham region, now known as the Ozark Plateau (Hanford and Manger, 1993). Sediment was transported to the marine environment by rivers that drained the highlands. The plant remains were probably transported from the terrestrial sources by the same rivers that transported the sediment. This hypothesis is supported by the presence of fossil plant-bearing delta deposits that occur at a slightly higher stratigraphic level in the Fayetteville Formation. That deltaic unit, called the Wedington Sandstone, is located in eastern Oklahoma and northwest of Arkansas (including the Durham area). The plant materials recovered at the White River locality were transported from the terrestrial habitat to the marine environment, where they sank to the bottom when sufficiently waterlogged and were rapidly buried in the marine mud. The presence of foliar remains in the concretions suggests that the plant material did not undergo long-distance transport from the terrestrial source area because mechanical and biological degradation normally rapidly separates these plant organs into disarticulated elements and destroys them.

The nodule that preserves the *Lyginopteris* stem is 35 cm long, 2–5 cm wide and 1–2 cm thick. It consists mainly of pyrite, but phosphate and calcite also are present. Along with the *Lyginopteris* stem, the nodule (Fig. 1a) contains one *Lyginopteris*-type rachis (Plate I, 4) not connected to the stem, two *Megaloxylon* stems, at least two rachises assignable to *Megaloxylon*, and a fern stipe of *Senftenbergia* or *Ankyropteris*.

The nodule was cut in slabs (Fig. 1a) and acetate peels were made from smoothed surfaces etched with

either hydrochloric or nitric acid, but the peels were unsatisfactory for detailed study. Nitric acid etching dissolves the coalified plant material faster than the surrounding pyrite, forming a negative of the plant anatomy as represented by the cell walls. The best results were obtained by etching cut polished surfaces with concentrated nitric acid for 35 s, gluing a coverslip to the rock surface with mounting medium and viewing specimens under reflected light. A few serial wafers were also prepared using a Buehler Isomet slow speed saw, to reveal features that change rapidly from level to level, such as the leaf trace divergences. Before etching, all section surfaces were smoothed by grinding with 600 grit Carborundum. Slabs used for serial wafers were embedded in plastic prior to cutting.

Terminology used to describe the specimen follows that of Blanc-Louvel (1966). The cambium, phloem, inner cortex and periderm of the stem are not preserved anatomically. However, a distinct zone lacking cellular preservation is present between the secondary xylem and the middle cortex. This zone represents the several missing layers of the stem interior including cambium, phloem, inner cortex and periderm. For the purposes of this paper it is named the cambio-phloic layer. The outer limit of this layer is well defined by a deep furrow left by nitric acid etching, probably corresponding to the periderm. The stem is somewhat compressed. Therefore a deformation model was developed to account for the position of the different tissues preserved in the specimen and to help in reconstructions, particularly of the primary xylem architecture. All of the studied slabs and sections of the nodule are reposited in the Ohio University Paleobotanical Herbarium as nos. 13717–13754.

3. Systematics

Class SPERMATOPSIDA
Family LYGINOPTERIDACEAE

Genus ***Lyginopteris*** Potonié, 1899.

Lyginopteris royalii Tomescu et al., sp. nov.

Holotype: Stem in nodule M1664, slabs and slides nos. 13717–13754; Plate I (1– 3); Plates II, III.
Repository: Ohio University Paleobotanical Herbarium, Athens, Ohio, U.S.A.
Type locality: Exposures in the bed and on the banks of White River, approximately 0.3 km NE of Durham, Washington County, Arkansas, U.S.A. (SW $\frac{1}{4}$, sec. 20, T.15 N., R.28 W. and NW $\frac{1}{4}$, sec. 29, T.15 N., R.28 W., Durham $7\frac{1}{2}$' quadrangle).
Stratigraphic horizon: Lower unnamed shale member of the Fayetteville Formation, Hombergian Stage, Chesterian Series.
Age: Late Mississippian–middle Chesterian (= E_1 or Pendleian stage of the Namurian A in Western Europe).
Etymology: The specific epithet is proposed in recognition of the many contributions to the knowledge of the Fayetteville Formation flora by Royal H. Mapes, Department of Geological Sciences, Ohio University.
Diagnosis: Characters of species same as those of genus *Lyginopteris* sensu Blanc-Louvel (1966). Diameter of stem small: 10–11 mm. Primary xylem architecture eustelic. Foliar bundles extend through

PLATE I

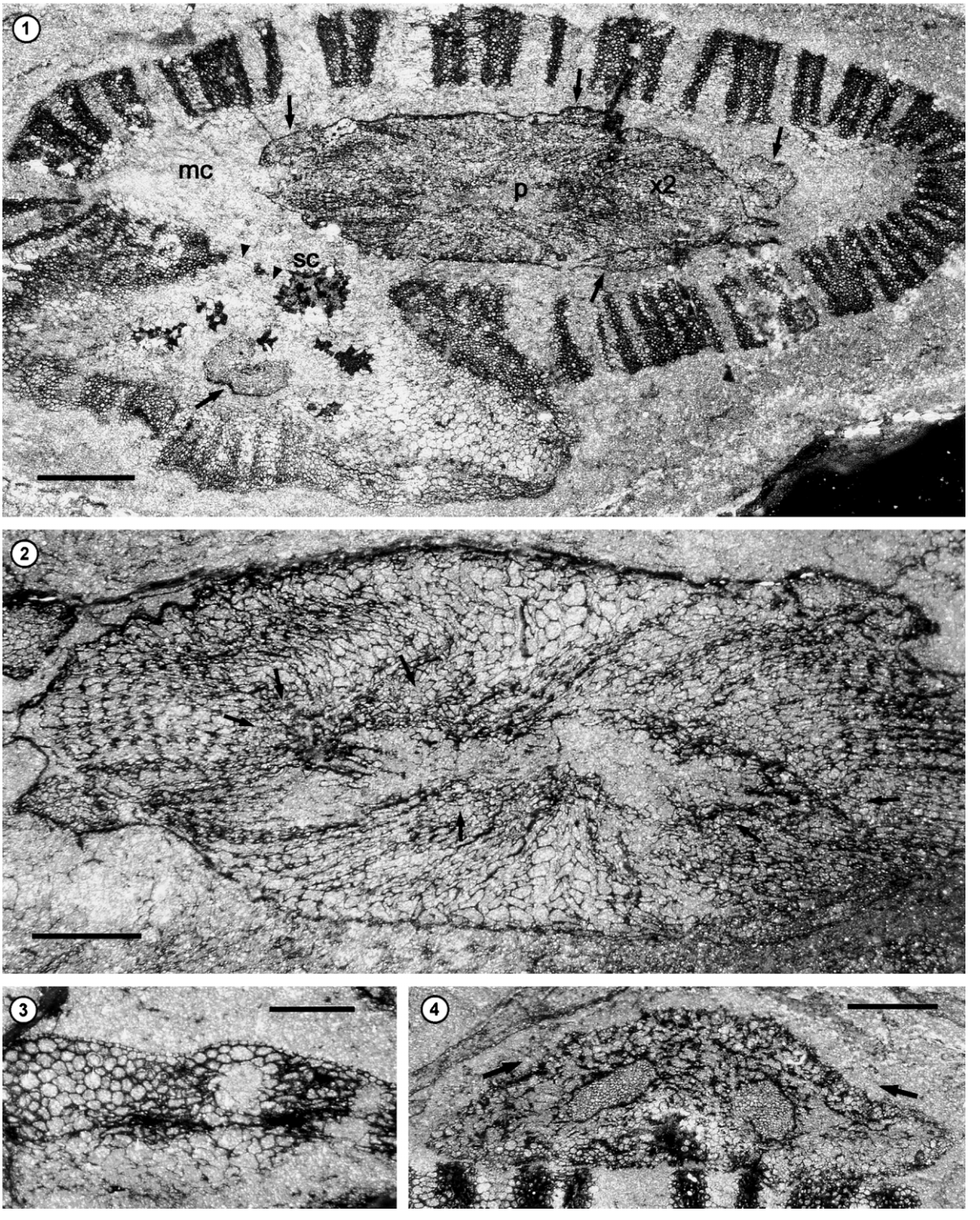
Lyginopteris royalii.

1. Transverse section of stem at level of frond divergence. Four foliar bundles (arrows) are diverging from the secondary xylem (x2); a fifth one has entered a frond base and the accompanying sclerenchyma bundle (sc) is connected to the outer cortex by tangentially elongated parenchyma cells (at arrow points); several smaller sclerenchyma nests accompany the foliar bundle in the frond base; mc, middle cortex; p, pith; bar = 1 cm. OUPH no. 13717.
2. Transverse section of the compressed secondary xylem cylinder showing deformation pattern. Three diverging foliar bundles (lower left, upper and lower right) are in the cambio-phloic layer and the fourth (upper left) is in the middle cortex. Distorted and inconspicuous primary bundles (arrows) line the periphery of the pith; bar = 0.5 mm. OUPH no. 13718.
3. Detail of the outer cortex of a frond base showing the epidermis in transverse section; bar = 0.25 mm. OUPH no. 13719.

Lyginopteris-type rachis.

4. Transverse section showing the double vascular bundle, the cortex containing sclerenchyma, and a pyrite halo (above specimen, between arrows) lined with very fine dark, coaly debris that could represent the remnants of the epidermis; bar = 0.5 mm. OUPH no. 13720.

PLATE I



five internodes before entering the rachis bases; foliar bundles do not divide along their trajectory through the stem. Longitudinally oriented sclerenchyma strand accompanies the diverging foliar vascular bundle adaxially in the cortex and is incorporated in the outer cortex above the level of divergence of the foliar rachis. Capitate glands absent.

4. Description

4.1. General features

Lyginopteris royalii is represented by a single anatomically preserved specimen 29 cm long. The stem is slightly curved (Fig. 1a) and moderately compressed so that the cross sections vary from oval to flattened (Plate I, 1), and are approx. 11×5 mm in diameter. Deformation models suggest that deformation in a longitudinal plane perpendicular to the direction of the main stress is minimal (below 10% of the original diameter - Niklas, 1978), therefore the initial diameter is estimated to have been 10–11 mm. Rachis bases are thick; seven diverge at intervals ranging 2–5.5 cm (Fig. 1b).

Internally, the stem has a eustele of five sympodia that line the periphery of the parenchymatous pith and reflect the 2/5 phyllotaxis. The secondary xylem is manoxylic. Cambium, phloem, inner cortex and periderm are crushed together and incompletely preserved. The specimen has thick middle and outer cortex and the epidermis is preserved on rachis bases. Sclerenchyma bundles accompany the diverging foliar vascular bundles adaxially.

Coprolites occur in agglomerations within several tissues of the stem: in the secondary xylem (Plate III, 6), the middle cortex and the parenchyma zones of the outer cortex. They are ovoid and their size ranges 112×134–164×216 μm (mean = 135.8×177.0 μm). The surface of the coprolites is relatively smooth and they consist of plant material, as reflected by their contents of cell walls. Phytophagy probably occurred after death of the plant, as no wound-response growth was observed in any of the tissues where coprolites were present. These characteristics place the coprolites in the category produced by the oribatid mites (of large size), as described by Labandeira et al. (1997).

4.2. Pith

Pith parenchyma is more compacted by compression than other stem tissues and the cells are incompletely preserved. Cell contours are sometimes partly marked by intercellular spaces represented by small voids in the sections. Rarely, individual secretory cells and sclereids or sclerenchyma nests occur in the pith. Complete pith parenchyma cells range 32×77–64×107 μm (mean = 44.0×90.4 μm) in cross section and 40×57–78×95 μm (mean = 54.0×74.8 μm) in longitudinal section.

4.3. Primary xylem

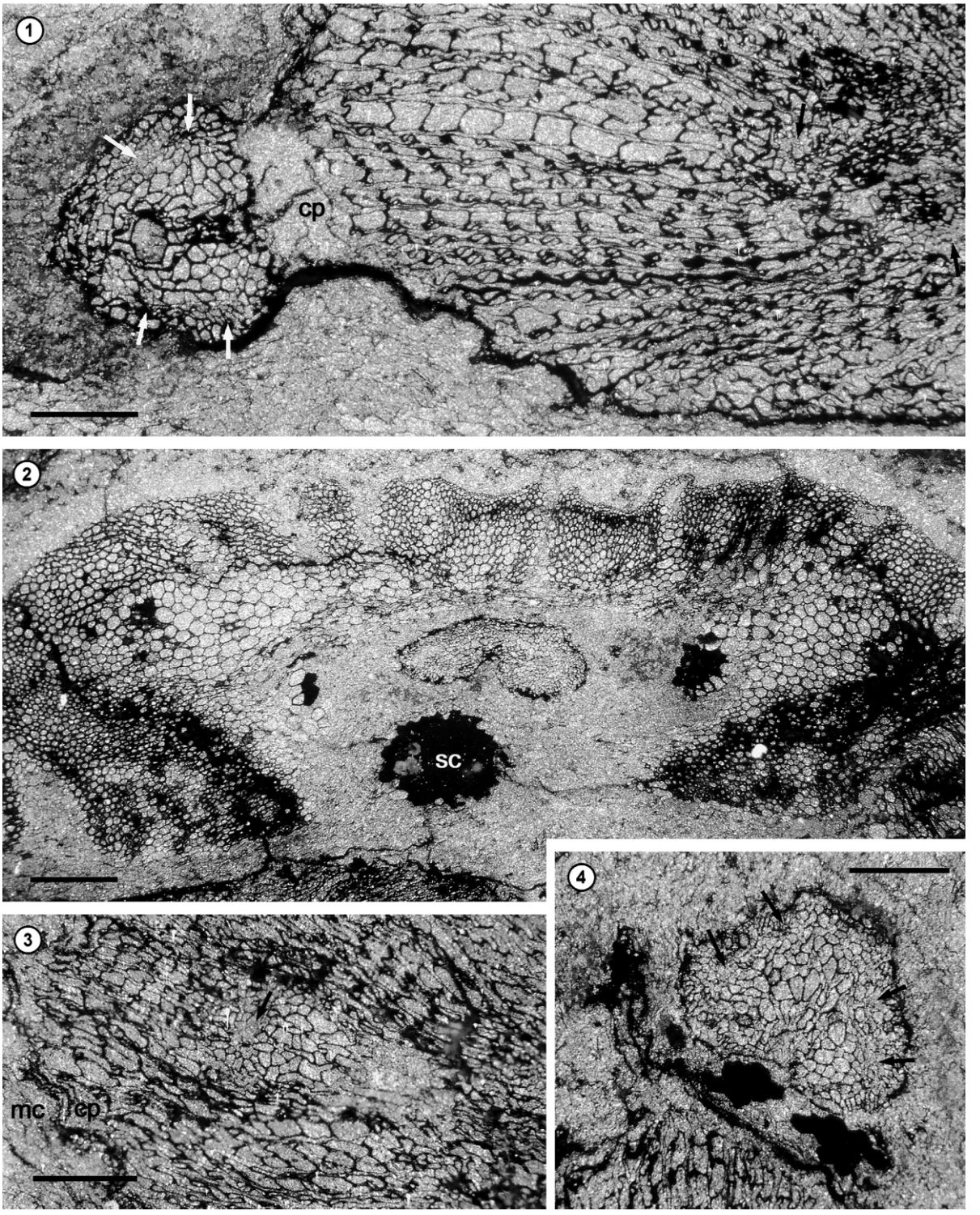
The primary xylem forms a eustele of five mesarch sympodia (cauline bundles) located at the margin of the pith, adjacent to the inner limit of the secondary xylem cylinder (Plate I, 2; Plate II, 1).

PLATE II

Lyginopteris royalii.

1. Transverse section of the stem showing two primary bundles (black arrows at right) and secondary xylem. The cambio-phloic layer (cp) is thickened between the secondary xylem and a diverging foliar bundle but lacks cellular preservation. The mesarch foliar bundle bearing four protoxylem strands (white arrows) is compressed laterally forming a false lacuna that contains cambio-phloic tissue; accompanying sclerenchyma is present between the two lobes of the compressed bundle; bar = 0.25 mm. OUPH no. 13721.
2. Transverse section of a frond base showing the vascular bundle and accompanying sclerenchyma. The main sclerenchyma bundle (sc) remains at the level of the outer cortex; bar = 0.5 mm. OUPH no. 13722.
3. Transverse section of the stem showing a mesarch foliar bundle in the secondary xylem. Centripetal metaxylem is more developed than centrifugal metaxylem. Note protoxylem parenchyma (arrow); cp, cambio-phloic layer; mc, middle cortex; bar = 0.25 mm. OUPH no. 13723.
4. Transverse section of the stem showing a foliar bundle in the middle cortex. The bundle is compressed laterally and contains four protoxylem strands (arrows) represented by protoxylem parenchyma. It is accompanied by an adaxial double sclerenchyma bundle. Below the bundle the cambio-phloic layer, lacking cellular preservation, lines the outer margin of the secondary xylem; bar = 0.25 mm. OUPH no. 13724.

PLATE II



Due to compression, the original shape of the primary xylem bundles is difficult to assess. Reconstruction of their original positions required development of a deformation model (see Section 5).

Each mesarch sympodium displays one protoxylem strand; the strands are not always obvious in the highly distorted primary xylem bundles. Protoxylem is represented by a protoxylem parenchyma strand; individual protoxylem tracheids are hard to identify. The diameter of the protoxylem cells varies 13–31 μm (mean = 19.1 μm), whereas the metaxylem elements range in diameter 21 × 32–55 × 71 μm (mean = 36.7 × 49.8 μm). Well preserved foliar bundles show centripetal metaxylem more developed than centrifugal metaxylem (Plate II, 3). Metaxylem tracheids have scalariform thickening patterns (Plate III, 2).

4.4. Secondary xylem

The secondary xylem cylinder (Plate I, 2) is about 1.5 mm thick, measured on a direction perpendicular to the stress that compressed the stem (where elongation would be smaller than 3.5% of the original diameter for a hollow cylinder- Niklas, 1978). The secondary xylem is manoxylic, comprising radial files of tracheids, mostly single or grouped by 2, separated by parenchyma rays 1–5 (but most usually 1–2) cells wide (Plate II, 1) and very high (usually over 30 cells high). The tracheids have multiseriate pits on their radial walls (Plate III, 4) and their diameter varies between 32 × 66 and 85 × 135 μm (mean = 53.9 × 98.6 μm). Ray parenchyma cells are typically 32–50 μm high (mean = 39.7 μm).

4.5. Cambio-phloic layer

The cambio-phloic layer is highly compressed in most cases. Its thickness is very variable. This layer can be observed best around leaf traces where the foliar bundle is just outside of the secondary xylem (Plate I, 4; Plate II, 1, 3, 4). Except for pits corresponding to sclerenchyma cells (Plate III, 7) and for extremely rarely preserved cell walls, cellular preservation is minimal.

4.6. Middle cortex

The thin-walled parenchyma of the middle cortex is generally incompletely preserved, except in the region near the outer cortex limit (Plate II, 1, 2; Plate III, 7). The size of individual cells varies 48 × 90–119 × 216 μm (mean = 81.1 × 126.3 μm) in cross section and between 39 × 55–82 × 99 μm (mean = 63.1 × 80.2 μm) in longitudinal section. A few solitary secretory cells and sclereids are scattered in the middle cortex. The secretory cells range 30 × 30–67 × 97 μm (mean = 45.7 × 60.0 μm) in cross section.

4.7. Outer cortex

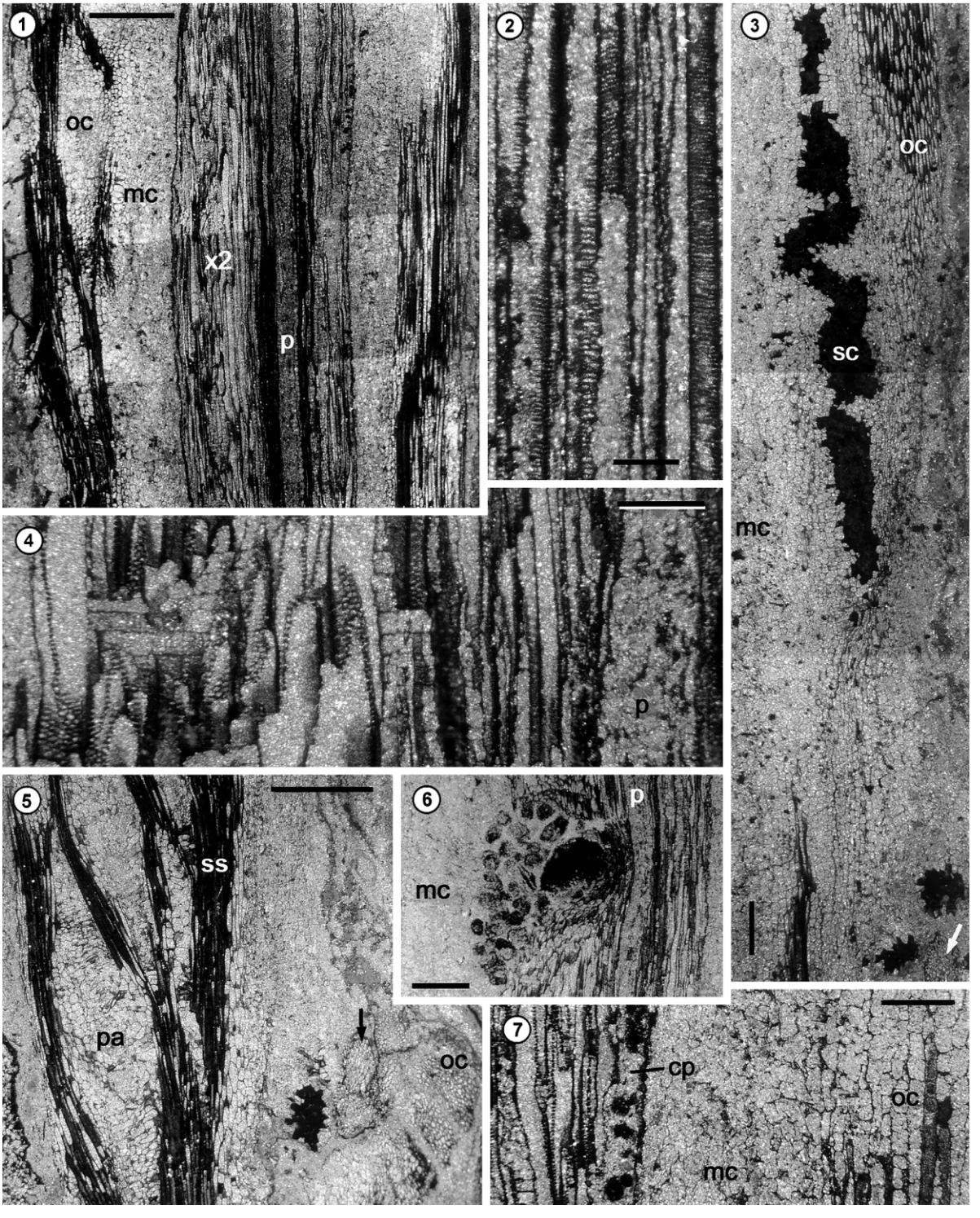
The outer cortex displays the *Dictyoxylon* structure characteristic of *Lyginopteris* (Plate I, 1; Plate III, 5). Fibers forming the radially broadened anastomosing strands have diameters of 43–71 μm (mean = 56.5 μm).

Plate III

Lyginopteris royalii.

1. Radial section of the stem showing the general structure; mc, middle cortex; oc, outer cortex; p, pith; x2, secondary xylem; bar = 1 mm. OUPH no. 13725.
2. Longitudinal section of the primary xylem showing tracheids with scalariform secondary wall thickenings; bar = 25 μm. OUPH no. 13726.
3. Radial section of the stem showing the relationship between the outer cortex (oc) and a sclerenchyma bundle (sc) accompanying a diverging foliar bundle (arrow). The sclerenchyma bundle (cut slightly obliquely) follows the outer cortex of the stem above the petiole base and tapers as the cortex closes above the petiole base. Smaller sclerenchyma bundles accompany the foliar vascular bundle in the petiole base; mc, middle cortex; bar = 0.5 mm. OUPH no. 13727.
4. Radial section showing pith (p), secondary xylem with multiseriate alternate pits of tracheids, and rays; bar = 0.15 mm. OUPH no. 13725.
5. Tangential section of the stem showing the sclerenchyma strands (ss) and parenchyma (pa) of the *Dictyoxylon* cortex. A diverging frond base cut obliquely shows the vascular bundle (arrow), accompanying sclerenchyma and outer cortex (oc) with little differentiation of sclerenchyma bands; bar = 1 mm. OUPH no. 13728.
6. Radial section showing mite coprolites present in the secondary xylem; mc, middle cortex; p, pith; bar = 0.5 mm. OUPH no. 13725.
7. Radial section showing outermost tracheids of the secondary xylem (at left), cambio-phloic layer (cp) with sclerenchyma cells, middle cortex (mc), and outer cortex (oc); bar = .2 mm. OUPH no. 13725.

PLATE III



The voids of this anastomosed network are filled with parenchyma more or less elongated in a tangential direction. The longest reach 187 to 341 μm (mean = 253.9 μm) and their diameter varies 36 × 52–74 × 110 μm (mean = 54.4 × 82.6 μm). The outer cortex of rachis bases does not exhibit the same pattern. Here there is very little differentiation of fibers and parenchyma cells are not elongated (Plate I, 3; Plate II, 2).

4.8. Epidermis

In this specimen the epidermis is preserved incompletely, appearing only on rachis bases (Plate I, 3). Individual epidermal cells are very small, measuring 7–29 μm (mean = 18.4 μm) radially and 15–31 μm (mean = 22.7 μm) tangentially in cross sections. Epidermal capitate glands that are so characteristic in other species of *Lyginopteris*, are absent from this specimen, even in the zones where the epidermis is well preserved.

4.9. Foliar bundle architecture and sclerenchyma bundles

Foliar vascular bundles are produced by tangential division of the cauline primary bundles. They diverge from the stele at a very low angle, following a slightly dextrorse coiling pattern upward, and extend through five internodes before entering a rachis base. Each diverging bundle displays one protoxylem strand (Plate II, 3). Where the bundle reaches the cambio-phloic layer, it is bilobed in cross sections, and the protoxylem strand has divided to form four strands (Plate II, 1, 4). As in the cauline bundles, protoxylem strands are represented by protoxylem parenchyma and protoxylem tracheids are hard to identify. Almost no secondary xylem accompanies the foliar bundles. The bundles do not divide along their trajectory through the stem, though they acquire a butterfly shape with four protoxylem strands in the rachis bases (Plate I, 1). The diameter of the tracheids in the foliar bundles ranges 244.8.37–844.8.88 μm (mean = 40.8 × 56.4 μm).

A small number of sclerenchyma cells is present adaxial to the foliar bundle in the cambio-phloic layer (Plate II, 1). Distally, the sclerenchyma forms an increasingly thick bundle accompanying the foliar bundle. The sclerenchyma bundle can be simple or double at initiation (Plate II, 4), though in the latter case the two bundles eventually fuse. Individual sclereids in the sclerenchyma bundles range 35 × 45–91 × 142 μm (mean = 60.1 × 77.3 μm) in cross section and 40 × 52–67 × 112 μm (mean = 53.1 × 73.5 μm) in longitudinal section. At the level where the vascular bundle enters the rachis base, the accompanying sclerotic bundle (Plate III, 3) continues upward contributing to the closing of the outer cortex of the stem above the rachis. In an acropetal series of transverse sections from the level where the sclerenchyma bundle has reached the tangent of the *Dictyoxylon* cortex (Plate I, 1; Plate II, 2), the gap in the outer cortex becomes progressively narrower, the diameter of the sclerenchyma bundle diminishes, and the two are progressively linked by tangentially elongated cortical parenchyma cells (Plate I, 1 at arrow points). More distally, the tangentially elongated cells intergrade with thicker-walled cells, until the gap is completely filled with fibers characteristic of *Dictyoxylon* cortex. In the rachis the vascular bundle is accompanied by one or more sclerotic nests (Plate I, 1; Plate II, 2; Plate III, 3, 5).

4.10. Lyginopteris-type rachis

The unattached rachis occurring in the same nodule as the *Lyginopteris* specimen has an obtuse triangular to semicircular shape in cross section and contains two flattened vascular bundles. The bundles delimit the two branches of a V (Plate I, 4) and are exclusively primary xylem. Each of the bundles contains five protoxylem strands, also represented by very narrow, thin walled cells interpreted as protoxylem parenchyma. The metaxylem tracheids have diameters of 16 × 26–30 × 39 μm (mean = 22.1 × 32.0 μm). The cortex contains parenchyma cells of different sizes, unevenly preserved, and scattered sclerenchyma cells. The distribution of these cell types is not consistent with a clear zonation of the cortex. The epidermis of the specimen is not preserved. However, the outermost layer of cells of the rachis is surrounded by a pyrite halo (Plate I, 5 above specimen, between arrows) that is lined with very fine dark, coaly debris; this lining, present at several places around the rachis, could represent the actual outer margin of the epidermis.

5. Discussion

Lyginopteris royalii is characterized by eustelic architecture of the primary xylem. The pith and middle cortex contain very rare secretory or sclerenchyma cells. The protoxylem strand of each bundle divides twice, forming four protoxylem strands per bundle, with no further divisions of the bundles before entering the rachis bases. The foliar bundles are accompanied in the cortex by adaxial sclerenchyma bundles made of more or less isodiametric sclereids.

The other eustelic species of *Lyginopteris* are *L. oldhamia*, *L. heterangioides*, *L. lacunosa* and *L. austriaca*. Of these, *L. royalii* most resembles *L. heterangioides* and *L. lacunosa* in having simple, undivided, foliar vascular bundles. However, species boundaries are not clear. Bertram (1989) considers *L. austriaca* dictyostelic based on the tangentially flattened stelar xylem groups of the stele, whereas Blanc-Louvel (1966) describes cauline bundles of a eustele in this species as anastomosing. Blanc-Louvel also considers the three species *L. heterangioides*, *L. lacunosa* and *L. austriaca* to represent different types of branches of *L. oldhamia*.

In *L. oldhamia* and *L. austriaca* each foliar bundle divides once in the cortex. By contrast, *L. heterangioides* and *L. lacunosa* have simple foliar bundles. *L. heterangioides* differs from *L. lacunosa* by having groups of metaxylem tracheids in the pith (Kubart, 1913). Bertram (1989) describes these same cells as metaxylem elements with their thickening pattern not preserved. Blanc-Louvel (1966), failing to obtain any diagnostic longitudinal section of these cells, questions their identity as metaxylem tracheids, and therefore the only difference between the two species, stressing that they also may represent simple sclerenchyma cells forming sclerotic nests.

If *L. heterangioides* and *L. lacunosa* represent distinct species, then *L. royalii* is closest to *L. lacunosa* by having only rare, solitary sclerenchyma cells in the pith. However it differs from *L. lacunosa* in two important features: *L. royalii* has sclerenchyma bundles that accompany the foliar bundles adaxially and it lacks the epidermal capitate glands.

None of the descriptions of *Lyginopteris* species mentions the presence of sclerenchyma bundles similar to those that characterize *L. royalii*. The only mention of sclerenchyma related to the foliar vascular bundles is that by Williamson and Scott (1895, p. 726 and photograph 4), who describe sclerotic masses that develop below the axils as characteristic transverse hypodermal bands in *L. oldhamia*, cautioning that these may be mistaken for axillary buds. However, the sclerotic masses are horizontally elongated (transversal), whereas those that characterize *L. royalii* are vertically elongated (longitudinal). Some other *Lyginopteris* species show frequent sclerenchyma cells and sclerotic nests. A few of the specimens figured by Blanc-Louvel (1966) attributed to different species (*L. oldhamia*, planche 76; *L. lacunosum*, planche 140, 3; *L. austriaca*, planche 145, 1), show distinct sclerotic nests adaxial to the foliar bundles. However, those nests are sporadically produced and have not been demonstrated to represent cross sections of longitudinally extended bundles of sclerenchyma cells. Another diagnostic character of *L. royalii* is the unique way of closure of the outer cortex above the node. The sclerotic bundle that accompanies the foliar bundle between the divergence from the stele and the entrance into the rachis, does not enter the rachis, but rather extends distally in the outer cortex and helps closing the gap above the node. This character is not known to occur in any other species of *Lyginopteris* or in closely related lyginopterid seed ferns.

The epidermis is rarely mentioned in descriptions of *Lyginopteris*, except for the very characteristic capitate glands. This is due to the fact that it is not always preserved. Williamson (1873) reports that he found nothing approaching a true epidermis after examining some hundreds of stems. As noted by several authors (Williamson and Scott, 1895; Bertram, 1989), the glands are not equally frequent in all specimens and they are not evenly distributed on a stem. This may be due to an uneven preservation of the epidermis, as pointed out by Williamson and Scott (1895), who consider that glands may became detached with the outer cortical layers. Capitate glands are reported in all known species of *Lyginopteris* where the epidermis is preserved. Epidermal glands could not be found in any of the studied sections of *L. royalii* and are absent from leaf bases where the epidermis is preserved. Hence our conclusion that the species *L. royalii* is deprived of epidermal capitate glands.

The genus *Lyginopteris* is considered to have included at least some species with liana or vine-like

architecture (Taylor and Millay, 1981; Galtier, 1988; Stewart and Rothwell, 1993). Features interpreted as characteristic to the liana or vine-like growth habit include: long internodes (high internode length/diameter ratio), slender stems (low stem section/frond surface area ratio), swollen bases and wide angle of attachment of rachises and adventitious roots borne on all sides of the stem. The biomechanical study of Speck (1994) provides (semi-) quantitative evidence that *Lyginopteris oldhamia* was a more or less liana-like semi-self-supporting plant. We suggest that the structure of the *Dictyoxylon* cortex of *Lyginopteris* represents another adaptation to the liana or vine-like condition. The network formed by the anastomosing sclerenchyma bands seems very fit to respond (by modification of the height and width of the network cells) to the stresses in torsion, compression or tension that may develop in the stem of such a plant, and to prevent the breaking of the cortex. The structure of the outer cortex also could prevent breakage of this layer by accommodating the increase in diameter of the stem due to secondary growth. On the other hand, the deformation of the cortex also may have hindered the persistence of an epidermis on the stems, except for the leaf bases and very young shoots.

In Blanc-Louvel's (1966) description of *Lyginopteris oldhamia*, the secondary xylem is surrounded by successive concentric layers: cambium, secondary phloem and primary phloem bundles, inner cortex, periderm (secondary cortex), middle cortex and the *Dictyoxylon* cortex (outer cortex). Bertram (1989) describes the same basic anatomy, but uses different terms in two instances. The layer called middle cortex by Blanc-Louvel is termed inner cortex by Bertram, and she describes Blanc-Louvel's inner cortex as a pericycle. The existence of a pericycle is characteristic only of roots and pteridophyte stems, so its description in *Lyginopteris* may reflect the earliest descriptions of the genus as a fern. As *Lyginopteris* is now known to be a seed fern (Oliver and Scott, 1904), we consider Blanc-Louvel's terminology more appropriate to the pteridospermous condition and use it in describing the specimen.

Observations made during the study of the phyllotaxis of *L. royalii* have drawn attention to deformation of the stem. The sympodia are sometimes flattened, and the position of their tracheids relative to each other is clearly disturbed. In cross sections some bundles seem stretched, whereas in other places two adjacent sympodia are extremely close to one another or almost fused. These observations combined with the assumption that the shape and position of the primary cauline bundles follow the deformations of the inner margin of the secondary xylem cylinder, suggest a model that accounts for the deformation of the stem and helps in reconstructing the original positions of the sympodia in the stele.

When a cylinder horizontally embedded in sediment is vertically compressed, there is very little deformation in a direction perpendicular to that of the main stress. This was suggested by Walton (1936) and demonstrated experimentally by Niklas (1978) and Rex and Chaloner (1983). Consequently, such deformation results in a reduction of the circumference of the secondary xylem cylinder. As shown by the position and shape of the cauline bundles, the reduction of the inner circumference is not distributed evenly. Reduction (shortening) alternates with elongation in successive regions of the circumference. Reduction (shortening) of the circumference occurs in the regions positioned close to the direction of the main stress and perpendicular to the main stress, whereas elongation occurs in the regions between those (Fig. 2a and b).

This particular pattern of deformation is most likely to occur if the radial files of tracheids in the secondary xylem function as more or less rigid plates. Under stress in compression these units would be tilted, tending to approach as close as possible a plane perpendicular to the direction of the main stress. This would lead to: (1) compression of the majority of tracheids; (2) sliding of the plates of tracheids against each other, by shearing of the numerous rays present in the manoxylic secondary xylem (Fig. 2b). As a result of this: (1) the inner edges of the plates of tracheids would be crushed together in the regions aligned with the main stress and in the areas located perpendicular to the main stress, with reduction (shortening) of the circumference in these regions. In addition, (2) the inner edges of the plates of tracheids oblique to the direction of the main stress would be pulled away from each other by the sliding of the plates (Fig. 2b), resulting in elongation of those regions of the circumference.

As emphasized by Mapes and Gastaldo (1986), non-swamp fossil plant assemblages are different

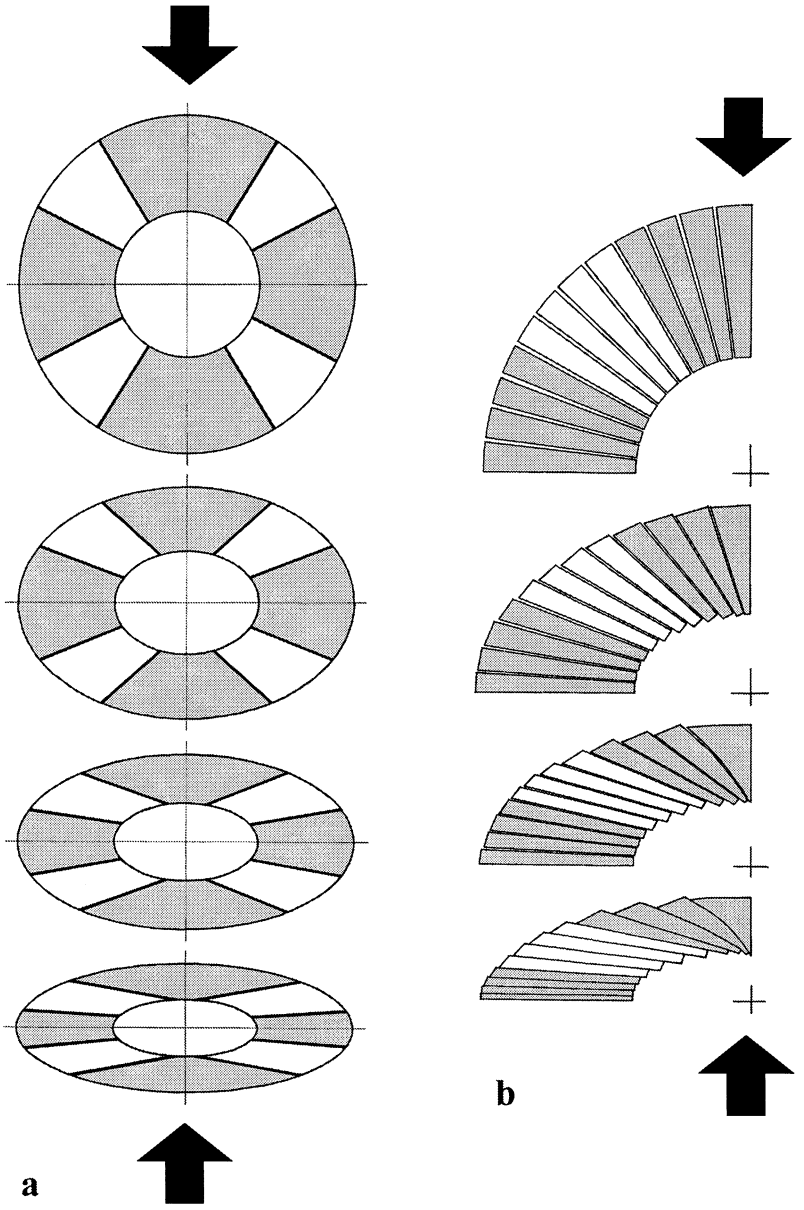


Fig. 2. Qualitative deformation model of the secondary xylem cylinder, used in reconstructing the primary xylem architecture of the *Lyginopteris royalii* stem. Successive deformation stages are shown on transverse sections for (a) the secondary xylem cylinder, where areas have been colored in white and gray to emphasize different deformation patterns of the inner circumference: elongation (white) and shortening (gray); (b) one quarter of the secondary xylem cylinder, where groups of radial rows of tracheids, separated by thin rays, are detailed to emphasize shearing along rays: areas are colored differently to show the same deformation patterns as in (a); arrows indicate direction of main stress.

from coal-swamp floras. By contrast to the latter, that are commonly deposited in situ and reflect exclusively swamp plant communities, the non-swamp assemblages usually consist of allochtonous plant remains and therefore may represent several ecologically distinct plant communities. Whereas most compression assemblages are paraautochtonous, in the sense that they are composed of bits of plant material drawn

from one plant community and deposited within that plant community, this permineralized assemblage from White River is thought to have been transported some distance from the source. In this respect, non-swamp assemblages can be very important in reconstructing the ecological diversity of the plant communities that inhabited the continental landscapes.

The Mississippian Period still forms a gap in our understanding of the land floras, as it did in 1967 when Taylor and Eggert gave a first report of the Fayetteville shale flora. This is due to the relative rarity of localities that preserved plant remains of Mississippian age, when compared to the well-known Pennsylvanian floras. The Upper Mississippian non-swamp assemblage of the Fayetteville Formation is thus important by both its age and its type (allochtonous). In addition, although its description is in an incipient stage, the Fayetteville shale flora represents one of the most diverse anatomically preserved Mississippian assemblages worldwide, and has already yielded several new species — *Lepidostrobus fayettevillense* (Taylor, Eggert, 1968), *Megaloxylon wheelerae* (Mapes, 1985) — and new genera — *Rhynchosperma* (Taylor and Eggert, 1967b), *Quaestora* (Mapes and Rothwell, 1980). The new *Lyginopteris* species reported here is the first to be described from North America and further supports the importance of the Fayetteville Formation flora. *Lyginopteris royalii* corroborates the earlier report of this genus in North America and extends the North American stratigraphic range of the genus to the Namurian A.

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References

Arnold, C.A., Steidtmann, W.E., 1937. Pteridospermous plants from the Pennsylvanian of Illinois and Missouri. American Journal of Botany 24, 644–650.

Bertram, U., 1989. Untersuchungen an Coal Balls aus dem Namur A von Ostrau unter spezieller Berücksichtigung der Gattungen *Heterangium*, *Lyginopteris* and *Microspermopteris*. Palaeontographica Abt. B 214 (5/6), 125–224.

Blanc-Louvel, C., 1966. Étude anatomique comparée des tiges et des pétioles d'une ptéridospermée du Carbonifère du genre *Lyginopteris* Potonié. Mémoires du Muséum National d'Histoire Naturelle, Nouvelle Série, Série C, Sciences de la Terre, Tome 18, Fascicule unique.

Eggert, D.A., Taylor, T.N., 1971. *Telangiopsis gen. nov.*, an Upper Mississippian pollen organ from Arkansas. Botanical Gazette 132 (1), 30–37.

Galtier, J., 1988. Morphology and phylogenetic relationships of Early Pteridosperms (3.). In: Beck, C.B. (Ed.), Origin and Evolution of Gymnosperms. Columbia University Press, New York, pp. 135–176.

Galtier, J., 1997. Coal-ball floras of the Namurian-Westphalian of Europe. Review of Palaeobotany and Palynology 95, 51–72.

Hanford, C.R., Manger, W.L., 1993. Sequence stratigraphy of a Mississippian carbonate ramp, north Arkansas and southwestern Missouri: a field guide prepared for the AAPG Annual Convention, New Orleans, April 25–28.

Kubart, B., 1913. Über die Cycadofilicineen *Heterangium* und *Lyginodendron* aus dem Ostrauer Kohlebecken. Verhandl. Gesellschaft dt. Naturforscher Ärzte 85. Versammlung zu Wien, Leipzig, pp. 653–654.

Labandeira, C.C., Phillips, T.L., Norton, R.A., 1997. Oribatid mites and the decomposition of plant tissues in Paleozoic coal-swamp forests. Palaios 12, 319–353.

Lacey, W.S., Eggert, D.A., 1964. A flora from the Chester Series (Upper Mississippian) of southern Illinois. American Journal of Botany 51 (9), 976–985.

Mapes, G., 1985. *Megaloxylon* in Midcontinent North America. Botanical Gazette 146 (1), 157–167.

Mapes, G., Schabilion, J.T., 1976. Petrified Pteridosperm Ovules and Lepidodendralean Remains from the Upper Mississippian of Arkansas. Botanical Society of America Miscellaneous Publication, Allen Press, Lawrence, KS, 27 pp.

Mapes, G., Rothwell, G.W., 1980. *Quaestora amplecta* gen. et sp. n., a structurally simple medullosan stem from the Upper Mississippian of Arkansas. American Journal of Botany 67 (5), 636–647.

Mapes, G., Gastaldo, R.A., 1986. Late Paleozoic non-peat accumulating floras. In: Broadhead, T.W. (Ed.), Land plants. Notes for a short course, organized by R.A.Gastaldo. University of Tennessee, Department of Geological Sciences, Studies in Geology, 15, 115–127.

Mapes, R.H., 1966. Late Mississippian lycopod branch from Arkansas. Oklahoma Geology Notes 26 (4), 117–120.

Mapes, R.H., 1979. Carboniferous and Permian Bactritoidea (Cephalopoda) in North America. University of Kansas Paleontological Contributions Article 64, 1–75.

Millay, M.A., Taylor, T.N., 1977. *Feraxotheca* gen. n., a lyginopterid pollen orgen from the Pennsylvanian of North America. American Journal of Botany 64, 177–185.

Niklas, K.J., 1978. Morphometric relationships and rates of evolution among Paleozoic Vascular Plants. Evolutionary Biology 11, 509–543.

Noé, A.C., 1924. Coal balls here and abroad. Transactions of the Illinois State Academy of Science 17, 179–180.

Oliver, F.W., Scott, D.H., 1904. On the structure of the Paleozoic seed *Lagenostoma lomaxi*, with a statement of the evidence

upon which it is referred to *Lyginodendron*. Philosophical Transactions of the Royal Society of London 197, 193–247.

Pfefferkorn, H.W., Gillespie, W.H., 1982. Plant megafossils near the Mississippian – Pennsylvanian boundary in the Pennsylvanian boundary in the Pennsylvanian system stratotype, West Virginia/ Virginia. In: Ramsbottom, W.H.C., Saunders, W.B., Owens, B. (Eds.), Biostratigraphic Data for a mid-Carboniferous Boundary. Palaeobotanical Contributions of the Subcommission on Carboniferous Stratigraphy, Leeds, 128–133.

Read, C.B., Campbell, G., 1939. Preliminary account of the New Albany Shale flora. The American Midland Naturalist 21 (2), 435–453.

Rex, G.M., Chaloner, W.G., 1983. The experimental formation of plant compression fossils. Palaeontology 26 (2), 231–252.

Saunders, W.B., 1973. Upper Mississippian ammonoids from Arkansas and Oklahoma. Geological Society of America, Special Paper 145, 1–110.

Serlin, B.S., Smoot, E.L., Taylor, T.N., 1979. A petrified calamitean axis from the Upper Mississippian. Botanical Society of America, Miscellaneous Series Publications 157, 37.

Speck, T., 1994. A biomechanical method to distinguish between self-supporting and non self-supporting fossil plants. Review of Palaeobotany and Palynology 81, 65–82.

Stewart, W.N., Rothwell, G.W., 1993. Paleobotany and the Evolution of Plants. Cambridge University Press, Cambridge.

Taylor, T.N., Eggert, D.A., 1967a. Petrified plants from the Upper Mississippian (Chester Series) of Arkansas. Transactions of the American Microscopical Society 86 (4), 412–416.

Taylor, T.N., Eggert, D.A., 1967b. Petrified plants from the Upper Mississippian of North America I: The seed *Rhynchosperma* gen. n. American Journal of Botany 54, 984–992.

Taylor, T.N., Eggert, D.A., 1968. Petrified plants from the Upper Mississippian of North America II: *Lepidostrobus fayettevillense* sp. n. American Journal of Botany 55, 306–313.

Taylor, T.N., Millay, M.A., 1981. Morphologic variability of Pennsylvanian lyginopterid seed ferns. Review of Palaeobotany and Palynology 32, 27–62.

Walton, J., 1936. On the factors which influence the external form of fossil plants: with descriptions of the foliage of some species of the Palaeozoic Equisetalean genus *Annularia* Sternberg. Philosophical Transaction of Royal Society 226, 219–237.

White, C.D., 1937. Fossil flora of the Wedington sandstone member of the Fayettevile shale In: Shorter Contributions to General Geology. U.S. Geological Survey Professional Paper 186, 13–41.

Williamson, W.C., 1873. On the organization of the fossil plants of the Coal-measures. Part IV. *Dictyoxylon*, *Lyginodendron*, and *Heteranglum* Philosophical Transactions of the Royal Society of London B164, 377–408.

Williamson, W.C., Scott, D.H., 1895. Further observations on the organization of the fossil plants of the Coal Measures. Part III. *Lyginodendron* and *Heterangium*. Philosophical Transactions of the Royal Society of London B186, 703–779.

Winston, R.B., Phillips, T.L., 1991. A structurally preserved Lower Pennsylvanian flora from the New Castle coal bed of Alabama. Geological Survey of Alabama Circular 157 (Tuscaloosa), 21 pp.

Zangerl, R., Woodland, B.G., Richardson Jr., E.S, Zachry Jr., D.L., 1969. Early diagenetic phenomena in the Fayetteville black shale (Mississippian) of Arkansas. Sedimentary Geology 3, 87–119.