

## A DEVONIAN LYCOPOD STEM WITH WELL-PRESERVED CORTICAL TISSUES

by HENRY N. ANDREWS, CHARLES B. READ, and SERGIUS H. MAMAY

**ABSTRACT.** *Phytokneme rhodona* is a new genus and species of lycopod stems from the late Devonian of Kentucky, U.S.A. The description is based on an unbranched axis a little over 3 cm in diameter in which the gross cellular preservation is essentially perfect. The cylindrical core of primary xylem is surrounded by a few radially aligned tracheids. The middle cortex is unique, being composed of a ground tissue of irregularly shaped but essentially isodiametric cells and a network of ray-like strands; the outer cortex is composed of elongate fibrous cells. The leaf traces depart in a low spiral producing a nearly whorled arrangement. In the outer cortex each trace is accompanied by a large chambered air space; otherwise there is no aerenchymatous tissue in the stem. This is perhaps the best-preserved Palaeozoic lycopod stem that has been found to date and adds to our knowledge of the extra-stelar tissues.

THE following account is based on a remarkably well-preserved lycopod stem from the Devonian of Kentucky, U.S.A. It is of special interest because the cortical tissues, which are almost invariably poorly preserved or quite lacking in Palaeozoic petrified lycopod specimens, are essentially intact. The cellular structure of the entire stem is preserved with the exception of a part of the phloem; however, even this is intact in some parts of the specimen.

A few other Palaeozoic lycopod stems have been found with the cortical tissues preserved. We believe that the photographs of our Kentucky specimen testify to the outstanding excellence of its preservation and it is worth placing on record on that account alone. However, where significant comparisons are possible, they do not seem to be close enough to justify the use of any previously established binomial. There is a possibility that the fossil may be the stem of the plant that bore the cone *Lepidostrobus kentuckiensis* Scott, 1915 (see also Scott and Jeffrey 1914). Certain differences in the anatomy of the two, and the fact that they were not found in organic connection, render it inadvisable to imply a relationship that we cannot be certain of, we have therefore chosen to describe the fossil under a new name.

Several recent studies of the Palaeozoic lycopods have emphasized their distinctive cauline anatomy as well as their extraordinary if not unique growth habit and physiology. For example, studies by Arnold (1960) and Lemoigne (1966) indicate that the vascular cambium produced only secondary xylem. Investigations by Andrews and Murdy (1958) and by Eggert (1961) have been concerned with the ontogeny of certain arborescent species; apparently the trunk or primary axis attained a height of many metres in some cases before the initial division took place; this was followed by numerous dichotomies, equal or unequal, which resulted in progressively smaller branch orders, to a certain minimum point at which growth ceased. This is quite in contrast to the growth pattern of other groups of plants such as the arborescent Dicotyledoneae and Coniferae.

Our study is based on a single petrified specimen of a lycopod axis 28 mm in diameter and about 24 cm long. S. R. Ash informed us (personal communication 1969) that the

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specimen was found by R. E. Thaden in a road cut along Kentucky Highway 206 south of the bridge crossing the Green River north of Columbia in the Knifley quadrangle, south-central Adair County, Kentucky (approx. lat.  $37^{\circ} 11' 19''$  N., long.  $85^{\circ} 07' 36''$  W); the fossiliferous bed is approximately 4 ft below the top of the Chattanooga Shale. According to J. W. Huddle (personal communication 1970), the Chattanooga Shale is presumably of Late Devonian age in all of Adair County.

#### DESCRIPTION OF SPECIMEN

As a matter of general orientation it may be helpful first to refer to Plate 1 which shows the central stele and a representative sector of the tissues peripheral to it. The cylindrical core of primary xylem (X) measures 3 mm in diameter; a few radially aligned tracheids surround this in some of the thin-section preparations. There follows a narrow band of poorly preserved tissue that we interpret as phloem. Outside this there is a very narrow inner cortex (IC) in the form of a thin cylinder with regularly spaced arches that extend inward to the xylem; the greater part of the axis is made up of a broad middle cortex (MC) and a sharply defined outer cortex (OC).

The primary wood (Pl. 2, figs. 1, 3) has the form of a nearly perfect cylinder, there being only slight fluting at the periphery. It is composed entirely of scalariform tracheids; the outermost ones are quite small, ranging from about  $14 \times 14 \mu\text{m}$  to  $26 \times 20 \mu\text{m}$  in diameter while those towards the centre are appreciably larger, attaining dimensions of  $90 \times 120 \mu\text{m}$ .

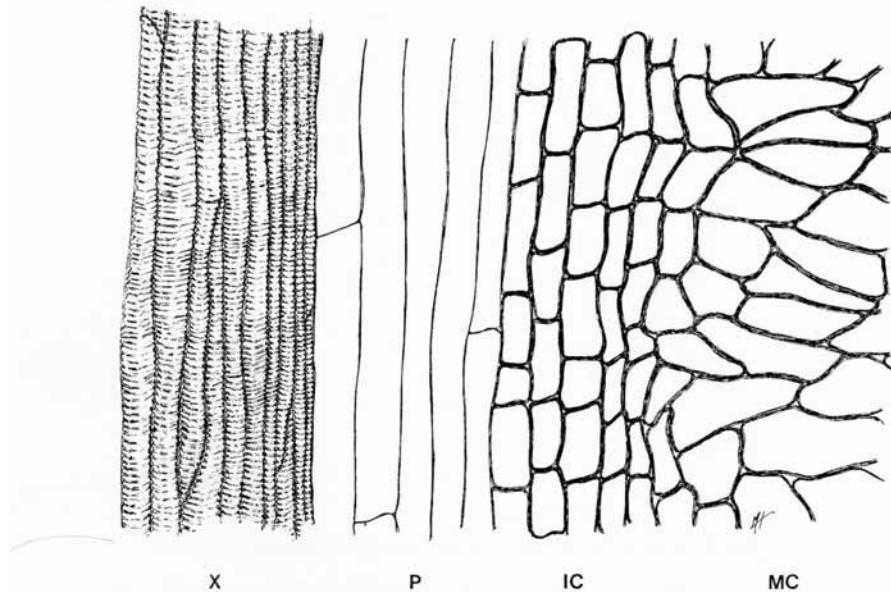
The primary wood cylinder is surrounded by a band of radially aligned secondary tracheids, two to four cells thick. This band was apparently produced by a vascular cambium and is not only narrow but also irregular in amount (Pl. 2, figs. 2, 3); it is in fact so narrow and irregular in development and the tracheids, at many points so similar in size to those of the primary wood, that it is difficult to distinguish it in longitudinal section.

Immediately peripheral to the xylem there is a band of phloem and inner cortex; in view of the way in which they are associated it seems expedient to deal with them together. The inner cortex (Pl. 1; Pl. 2, figs. 2, 3) is a continuous band some 10–12 cells thick radially; it is separated from the outermost xylem by a distance of about 0.3 mm except that there are rather regularly spaced arches or bridges (about 0.6 mm apart tangentially) which extend into, and are in contact with, the xylem. There is thus a ring of tangentially elongate spaces between the xylem and inner cortex which we interpret as the site of the phloem (Pl. 2, fig. 2).

In transverse section the inner cortical cells appear a little less angular than the tracheids and intercellular spaces were probably present. The cells range from 24 to  $50 \mu\text{m}$  in diameter with many of them very close to  $35 \mu\text{m}$ . In longitudinal view (text-fig. 1) they are readily distinguished from any other tissue; they are elongate, varying from 45 to  $185 \mu\text{m}$ , with transverse or oblique end walls. The leaf traces depart through the arches of inner cortex and will be considered separately.

The oval-shaped (in transverse section) phloem areas between the xylem and inner cortex constitute the only poorly preserved tissue in the specimen. In most of our preparations the central part of the phloem has been lost through decay; in Plate 2, fig. 3, there are a few phloem cells immediately outside the xylem and a few just within

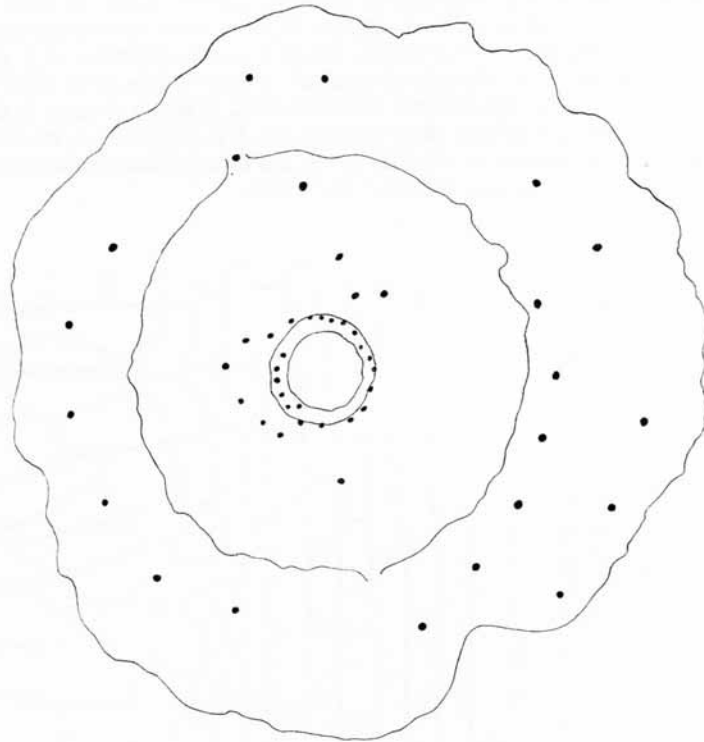
the inner cortex. One of our longitudinal sections, however (slide 7) shows cellular continuity between the xylem and inner cortex. Between these two tissues (text-fig. 1) there are greatly elongate, thin-walled cells about  $30\ \mu\text{m}$  in diameter; it is presumed that they are sieve cells or the functional equivalent of sieve cells of modern vascular plants, although no pitting details have been observed. It was not possible to obtain a satisfactory photograph of this zone and text-fig. 1 is offered as a camera lucida drawing which shows the size and relationships of the tissue systems from the periphery of the xylem to the inner margin of the middle cortex.



TEXT-FIG. 1. A drawing of a portion of slide no. 7 showing: x, peripheral part of xylem; p, phloem; ic, inner cortex; mc, inner part of middle cortex.

The middle cortex (Pl. 1, MC; Pl. 3, figs. 1-3) is, to the best of our knowledge, a unique tissue but if not unique it is most unusual. It is about 5 mm in radial thickness and consists of two fairly distinct types of cells: a groundwork of large, thin-walled irregularly shaped cells that is traversed by more or less radially aligned strands of elongate cells. These strands tend to stand out most conspicuously at lower magnifications (Pl. 1). Although essentially radially aligned they may be irregular and tend to anastomose and divide (Pl. 3, fig. 1). The great variation in their size is apparent in a tangential-longitudinal section (Pl. 3, fig. 2) where they appear as clusters of small cells (about 3-30) scattered among the larger cells of the ground tissue. It is even more difficult to delimit the strands in a radial section (Pl. 3, fig. 3).

The outer cortex is also broad and distinctive. It is 5-6 mm wide (Pl. 1, OC), and consists of cells that seem best described as short fibres. In a transverse section they



TEXT-FIG. 2. Diagram of a transverse section showing leaf trace distribution; slide H1.

appear quite uniform in size and shape, ranging from 85 to 105  $\mu\text{m}$  in diameter. In longitudinal view (Pl. 2, fig. 5; Pl. 4, fig. 2) they appear elongate with tapered ends and range from 0.75 to 1.2 mm long. Intercellular spaces at the corners of the cells are quite

#### EXPLANATION OF PLATE 1

Fig. 1. A representative sector of the stem in transverse section. x, cylindrical core of primary xylem; ic, inner cortex; mc, middle cortex; oc, outer cortex. Slide H1;  $\times 14$ .

#### EXPLANATION OF PLATE 2

Fig. 1. The xylem. x, primary xylem; sx, the narrow band of radially aligned tracheids, presumably secondary xylem. Slide H1;  $\times 33$ .

Fig. 2. Portion of the central part of the stem from the periphery of the primary xylem to the inner part of the middle cortex. x, primary xylem; ph, areas that were occupied by phloem; ic, inner cortex; lt, leaf traces; mc, inner part of the middle cortex. Slide H1;  $\times 46$ .

Fig. 3. A portion of fig. 2, enlarged. lt, leaf traces; ic, inner cortex; ph, phloem. Slide H1;  $\times 140$ .  
Figs. 4, 5. Transverse and radial-longitudinal sections, respectively,  $\times 140$ , showing the contact between middle and outer cortices. mc, middle cortex; oc, outer cortex, 4, slide H1. 5, slide 4.

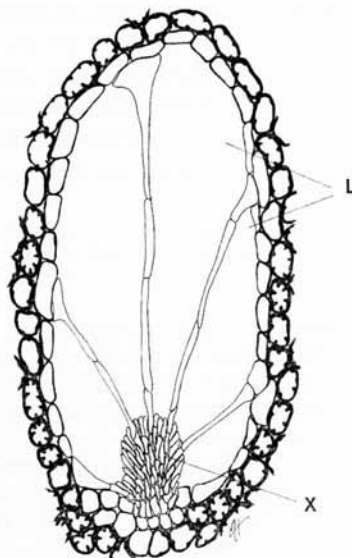
conspicuous and the walls are irregularly thickened (Pl. 2, fig. 4; Pl. 4, fig. 4). The latter feature varies considerably as may be noted in Plate 2, fig. 4; although we are inclined to regard it as a natural feature it is possible that it is due in part to alterations of the cell walls during fossilization.

In some of our sections sporadic patches of radially aligned cells may be observed at the periphery of the outer cortex (Pl. 4, fig. 3) and at the outer margin of the middle cortex (Pl. 3, fig. 4).

The leaf traces depart from the periphery of the primary xylem. Where they are particularly well preserved (Pl. 2, fig. 3) it may be observed that they consist of a small central strand of about a dozen annular tracheids surrounded by very thin-walled cells that are presumed to be phloem; this phloem sheath is usually one cell thick on the inner and lateral sides of the tracheidal strand and three to four cells thick on the outer side. The leaf traces depart from the xylem core in a helical arrangement but the angle of the spiral is so low as to present a nearly whorled arrangement. Several traces are evident in Plate 2, fig. 2 where they are passing through the outer part of the inner cortex.

The traces are particularly conspicuous in the outer cortex and parts of two 'whorls' are evident in Plate 1; see also text-fig. 2. Reference should be made to Plate 4, fig. 1 and text-fig. 3 for details of the trace in this part of the stem. The trace itself remains attached to the inner wall of the apparent gap; this is evident in the ring of traces in the inner part of the outer cortex in Plate 1. The oval-shaped gap (trabecula) has not resulted from decay but is a natural chamber (text-fig. 3) and several delicate parenchymatous strands serve to attach the trace to the wall of the chamber. These slender, multicellular filaments which traverse the trabecula are generally poorly preserved but in a few instances they are intact. It seems probable that the trabeculae facilitated the passage of oxygen from the leaves through the outer cortex, which must have been otherwise quite impermeable. Diffusion of oxygen through the middle cortex was presumably much more readily achieved by virtue of the parenchymatous cell structure and, in some lycopods, by the presence of intercellular spaces.

The leaf traces form an acute angle with the long axis in the inner and outer cortex; thus in a transverse section of the axis the traces too are cut in a near-transverse section and are quite readily discernible. They follow a more nearly horizontal course in the middle cortex and it is difficult to distinguish them from the numerous black pyrite particles that are especially abundant in the cells of this tissue. Also, the chambered cavities, which render the location of the traces so distinct in the outer cortex, are lacking in the middle cortex.



TEXT-FIG. 3. A leaf trace in the outer cortex, transverse section showing xylem strand and lacunae; slide A3.

## SYSTEMATIC DESCRIPTION

Genus PHYTOKNEME gen. nov.

*Type species. Phytokneme rhodona* gen. et sp. nov.*Diagnosis.* As for species.*Phytokneme rhodona* sp. nov.

Plates 1-4; text-figs. 1-3

*Diagnosis.* Petrified axis with lycopodiaceous stele and cortex of three distinct parts: a narrow inner band and broad middle and outer bands. Middle cortex parenchymatous, composed of irregularly shaped but essentially isodiametric ground tissue and network of ray-like strands; outer cortex of elongate fibrous cells. Leaf traces depart in a low helix approaching whorls; traces accompanied by a large, chambered air space in their passage through the outer cortex.

*Derivation of name.* Greek: *phyto*, plant; *kneme*, spoke of a wheel; the specific name is a Greek adjective meaning 'waving', a reference to the distinctive ray structure of the middle cortex.

*Horizon.* Phosphatic nodule zone about 4 ft below the top of the Chattanooga Shale, Upper Devonian.

*Locality.* Knifley quadrangle, south-central Adair County, Kentucky (lat. 37° 11' 19" N., long. 85° 07' 36" W.).

*Deposition of type specimen.* All of the slides (thin sections) on which this study is based were prepared from one specimen, no. 42726, preserved in the Paleobotanical Collections, U.S. National Museum, Washington, D.C., U.S.A.

*Discussion.* It may be appropriate first to indicate the reasons for assigning the fossil to the lycopod group. The cylindrical, slightly fluted, solid core of primary scalariform tracheids presents a typical lycopod stele. It seems evident that the numerous, small leaf traces supplied correspondingly small (microphyllous) leaves. The leaves were arranged in a helical pattern but the angle is so close to the horizontal as to make them appear nearly whorled. Such an arrangement has been demonstrated in the Late Devonian *Cyclostigma kiltorkense* Haughton as described and illustrated by Nathorst (1902) whose specimens came from the Arctic (Bear Island) and by Johnson (1913) whose specimens came from Ireland. Nathorst, in his Plate 11, fig. 6, shows a compression specimen with

## EXPLANATION OF PLATE 3

Figs. 1-3. The middle cortex,  $\times 35$ . 1, transverse slide H1. 2, tangential; slide 4. 3, radial slide 7. R, strand tissue. Orientation of the figures: the *a-b* line for figs. 7 and 9 follows a radius, *a* being towards the centre of the stem; for fig. 8, the line follows the main axis, *a* being down and *b* up.  
Fig. 4. Showing sporadic meristematic activity in the outer part of the middle cortex. OC, outer cortex; MC, middle cortex. Slide B11;  $\times 35$ .

## EXPLANATION OF PLATE 4

Figs. 1, 2. Transverse and longitudinal views respectively of the outer cortex,  $\times 38$ . LT, leaf trace. 1, slide A3. 2, slide 9.  
Fig. 3. A peripheral cushion of the outer cortex showing meristematic activity on the outer edge, see also upper right part of Plate 1. Slide H1;  $\times 46$ .  
Fig. 4. Transverse view of a few cells of the outer cortex showing the irregularly thickened walls. Slide H1;  $\times 700$ .

leaf scars in what appear, superficially, to be a nearly whorled arrangement; Johnson (1913) shows a similar arrangement in a specimen on Plate 40, fig. 2. He also figures leaf-bearing specimens which are described as having the leaves arranged in 'horizontal or obliquely ascending whorls of 10-20 members'. The leaves are 12-15 cm long, 1 mm wide at the point of attachment, tapering towards the distal end and with a single vein running the entire length of the leaf.

Banks (1944, p. 653) in describing *Colpodexylon deatsii* from the Upper Devonian of New York notes, with reference to the leaf arrangement: 'The helix is so tight that the cushions appear whorled. Proof of the spiral arrangement is obtained by removing stems from the matrix and tracing leaf cushions around the axis. Never in a complete turn around the stem is the first cushion reached again, rather one arrives at a cushion in the next row above the first.'

To the best of our knowledge there is no information available on the anatomy of *Cyclostigma kiltorkense*, and the deeply lobed stele of *Colpodexylon deatsii* is quite different from that of our fossil.

Although relatively few of the petrified arborescent lycopod axes that have been found in the Palaeozoic have well-preserved cortical tissues there are several that afford some information on this tissue system. In many, if not most specimens, the cortex (which we define here as that region between the phloem and the periderm, when the latter is present) is composed of three zones, a very narrow inner cortex and appreciably broader middle and outer bands. The cellular make-up of the three varies in different species or genera:

In *Lepidodendron harcourtii* as figured by Williamson (1881, pl. 52, fig. 9) the three zones, although distinct, all appear to be quite uniformly parenchymatous, apparently differing chiefly in cell size.

In *Lepidodendron scleroticum* Pannell (1942) the middle cortex consists of parenchyma with interspersed 'sclerotic nests'; it is uncertain as to whether these clusters of cells are actually sclereids or of a secretory nature; they are distinguished by their dark contents. The outer cortex of this plant is composed of a parenchyma ground tissue interspersed with radial-longitudinally aligned fibrous strands.

Neither *L. harcourtii* nor *L. scleroticum* display a tissue system that is closely comparable to the middle cortex of *Phytokneme*; several other lycopod axes, however, may have had something comparable. In his description of *Lepidodendron fuliginosum*, Seward (1910) refers to a broad middle cortex 'composed of rather small lacunar parenchymatous tissue consisting of sinuous tubular elements interspersed among isodiametric cells of various sizes' (p. 145). And in reference to *L. harcourtii* he notes that 'Remains of a lacunar tissue are seen in the middle cortical region' (p. 161). Seward's figures suggest that the fossils he described were not as well preserved as our specimen and it is therefore not possible to draw a satisfactory comparison. It may also be noted that there is no lacunar tissue in the cortex of *Phytokneme*, other than the trabeculae in the outer cortex; a small degree of decay in the middle cortex could readily result in a lacunar effect however. In this connection it is pertinent to refer to Calder's (1933) study of *Bothrodendron mundum*; in reference to the cortical tissues she states: 'In only two of the small branches in the Kidston Collection specimens (No. 734) is the middle cortex preserved; it is composed of very loosely-woven "hyphal" tissue with well-developed lacunae' (p. 668). The specimen referred to is much smaller than ours and

we do not imply a close relationship; the three cortical zones in *B. mundum* and *Phytokneme* seem quite similar with the exception of the lacunae in the former. We suggest that the middle cortex in the two may have been very much alike and that the 'lacunae' in *B. mundum* is a decay artifact.

*Lepidodendron kazachstanica* Senkevitch as described by Yurina (1969, p. 52) presents certain points of comparison with our fossil. The Devonian Kazakhstan lycopod seems to be similar to *Phytokneme rhodona* in its stelar structure, the nearly whorled arrangement of the leaf traces and the anatomy of the outer cortex. However, the middle cortex is not sufficiently well preserved to allow close comparison with the unique features present in our plant.

Bower (1893) gives a fairly detailed summary of the cortical anatomy of several Palaeozoic lycopod stems and cones as well as some of the modern lycopodiums; although there is considerable variation in different plants he shows that a threefold differentiation of the cortex is quite common. In *Lepidodendron fuliginosum* '... it consists chiefly of multicellular filaments which are intertwined together in irregular fashion; the tissue resembles in its general character that of the central strand of *Fucus* rather than the tissue of a vascular plant' (p. 346). He also figures a portion of the middle cortex of *Lepidodendron selaginoides* and describes it as 'a tissue of very spongy character, with large intercellular spaces, which were traversed by trabeculae consisting of one or more cell-rows' (p. 345).

A casual survey of some living species of *Lycopodium* reveals considerable variation in cortical anatomy but in most cases it is possible to distinguish inner, middle, and outer cortical zones. In *L. clavatum* L. there is a broad middle cortex of large, thin-walled cells, an outer cortex of smaller thin-walled cells and an inner cortex of slightly thicker walled cells. In *L. annotinum* L. there is a broad middle cortex of very thick-walled cells, with narrower inner and outer bands of thin-walled cells. In *L. alopecuroides* L. and *L. inundatum* L. the cellular differentiation in the cortex as a whole is less marked than in the above two and the middle part is aerenchymatous, the air passages tending to be radially aligned. *L. selago* L. has a very narrow inner and outer cortex of closely compacted cells and a broad middle cortex that Bower has aptly described as being composed of 'interlaced filaments'; air passages are present but they form a very irregular network. The aerenchymatous nature of the cortex of *L. inundatum* and *L. alopecuroides* may be attributed to the moist habitat that they live in; it is a little puzzling, however, to find this in *L. selago* which tends to favour alpine regions.

As noted above we have also given due consideration to the possibility that *Phytokneme rhodona* is the stem that bore the cone described by Scott and Jeffrey (1914) under the name *Lepidostrobus fischeri*. This specific name proved invalid because it had been used previously by Renault, and Scott (1915) accordingly changed the name to *L. kentuckiensis*.

The stele of *L. kentuckiensis* is similar to that of *Phytokneme* and the description of the tissues that we interpret as being homologous with the middle and outer cortices of our fossil are described as follows by Scott and Jeffrey: The 'inner' (middle) cortex is composed 'chiefly of rather large, short cells, about 80–120  $\mu$  in diameter. They are sometimes enclosed in loops of narrower cells which appear to wind round them' (p. 357). The tissue peripheral to this (outer cortex) '... consists of long, prosenchymatous elements, more or less hexagonal in transverse section, with a diameter of about



36–50  $\mu$ . The whole tissue shows a tendency to radial arrangement, . . . This radial seriation is more marked in the external part of the zone . . . (p. 357).

In summary, the importance of the specimen described here lies in the information that it affords concerning the cortical tissues of the Palaeozoic lycopods. In many or most species the cortex is composed of three tissue systems, inner, middle and outer. The middle cortex, generally, is a broad parenchymatous zone which may be ramified to some degree by air chambers; it seems evident that it was very readily decayed and although probably always present in life it was rarely preserved with the perfection that it appears in *Phytokneme*. Our stem may be a cauline axis of the plant that bore the cone *Lepidostrobus kentuckiensis* and, on the basis of comparative phyllotaxy, it may give a clue to the anatomy of lycopods such as *Cyclostigma kiltorkense*.

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The paper is dedicated to Professor Chester A. Arnold in the year of his official retirement as Professor of Botany at the University of Michigan, and in honour of his distinguished service to the fields of morphology and paleobotany.

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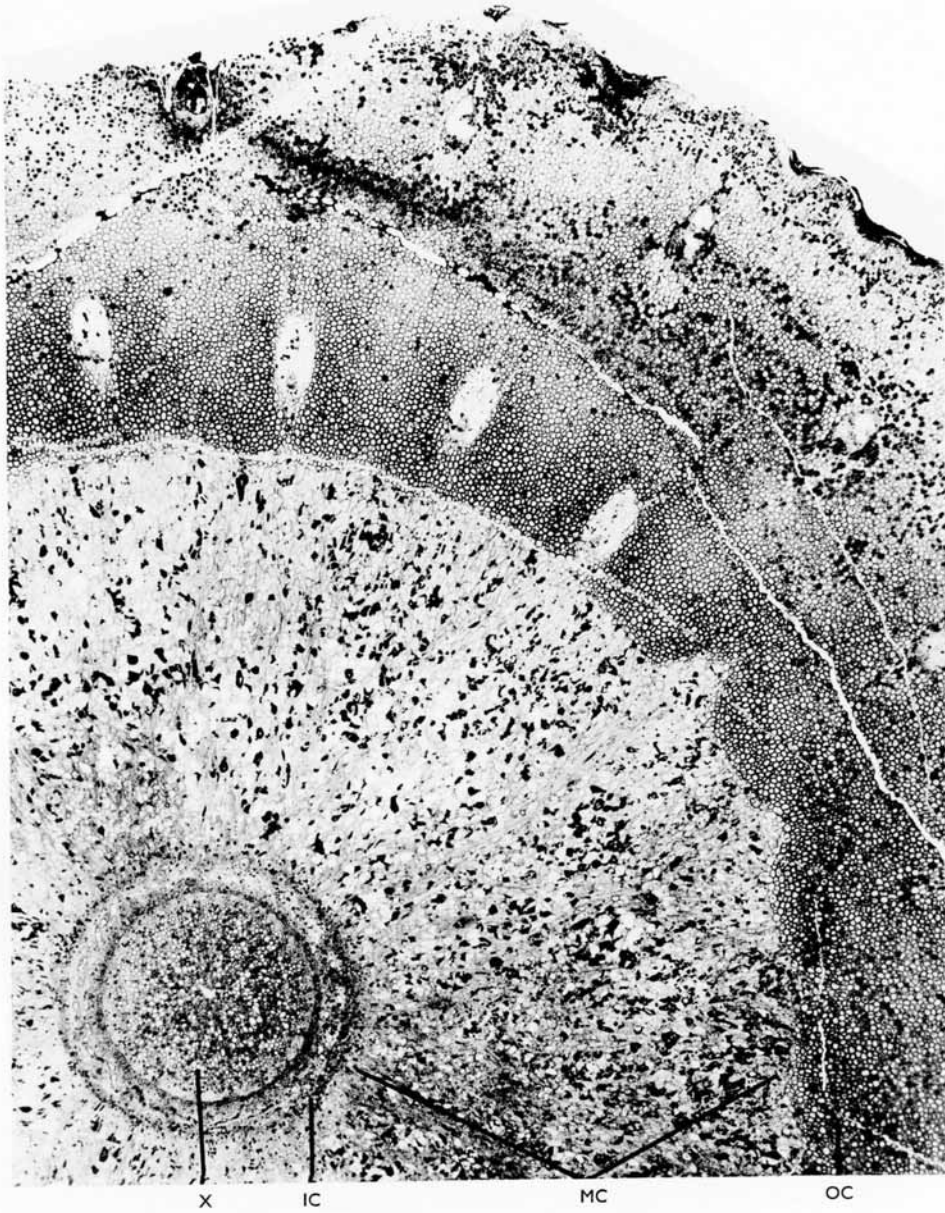
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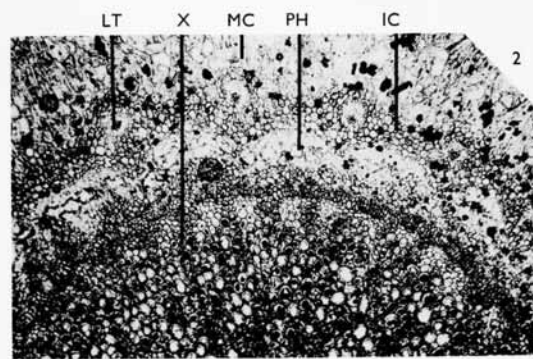
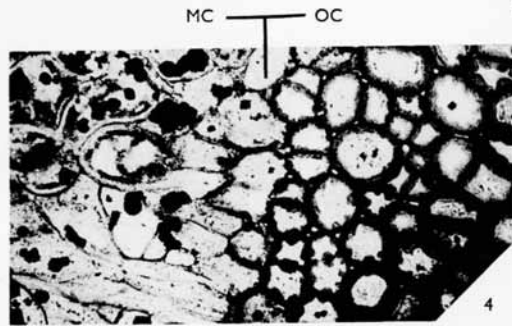
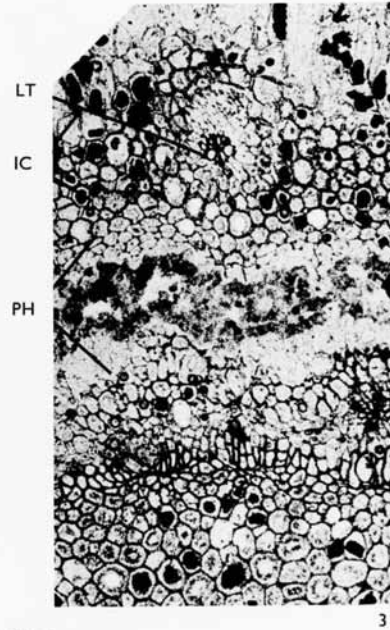
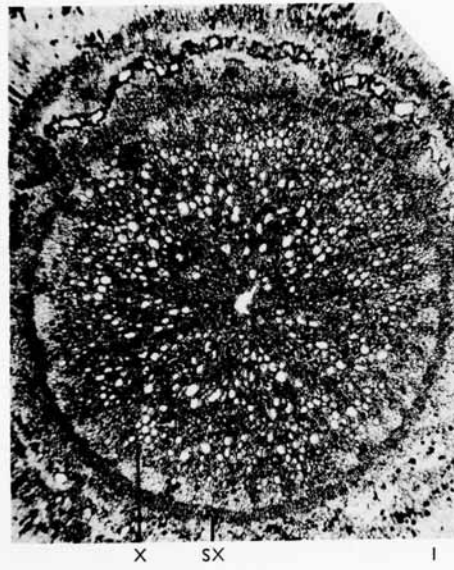
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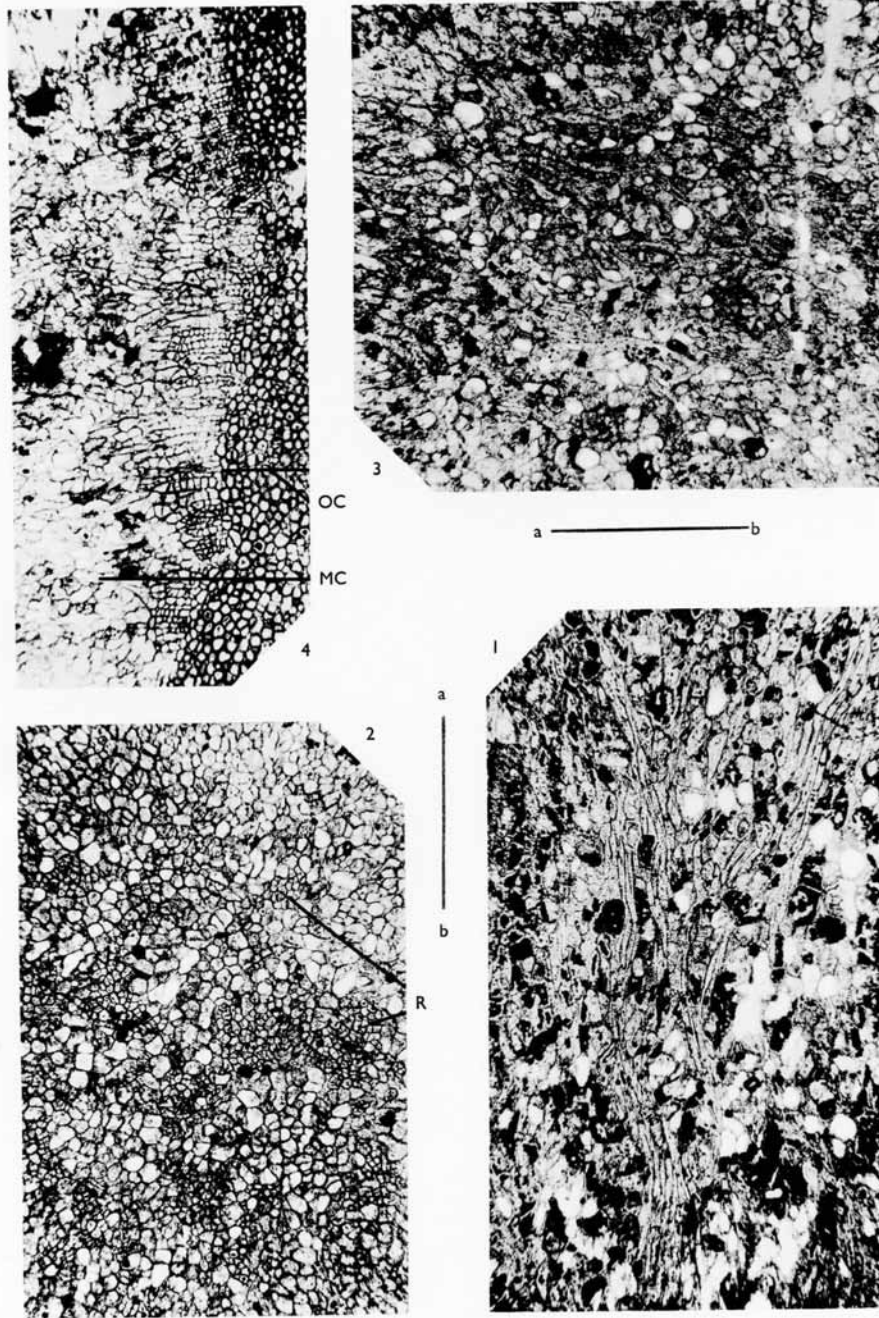
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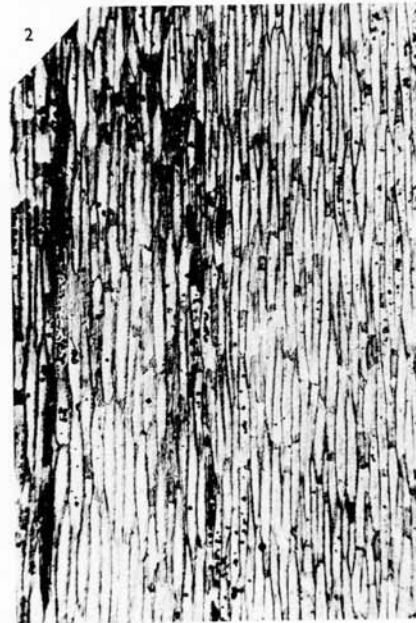
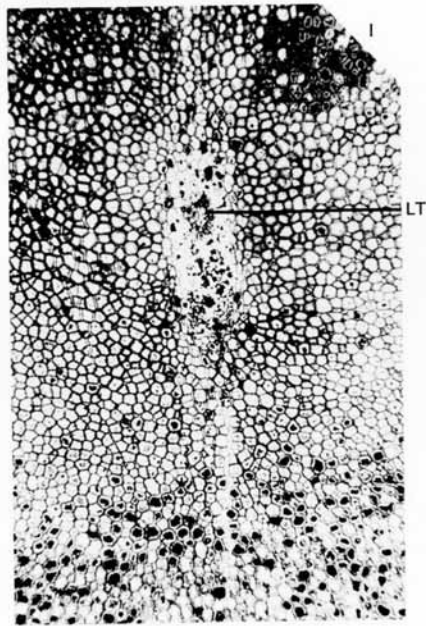
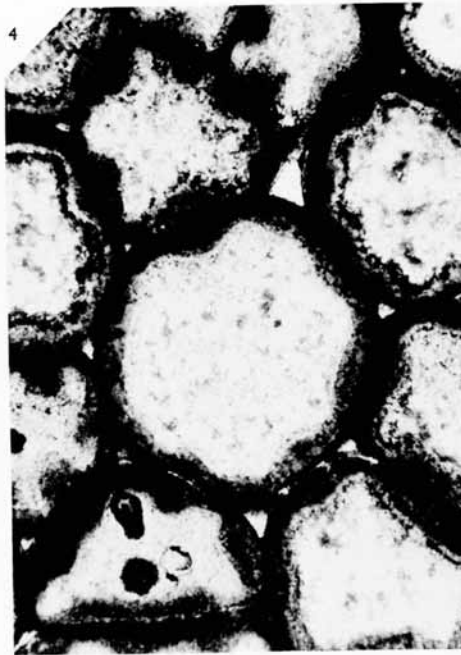
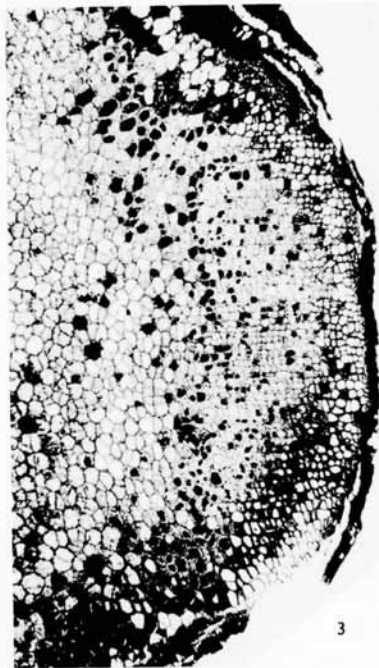
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