

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

THE UNIVERSITY OF MICHIGAN

Vol. XV, No. 10, pp. 249-267 (4 pls., 1 fig.)

AUGUST 1, 1960

A LEPIDODENDRID STEM FROM KANSAS AND ITS
BEARING ON THE PROBLEM OF CAMBIUM AND
PHLOEM IN PALEOZOIC LYCOPODS

BY
CHESTER A. ARNOLD



MUSEUM OF PALEONTOLOGY
THE UNIVERSITY OF MICHIGAN
ANN ARBOR

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

Director: LEWIS B. KELLUM

The series of contributions from the Museum of Paleontology is a medium for the publication of papers based chiefly upon the collection in the Museum. When the number of pages issued is sufficient to make a volume, a title page and a table of contents will be sent to libraries on the mailing list, and to individuals upon request. A list of the separate papers may also be obtained. Correspondence should be directed to the Museum of Paleontology, The University of Michigan, Ann Arbor, Michigan.

VOLS. II-XIV. Parts of volumes may be obtained if available.

VOLUME XV

1. *Leiopteria rafinesquii* Hall and A New Species of the Genus from the Thedford-Arkona Region of Southwestern Ontario, by George M. Ehlers and Edward P. Wright. Pages 1-13, with 2 plates.
2. Quasillitid and Alanellid Ostracods from the Centerfield Limestone of Western New York, by Robert V. Kesling, Emadeddin Kavary, Robert S. Takagi, John R. Tillman, and George R. Wulf. Pages 15-31, with 4 plates.
3. A New Species of *Mahonia* from the Oligocene Ruby flora of Southwestern Montana, by Herman F. Becker. Pages 33-38, with 1 plate.
4. Some Middle Devonian Stromatoporoids from Michigan and Southwestern Ontario, Including the Types Described by Alexander Winchell and A. W. Grabau, by J. J. Galloway and G. M. Ehlers. Pages 39-120, with 13 plates.
5. A Simple Device for Single-lens Stereophotography of Paleontological Specimens, by Herbert W. Wienert. Pages 121-124, with 1 plate.
6. Techniques in the Photography of Fossilized Plants, by Herbert W. Wienert. Pages 125-132, with 3 plates.
7. The Type Species of the Paleozoic Tabulate Coral Genera *Cladopora* and *Coenites*, by Erwin C. Stumm. Pages 133-138, with 1 plate.
8. Hydropores in Edriasteroids, by Robert V. Kesling. Pages 139-192, with 13 plates.
9. An Upper Cretaceous Ammonite Bitten by a Mosasaur, by Erle G. Kauffman and Robert V. Kesling. Pages 193-248, with 9 plates.
10. A Lepidodendrid Stem from Kansas and its Bearing on The Problem of Cambrium and Phloem in Paleozoic Lycopods. Pages 249-267, with 4 plates.

A LEPIDODENDRID STEM FROM KANSAS AND ITS BEARING
ON THE PROBLEM OF CAMBIUM AND PHLOEM IN
PALEOZOIC LYCOPODS

BY
CHESTER A. ARNOLD

CONTENTS

Introduction	249
The specimen	250
The pith and xylem	250
The extra-xylary tissues	251
Distinctive features	255
<i>Lepidodendron schizostelicum</i> , Arnold, sp. nov.	255
Specific diagnosis	255
The problem of cambium and phloem in the lepidodendrids	256
Conclusions	259
Summary	261
Literature cited	261
Plates	(after) 263

INTRODUCTION

ALTHOUGH the anatomy of the stems of the arborescent Paleozoic lycopods has been extensively investigated, our knowledge of the subject is still far from complete. There is much that is either unknown or is not well understood, and almost any unstudied but well-preserved specimen will yield new information. The xylem cylinder of many of them has been described in minute detail, and extensive information has been assembled on the structure and probable mode of development of the hard periderm that formed the outer layer of the trunks and branches. Of the nature of the tissues between the wood and the periderm, those that occupied positions where cambium and phloem normally occur, much remains to be learned. The tissues of this part of the lepidodendrid stem are seldom well preserved, and in the relatively few instances where they have been found intact, conflicting interpretations have resulted.

In a part of the specimen under consideration the tissues immediately outside the xylem are quite well preserved, and they shed some light on a long-standing controversy concerning cambium and phloem in the lepidodendrids.

dendrids. In addition, our specimen shows a unique feature in the structure of the xylem cylinder. This, along with a consideration of the extra-xylary tissues, constitutes the subject of this account.

THE SPECIMEN

The specimen described here was found in a coal ball from the well-known locality about four miles southwest of West Mineral, Kansas. The horizon from which it came is the Fleming coal of the Cherokee group, lower Des Moinesan series, Pennsylvanian system. The specimen was scarcely more than a fragment that unfortunately had been cut at a highly oblique angle. Furthermore, considerable finely disseminated pyrite was present in the tissues which greatly interfered with the study of some features.

The specimen consisted of a short piece of an uncrushed xylem cylinder and some of the adhering cortical tissues. The diameter of the original stem is unknown because an undetermined amount of external tissue was lost, but a radius of 3.5 cm. can be measured which allows for a minimum possible diameter of 7.0 cm. It probably represents a branch rather than a part of a main trunk, but the large pith and the well-developed secondary wood indicate that it probably did not come from an ultimate branch. The xylem cylinder is not quite round (Pl. I, Fig. 1) though it measures about 11.5 mm. in almost any direction. The pith is 7.0 mm. in diameter, the primary wood is about 1.0 mm. thick, and the secondary layer, which is thicker on one side than on the other, ranges from 1.0 to 2.0 mm. in width.

The pith and xylem.—Only about a quarter of the pith tissue is preserved (Pl. I, Fig. 1) but this is enough to show the distinct though somewhat irregular boundary between it and the primary xylem. The preserved part is at one side and is about 2.0 mm. wide. The cells throughout most of it are small and essentially isodiametric. Some of them show scalariform wall thickenings, but these cells are scattered and not markedly different in size and other characteristics from the surrounding cells. Along the side of the preserved part, however, toward the center of the axis there is a strip of tissue that is considerably crushed, and in it there are numerous large tracheary elements with scalariform bars. The original location and extent of this part of the pith is undetermined, but it is continuous with the small-celled intact part. It appears to represent tissue of the inner pith. Though the outer part of the original pith was mostly parenchymatous, there seems to have been a central part that contained rather large numerous tracheary elements. Therefore, if correctly interpreted, this stem did not possess a mixed protostele of the type found in *Lepidodendron vasculare* nor in the small twigs of *L. scleroticum*. It may have evolved from a

mixed protostele, but if so the transformation took place around the central part leaving the surrounded area more or less unchanged. Better preserved material will have to be examined before the structure of the pith in this stem can be fully elucidated.

The primary xylem shows an unusual feature. This is the presence of conspicuous raylike bands of parenchyma spaced at intervals of, roughly, a millimeter that extend into it from the secondary xylem, and which usually terminate only a few cells away from the pith (Pl. I, Fig. 2), though they sometimes pass completely through it (Pl. III, Fig. 2). These large rays have the effect of almost cutting the primary wood into separate sections. These bands obviously originated in the procambium. Since the primary xylem developed centripetally, the first-formed elements of the xylem were in separate segments of 20 or more, but they became partly joined during late stages in ontogeny.

Owing to insufficient material for study, the exact relationship of these parenchyma bands to the leaf traces is not conclusively shown. It has not been possible to prepare longitudinal sections that show them over more than a few millimeters in vertical extent, and in the small areas where they are revealed, details are badly obscured by pyrite. In the tangential sections, however, some traces can be seen that are flanked only by ordinary tracheids and are not associated with the raylike bands.

The primary xylem is in close contact with the secondary xylem, and no distinct corona shows. No clearly recognizable protoxylem elements have been seen, but limited material and deposition of pyrite along the contact zone renders satisfactory study of this region impossible. The smallest tracheids that have been observed in longitudinal section seem to have scalariform wall thickenings. Little, or only very little, parenchyma is present between the primary and the secondary xylem. There is, however, along the contact zone and between the rows of innermost serially aligned secondary tracheids a narrow and somewhat irregular band of small tracheids. Some of these may belong to the secondary xylem but others are probably protoxylem.

Except for the large raylike structures that transect the secondary xylem and terminate deep within the primary layer, the secondary xylem shows nothing unusual and need not be described in detail. Its tracheids, in common with those of the primary xylem, show the typical scalariform wall thickenings. Fimbrils (Barghoorn and Scott, 1958) are present between the scalariform bars but are difficult to see. Ordinary xylem rays are present but they are small and inconspicuous.

The extra-xylary tissues.—In the stem under consideration there is a zone about 8.0 mm. wide between the xylem and the outer cortex that is

structurally rather complex. This represents the region that in most petrified lepidodendrid stems is more or less empty of tissue, but is here rather well preserved (Pl. II, Fig. 1).

Surrounding the xylem, and in contact with it, is a compact zone of small cells that maintains a quite constant thickness all around the xylem cylinder, and does not exceed 0.10 mm. in depth (Pl. II, Fig. 2*d*; Pl. III, Fig. 1; Pl. IV, Figs. 1, 2). This shows as a slightly darkened band even under low magnification (Pl. I, Fig. 2). Though the cells of this layer vary in size, they are of the order of 20-25 microns in tangential diameter, in contrast to diameters of 100 or more microns for the adjacent xylem tracheids.

Although this layer of cells is to all appearances a primary tissue, it is not a cambium. There are some indications of limited cell divisions within it (Pl. IV, Fig. 2) but this was probably in accomodation to the increasing girth of the xylem cylinder during growth. Most of the cell divisions had occurred at the ends of the large rays. Some of the small cells appear slightly elongated in longitudinal section but this is not true of all of them. Although this is the tissue that can be best identified with phloem in this stem, it bears more resemblance to the parenchyma that separates the tracheids from the sieve elements in *Lycopodium* and *Selaginella*. If this tissue is phloem, it is atypical in lying directly against the xylem.

The layer described above is succeeded by a wider one that extends to the inner limits of the outer cortex. At about 0.50 mm. or less from its inner limit there is an irregular zone containing large spaces that are partly filled with black material (Pl. II, Fig. 2*e*). This appears identical with the "secretory zone" in *Lepidophloios fuliginosus* (Seward, 1900; 1910, Figs. 162, 167-69, 179). Leaf trace strands appear at intervals of 1 mm. or more along the circumference between this layer and the xylem (Pl. II, Fig. 2).

Externally to this the structure becomes more varied. At places the tissues display a loose arrangement suggestive of hyphal structure, and here and there are groups of cells with thickened walls. The leaf traces in this region are surrounded by radiating rows of cells (Pl. III, Fig. 4) that resemble the tissue that Scott (1900, Fig. 52; 1920, Fig. 60) shows around the trace in *Lepidophloios wüschianus*. The radiating cells, while apparently of secondary origin, are parenchymatous instead of vascular.

In the inner cortical zone are irregular bands of secondarily formed tissue that resemble periderm more than anything else (Fig. 1). It is predominately parenchymatous though a few cells appear to have thick walls and may be fibrous. These, however, are few and scattered. The bands average about 0.50 mm. in width, though they vary considerably. This tissue surrounds the xylem cylinder, at places lying adjacent to it

(though always slightly separated from it by the afore-mentioned layer of small-celled parenchyma) but elsewhere extending away from it and out into the inner cortex (Pl. II, Figs. 1, 2 *a-c, f*; Pl. III, Figs. 1, 3; Pl. IV, Fig. 1). Where it lies adjacent the xylem it somewhat resembles secondary phloem, but its cells do not show the same relation to the xylem cells as would secondary phloem cells, and the intervening layer is not a cambium. At the places where this layer bends away from the xylem and lies in the inner cortex, tissue more resembling ordinary primary cortical parenchyma flanks the xylem (Pl. II, Fig. 2; Pl. IV, Fig. 2).

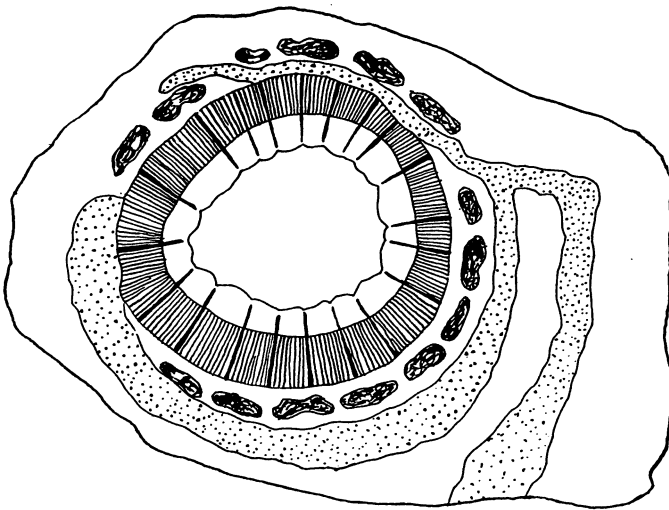


FIG. 1. Semidiagrammatic drawing showing relation of internal periderm (stippled) to xylem cylinder.

Where this periderm-like tissue lies nearest the xylem, its cells are rectangular, elongated in radial direction, and in regular radial rows. Whether it developed from a single-celled initiating layer or from general cell division throughout, is uncertain, though lack of any one cell layer that would seem to have been responsible for the development of the whole layer suggests the latter.

At a place farther away from the xylem the cells show a more pronounced tendency to be elongated in the tangential direction, though the regular radial alignment is retained (Pl. III, Fig. 3).

Lack of material prevented the preparation of a sufficient number of sections to fully reveal the cells of this tissue in longitudinal view. From

what can be ascertained about their vertical extent, however, the cells near the xylem seem to be as broad as they are long or only slightly longer than broad, and with transverse ends. Away from the xylem they seem to be longer, with rounded or tapering ends and frequently with transverse septa, thus showing considerable resemblance to the "chambered" cells that have been described in the periderm of some other arborescent lycopods.

When first observed it was thought that this rather anomalously developed band of periderm-like tissue was traumatic and had been formed over a surface laid bare by abrasion or by some other cause. It obviously had formed, however, within normal tissue because leaf traces are present in regular sequence on both sides. One would not expect to see leaf traces in scar tissue. The only plausible interpretation is that, in this stem, periderm formation took place deep within the cortex and as far inward as its innermost limits. Where so located, the periderm may bear some resemblance to simply constructed secondary phloem.

A striking similarity exists between the periderm-like tissue where it lies adjacent to the stele in our specimen and to the anomalously formed secondary tissue in *Lepidophloios fuliginosus*. The resemblance is especially strong in a figure by Calder (1934, Pl. I, Fig. 9), which shows a layer of parenchyma outside the xylem and with radially aligned cells slightly elongated in the radial direction. There is, however, an important difference. In Calder's figure, as in previously published figures depicting the species, this tissue lies adjacent to primary xylem, not outside typical secondary xylem as in the Kansas specimen. Regardless of this difference there is the pertinent question as to whether the two tissues might be the same, and whether the secondary layer in *L. fuliginosus* could be periderm tissue formed next to the primary xylem. In an effort to check this point several sections of this species were examined, one having been freshly cut and ground very thin. Immediately it was obvious that the two tissues are different. The elongate elements in *L. fuliginosus* show scalariform wall thickenings and are therefore true xylem elements, not periderm fibers. In this specimen the tissue next to the corona is poorly preserved but was apparently parenchymatous. In some published figures this region is merely shown as a structureless black layer. The outer part of the secondary tissue in this specimen consists mostly of tracheids. There is also some evidence that more than one cambium layer was responsible for the formation of the rather small amount of secondary parenchyma and tracheidal tissue. A further feature of interest is that the leaf traces do not take a horizontal course through this tissue but traverse it at the same steep angle they pursue through the cortex. They appear cut transversely, not horizontally, as

they are in the secondary xylem of other lepidodendrids. The amount of secondary accretion was not enough to change their course. It seems quite clear that regardless of superficial resemblances the anomalously formed secondary tissue in *Lepidophloios fuliginosus* is different from the internal periderm-like layers in the Kansas specimen.

The outermost tissues of the Kansas stem consist of woody periderm of the type commonly encountered in lepidodendrids, but the material was not sufficient to permit their detailed study in longitudinal section. This quite uniform tissue is interrupted only by several successive rows of "glands" of the type described for *Lepidodendron johnsonii* and a few other species. The positions of many of the "glands" is indicated only by empty spaces, but thin-walled cells with dark contents are preserved in a few. Chambered cells occur only in the innermost part of the periderm where the hard tissue merges with the somewhat sclerotic middle cortex.

DISTINCTIVE FEATURES

The peculiar raylike structures that extend across the secondary xylem and terminate near the inner edge of the primary wood only a short distance from the pith appear to distinguish this stem from those of the other arborescent lycopods. Aside from this it differs from other species only with respect to details. Although there are a number of lycopod genera of which the internal structure is unknown (i.e. *Asolanus*, *Omphaliophloios*, *Porodendron*, *Pinakodendron*) to which this somewhat aberrant stem could belong, it so closely resembles a *Lepidodendron* in its general features that it is tentatively assigned to that genus. *Lepidodendron* and *Lepidophloios* cannot be separated on purely anatomical evidence, so in the absence of leaf cushions, stems such as the one described here are customarily assigned to *Lepidodendron*, and the name *Lepidodendron schizostelicum*, sp. nov., is chosen for it in reference to the partly divided stele.

***Lepidodendron schizostelicum* Arnold, sp. nov.**

Specific Diagnosis.—Siphonostelic primary cylinder surrounded by well-developed secondary xylem; xylem cylinder dissected by conspicuous raylike structures that extend from the cambium zone inward and terminate near the inner limit of the primary xylem; pith parenchyma with intermixed tracheary elements; inner cortex containing irregular bands of periderm-like tissue; outer cortex with thick periderm. *Locality*: 4 miles southwest of West Mineral, Kansas. *Horizon*: Fleming coal, Cherokee group, Des Moines series, Pennsylvanian system. *Holotype*: No. 36880 UMMP.

THE PROBLEM OF CAMBIUM AND PHLOEM IN THE LEPIDODENDRIDS

As stated in the Introduction, the specimen from Kansas throws some light on the much misunderstood problem of the nature of cambium and phloem in the lepidodendrids. This appears to be the first discovery in which the tissue layer sometimes identified as cambium and sometimes as phloem has been found in position to show unmistakably that it is periderm tissue. No cambium or secondary phloem seems to be present. Aside from the anomalous position of this internal periderm layer, the arrangement of the tissues is the same as generally observed in lepidodendrids.

Doubts concerning the existence of phloem of cambial origin in lepidodendrid stems seem to have first been expressed by Seward (1900). In *Lepidophloios fuliginosus* he described a tissue a few cells outward from the xylem and called it the "meristematic zone." It is a narrow band of serially arranged polygonal cells that he did not identify further, though he noted certain resemblances to cambium. This "meristematic zone" is followed by the "secretory zone," which he postulated might have functioned as phloem, though structurally it was different. Seward concluded (1900, p. 154): "Indeed in no stem of *Lepidodendron*, *Lepidophloios*, or *Sigillaria* has typical phloem so far been satisfactorily demonstrated." After sixty years the situation has not materially changed though authors in the meantime have persisted in labeling as "phloem" that tissue in lepidodendroid stems that lies immediately external to the xylem.

It may be well to emphasize at this point that the term "phloem" is applicable only to tissue that, because of its structure, shows evidence of having been conducting tissue. Merely being located outside the xylem is not sufficient, though usually that is where it is. Location actually has nothing to do with the proper designation of phloem.

Seward's "meristematic zone" occupies a similar position and consists of the same kind of cells as the tissue that Scott labeled "phloem" in a drawing of the outer part of a transverse section of the stele of *Lepidophloios wünschianus* (Scott, 1900, Fig. 52; 1920, Fig. 60). Scott interpreted lepidodendrid stems in the conventional manner and assumed that the cambium which laid down the secondary xylem was also capable of forming secondary phloem. He did comment on the fact, however, that his "cambium" cells did not correspond exactly with the radially aligned xylem elements which they lie against. He admitted (1900, p. 142) that the phloem presents difficulties in interpretation, and that typical elongated elements cannot always be seen even in well-preserved material.

Weiss (1901) then proceeded to describe tissues he thought were cambium in *Lepidophloios fuliginosus*. He labeled as "cambium" the same tissue that Seward had called the "meristematic zone" and Scott had called

"phloem" (Weiss, 1901, Pl. III). The tissue he thought was phloem lay outside his cambium though it was clearly not of secondary origin. He even described and figured rather large cells surrounded by smaller cells that he called "sieve tubes" and "companion cells." He said that this phloem does not differ materially from that of living lycopods, and in so doing, of course, overlooked the significant fact that recent lycopod phloem does not contain companion cells. Weiss also tried to bolster his rather weak interpretations with functional necessity by saying: "Until it is disproved that the cells of this phloem region are of such nature as not to be able to conduct and store organic materials for use of the secondary meristem we must look upon it as functionally representing phloem . . ." Both Scott and Weiss insisted that Seward was wrong, yet they differed from each other almost as much as they differed from him. Weiss's figures, including the labeling, are reproduced by Hirmer (1927, figs. 275-79, p. 244).

In 1902 Seward reiterated his previous conclusion concerning the absence of true phloem in the lepidodendrids and amplified it somewhat. In the meantime he had prepared longitudinal sections of the controversial *Lepidophloios wünschianus*, and had found that vertically elongated elements could be seen only in the xylem, and that Scott's "phloem" consisted of cells that were actually shorter in the vertical than in the longitudinal dimension. Thus they could not have been formed from the same meristematic initials that had produced the secondary xylem. His ultimate conclusions were (1902, p. 46) that the lepidodendrids did not possess a cambium that was identical with that of other plants, that the tissue occupying the position of phloem in other plants did not exhibit phloem characteristics, and that the formation of secondary tissues was chiefly, if not entirely, confined to secondary xylem.

Though Scott admitted that there were difficulties in the interpretation of the tissues in lepidodendrid stems as cambium and phloem, he never questioned or took exception to the existence of secondary phloem in these stems as did Seward. In the second and third editions of his *Studies in Fossil Botany* he makes no reference to Seward's observations and conclusions, and repeats without significant change the text of the first edition. Since the third edition of his *Studies* has been a widely used reference work on the anatomy of Paleozoic plants, it is understandable why the idea is so prevalent that the stems of lepidodendrids possessed cambium and secondary phloem like other plants.

Of the views of the three participants in this mild controversy over the question of cambium and phloem in lepidodendrid stems, that brought forth by Seward seems to be the most objective and to be least influenced by preconceptions of how a stem is constructed. His interpretation, rather

than those of Scott and Weiss, seems to be the one that fits *Lepidodendron schizostelicum* and to find confirmation in it. Direct evidence seems to be conclusive that if there was a cambium in lepidodendrids such as *Lepidophloios fuliginosus*, *L. wünschianus*, *Lepidodendron schizostelicum*, and in most of the other familiar forms, it produced secondary xylem only.

Modern literature has contributed little to a better understanding of cambium and phloem in lepidodendrids. The main reason these tissues have received such scant attention is that they occupy parts of the axis that are usually least preserved. If the phloem is mentioned at all, it is usually in connection with a band of parenchyma around the xylem cylinder. Thus in her otherwise detailed account of *Lepidodendron scleroticum* Miss Pannell (1942) merely says that the cambium appears to have been composed of several layers of cells, and that the phloem area is small in proportion to the amount of secondary wood. The only figure intended to show these tissues (1942, Fig. 11) reveals nothing more than a band of partly disorganized cells. Evers (1951) states that the phloem cells are not preserved in *L. hallii*. Felix (1952) makes no mention of phloem in the three *Lepidodendron* species from Kansas which he described. Beck (1958), in his account of *Levicaulis arranensis* designates as phloem the band of parenchyma around the primary xylem: "The phloem is a homogeneous parenchymatous tissue composed of very small cells that are circular to irregular in transverse view, and elongated vertically, with horizontal end walls." His one figure (Pl. II, Fig. 20) shows a band of rather simple, partly disorganized parenchyma. Fry (1954) shows a parenchyma band in *Paurodendron* that is separate from both the xylem and the cortex, and states that it is apparently a remnant of the inner cortex, pericycle, and phloem. Andrews and Murdy (1958) show no phloem in their *Lepidophloios pachydermatikos*. Walton (1935) found no phloem or cambium in the trunks of *L. wünschianus* from Arran and none was preserved in the large pieces of trunk of *Lepidodendron johnsonii* from Colorado (Arnold, 1940).

The best account of tissue that may be genuine phloem in a lepidodendrid is in Calder's description of the stem of *Lepidodendron brownii* (Calder, 1933). The xylem, which is entirely primary, is surrounded by 2-3 rows of parenchyma cells, and between these and the inner cortex is a zone containing "phloem channels," so named because all but one are empty. The one channel containing tissue is filled with rather large radially elongated thin-walled cells that are greatly elongated vertically. These cells bear considerable resemblance to phloem elements, though sieve areas were not seen on their walls.

CONCLUSIONS

The internal periderm-like tissue of *Lepidodendron schizostelicum* is undoubtedly the same kind of tissue that Seward called the "meristematic zone," that Scott called "phloem," and Weiss called "cambium." Apparently none of the sections they examined showed this tissue at different distances away from the central axis. In fact, the tissues they saw might have lain against, or very close to, the central axis at all points, as cambium and phloem normally do. The situation in our specimen could well be exceptional; but that would place no difficulty in the way of regarding them as identical tissues. It is believed that Seward, Scott, and Weiss were all studying a tissue that was of the nature of periderm rather than cambium or phloem. In the material that Scott and Weiss figured, as well as in ours, the tissue in question is always separated from the secondary wood by a parenchyma layer in which the cells show no relation to the cells of the tissues it separates. Moreover, the cells of the former, though arranged in an orderly manner, indicative of origin through a series of cell divisions, do not show any such relation to the xylem elements. This lack of proper relation to the xylem is clearly revealed in the figures by Scott and Weiss, and of course the anomalous position of this tissue in our specimen is an additional reason for not interpreting it as cambium or phloem. The only conclusion in agreement with the facts is that the layer is cortical and has the structure of a periderm.

Some profound questions are bound to arise in connection with conclusions of the kind drawn here. Is it inherent in the cosmic order that a cambial initial must produce both xylem and phloem mother cells? Could a cambium exist that produces only one of these? Then there is the question of the nature of the growth mechanism that produced the secondary xylem. Did it result from a cambium that cut off derivatives only on one side, or was there no cambium as such, the radial alignment of the xylem elements having resulted from previous divisions in the procambium? The latter is suggested by the absence of anything resembling the cambium at the periphery of the xylem. Such an explanation is sometimes given for the orderly arrangement of tracheids in the veins of leaves. In the Devonian *Schizopodium* (Harris, 1929) there are no remnants of cambium outside the masses of radially aligned tracheids at the ends of the "arms" of the stellate xylem strand. In neither of these instances, however, are the masses of serially arranged cells as extensively developed as in many lepidodendrid stems, but they do show that a cambium may not be an absolute necessity for the type of cell arrangement that is exhibited.

The very sharp distinction between typical primary xylem and tissue having the appearance of having been secondarily formed in lepidodendrid

stems renders the above explanation improbable. A more likely explanation for the lack of visible cambium is that the relatively few examples in which those tissues external to the xylem are preserved are mature stems in which cessation of growth had accompanied complete differentiation of the cambial initials into vascular tissue. Since there is evidence of determinate terminal growth in lepidodendrids (Andrews and Murdy, 1958) it is possible that the lateral meristems also functioned for only a limited interval, and the state of maturity had something to do with preservation of the extra-xylary tissues.

Lack of secondary phloem in lepidodendrids does not imply absence of primary phloem, though the precise identification of such tissue is seldom possible. As stated, Calder's account of phloemlike tissue in *Lepidodendron brownii* is the most convincing of all supposed occurrences of lepidodendrid phloem. Authors commonly identify the parenchymatous layer immediately outside the xylem as phloem though diagnostic characteristics of phloem may not be demonstrable. True phloem contains sieve elements and is conducting tissue. It would be necessary to demonstrate the presence of sieve areas before the existence of phloem of any kind in lepidodendrid stems can be considered established beyond all doubt. It may be, as Seward suggested, that conduction in these plants was carried on by tissues not showing the characteristics of true phloem, but this would be difficult to prove.

The question also comes up as to whether the apparent lack of secondary phloem in a few lepidodendrid stems can be taken as evidence of its absence from all of them. It seems, however, that a difference of such fundamental character as the presence or absence of phloem would not exist among closely related forms. Such a difference would certainly be associated with other morphological characters that would set them apart in other respects.

Secondary phloem is nonexistent in living lycopods with the possible exception of the enigmatic *Isoetes*. Even there, none is formed outside the cambium. The fact that the *Isoetes* cambium forms no vascular tissue externally may turn out to be a significant feature with respect to possible relationship with the lepidodendrids. Even the primary phloem is relatively simple in living lycopods.

Some of the fallacies in attempts to recognize cambium and phloem in lepidodendrid stems as encountered in the literature are due to the following: (a) identification of cambium and phloem solely on the basis of location without regard to cell characteristics; (b) failure to distinguish between primary and secondary phloem; (c) erroneous comparisons with phloem in recent lycopods due to lack of familiarity with it; (d) the dog-

matic assumption that if a stem contains secondary xylem, it must also contain secondary phloem; (e) calling a tissue "cambium" though its cells are much smaller than the adjacent xylem elements, and do not "line up" with them; (f) calling a tissue "cambium" when it is separated from the secondary xylem by other tissue, thus requiring that the xylem mother cells "jump" a barrier during their development; and (g) disregard of extreme differences between length of xylem and the alleged cambium and phloem cells.

SUMMARY

A small *Lepidodendron* stem from a coal ball from the Cherokee group of the Pennsylvanian system of southeastern Kansas is described. The stem is distinguished by the presence of conspicuous raylike structures that extend across the secondary xylem and terminate in the primary xylem near the pith. Some of the tissues immediately external to the secondary xylem are exceptionally well preserved. No tissues showing histological characteristics of phloem can be recognized, but a band of internal periderm-like tissue, that at places is separated from the xylem only by a narrow layer of small-celled parenchyma might be mistaken for phloem if not critically examined. This tissue seems to be identical with that which Seward designated the "meristematic zone," and Weiss called "cambium" in *Lepidophloios fuliginosus* and Scott called "phloem" in *L. wünschianus*. Seward's conclusion that the cambium did not form secondary phloem in the lepidodendrids is supported. The stem is named *Lepidodendron schizostelicum*, sp. nov., in allusion to the xylem cylinder which is partly divided by conspicuous large raylike structures.

LITERATURE CITED

- ANDREWS, H. N., and MURDY, W. H. 1958. Lepidophloios—and Ontogeny in Arborescent Lycopods. *Amer. Journ. Bot.*, Vol. 45, pp. 552-60.
- ARNOLD, C. A. 1940. *Lepidodendron johnsonii* sp. nov., from the Lower Pennsylvanian of Central Colorado. *Contrib. Mus. Paleontol. Univ. Mich.*, Vol. 6, pp. 21-52.
- BARGHOORN, E. S., and SCOTT, R. A. 1958. Degredation of the Plant Cell Wall and its Relation to Certain Tracheary Features of the Lepidodendrales. *Amer. Journ. Bot.*, Vol. 45, pp. 222-27.
- BECK, C. B. 1958. "Levicaulis arrenensis," gen. et sp. nov., a Lycopoid Axis from the Lower Carboniferous of Scotland. *Trans. Roy. Soc. Edinburgh*, Vol. 63, pp. 445-56.
- CALDER, M. G. 1933. Notes on the Kidston Collection of Fossil Slides. No. 1. The Anatomy of the Axis of *Lepidodendron Brownii* Unger sp., with Special Reference to the Relationship Between this Stem and *Lepidostrobus Brownii* Unger sp. *Ibid.*, Vol. 57, pp. 547-55.

- 1934. Notes on the Kidston Collection of Fossil Slides. No. 5. On the Structure of Two Lower Carboniferous Stems, one of the Lepidophloios wünschianus type and the other of the Lepidodendron fuliginosum type. *Ibid.*, Vol. 58, pp. 113-24.
- EVERS, R. A. 1951. A Lepidodendron from Illinois. *Amer. Journ. Bot.*, Vol. 38, pp. 731-37.
- FELIX, C. J. 1952. A Study of the Arborescent Lycopods of Southeastern Kansas. *Ann. Missouri Bot. Gard.*, Vol. 39, pp. 263-88.
- FRY, W. L. 1954. A Study of the Carboniferous Lycopod, Paurodendron, gen. nov. *Amer. Journ. Bot.*, Vol. 41, pp. 415-28.
- HARRIS, T. M. 1929. *Schizopodium Davidi*, gen. et sp. nov.—a New Type of Stem from the Devonian Rocks of Australia. *Phil. Trans. Roy. Soc. London, Ser. B*, Vol. 217, pp. 395-410.
- HIRMER, M. 1927. *Handbuch der Paläobotanik*, München and Berlin.
- PANNELL, E. 1942. Contributions to our Knowledge of American Carboniferous Floras. IV. A New Species of Lepidodendron. *Ann. Missouri Bot. Gard.*, Vol. 29, pp. 245-60.
- SCOTT, D. H. 1900. *Studies in Fossil Botany*. London.
- 1920. *Studies in Fossil Botany*. Vol. I. 3d ed.; London.
- SEWARD, A. C. 1900. Notes on the Binney Collection of Coal-Measure Plants. Pt. I. *Proc. Cambridge Phil. Soc.*, Vol. 10, pp. 137-57.
- 1902. On the So-called Phloem of Lepidodendron. *New Phytol.*, Vol. 1, pp. 38-46.
- 1910. *Fossil Plants*. Vol. 2. Cambridge.
- WALTON, J. 1935. The Fossil Hollow Trees of Arran and their Branches (Lepidophloios Wünschianus Carruthers). *Trans. Roy. Soc. Edinburgh*, Vol. 58, Pt. 2, pp. 313-37.
- WEISS, F. E. 1901. On the Phloem of Lepidophloios and Lepidodendron. *Mem. and Proc. Manchester Lit. and Phil. Soc.*, Vol. 45, Mem. 7.

Submitted for publication April 18, 1960

PLATES

EXPLANATION OF PLATE I

	PAGE
<i>Lepidodendron schizostelicum</i> Arnold, sp. nov.	255
FIG. 1. Transverse section. $\times 6$.	
FIG. 2. Part shown on right side of Fig. 1 showing raylike structures that traverse the xylem cylinder and terminate near the pith. $\times 16$.	

PLATE I

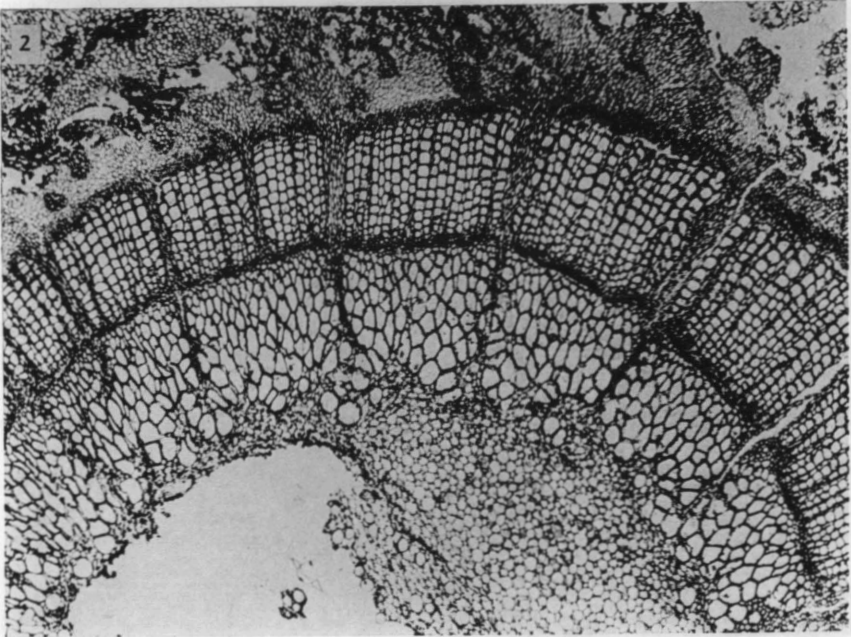
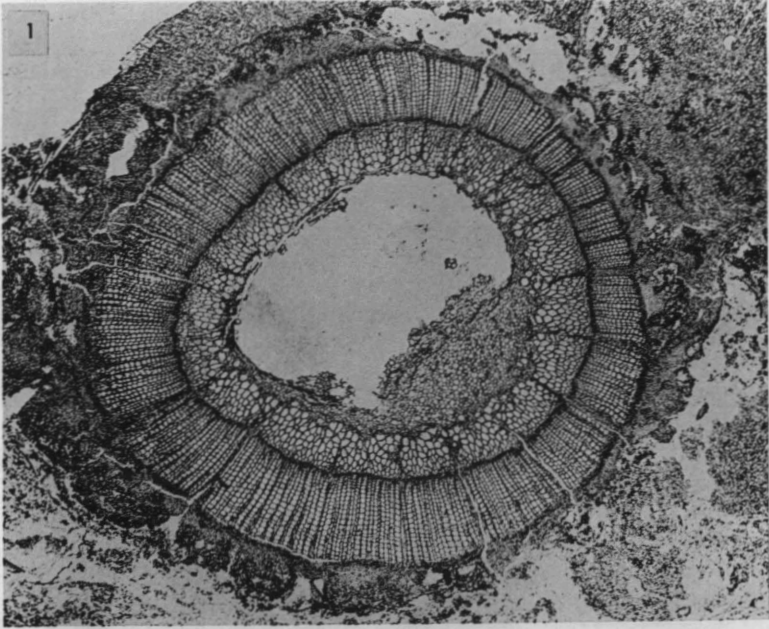
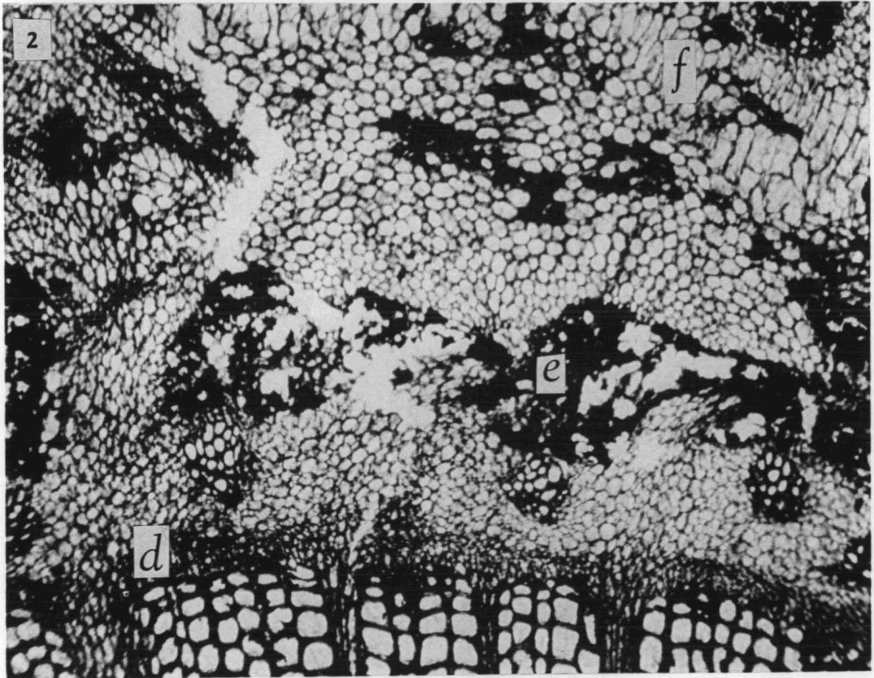
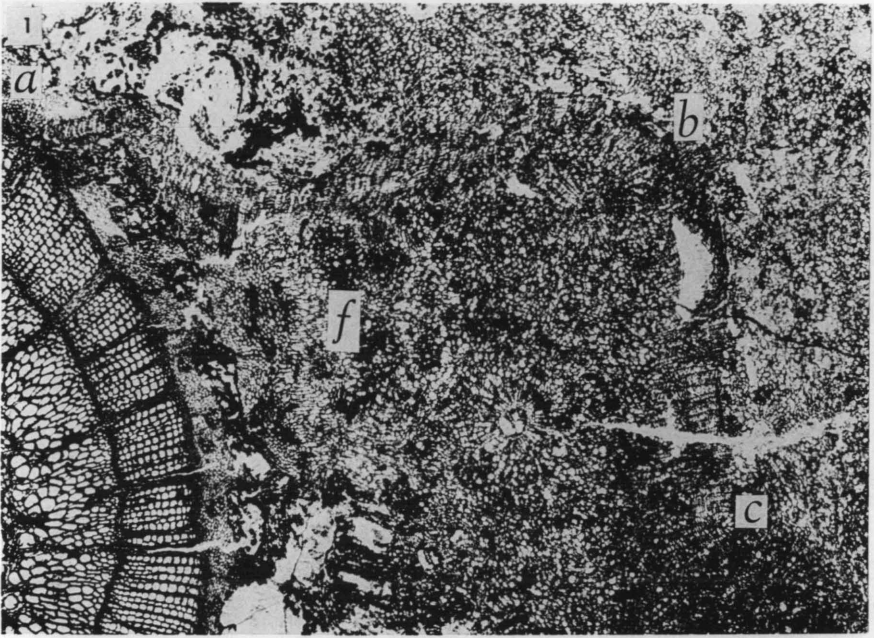


PLATE II



EXPLANATION OF PLATE II

	PAGE
<i>Lepidodendron schizostelicum</i> Arnold, sp. nov.	255

FIG. 1. Transverse section showing part of xylem cylinder and extra-xylary tissues. The band of internal periderm bends away from the xylem at *a* and extends out into the inner cortex, *b* and *c*. Another band of internal periderm is situated nearer the stele at *f*. $\times 10$.

FIG. 2. Secondary xylem bounded by narrow band of small-celled parenchyma, *d*, followed by inner cortical tissue containing leaf traces and "secretory zone," *e*, and internal periderm, *f*, which is also shown at *f* in Fig. 1. $\times 40$.

EXPLANATION OF PLATE III

	PAGE
<i>Lepidodendron schizostelicum</i> Arnold, sp. nov.	255
FIG. 1. Part of transverse section showing internal periderm adjacent the secondary xylem. $\times 50$.	
FIG. 2. Raylike structure extending across the primary xylem. $\times 50$.	
FIG. 3. Part of internal periderm band at approximate position of <i>c</i> in Pl. II, Fig. 1. $\times 50$.	
FIG. 4. Radiating cells surrounding leaf trace in inner cortical region inside the internal periderm but external to the "secretory zone." $\times 50$.	

PLATE III

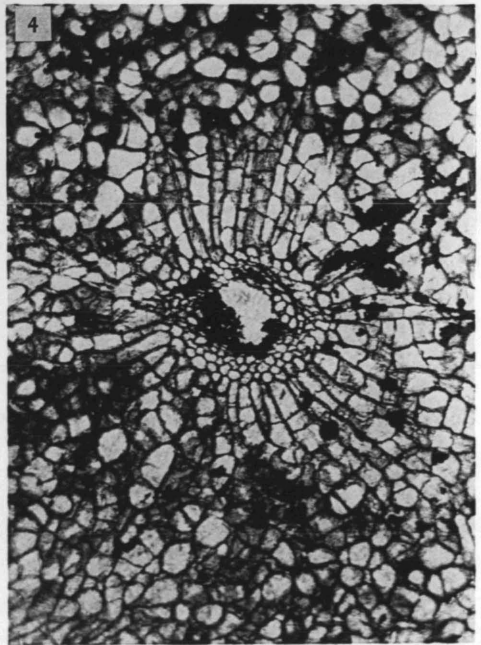
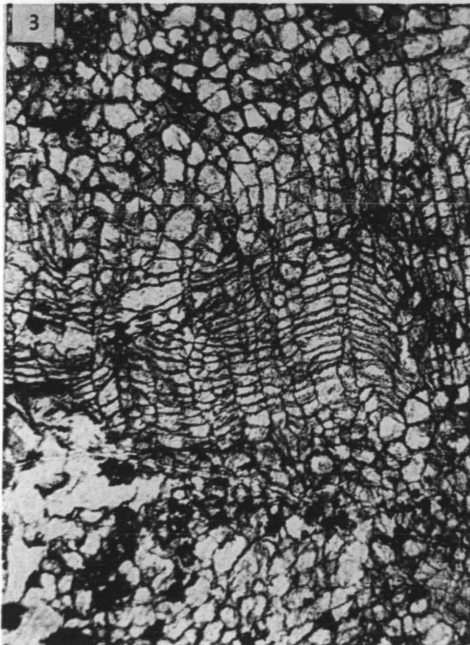
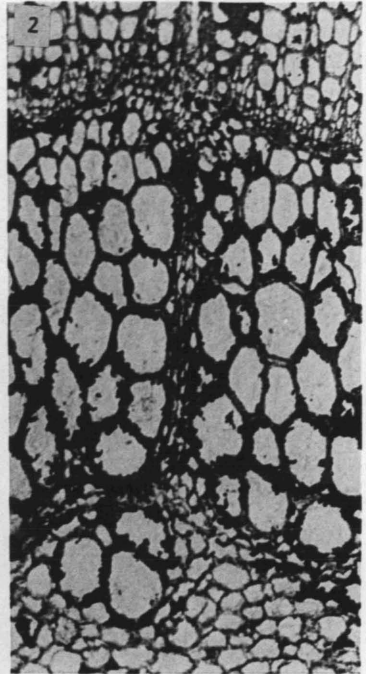
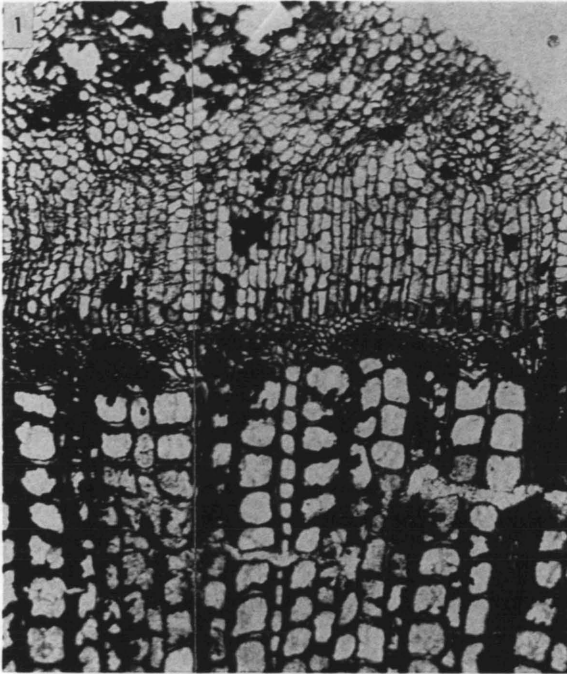
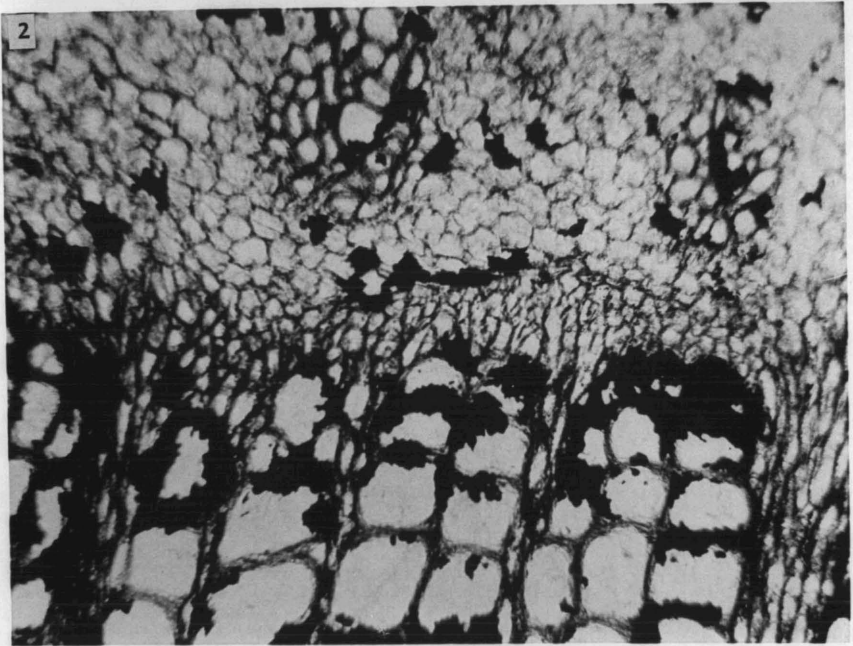
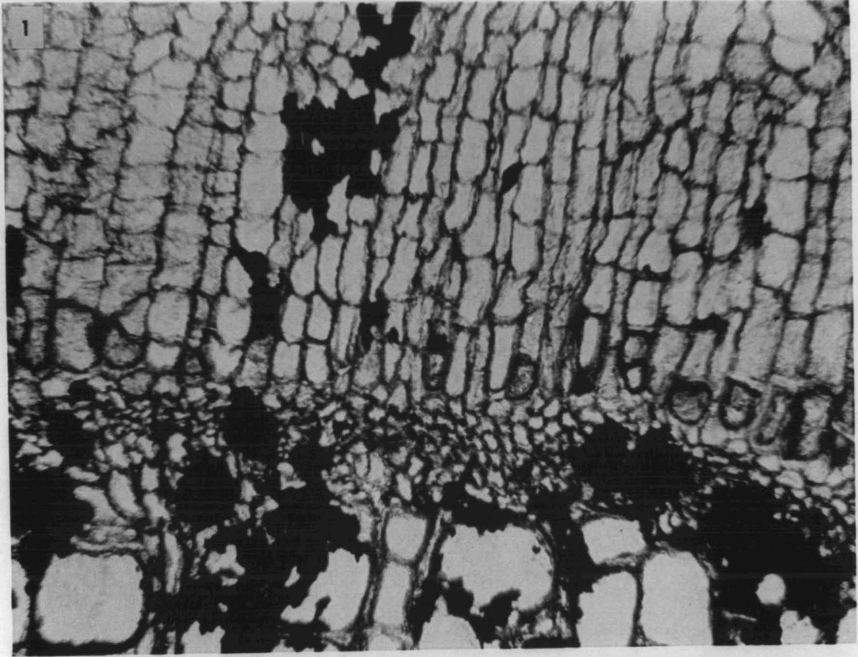


PLATE IV



EXPLANATION OF PLATE IV

	PAGE
<i>Lepidodendron schizostelicum</i> Arnold, sp. nov.	255

FIG. 1. Part of region where internal periderm lies adjacent the stele. The cells are slightly elongated in the radial direction and are radially aligned. A layer of small-celled parenchyma separates the internal periderm from the xylem. $\times 100$.

FIG. 2. Part of region at a slight distance along the circumference of the xylem cylinder from the place where Fig. 1 was taken showing an area in which ordinary inner cortex lies adjacent the xylem and separated from it by the small-celled parenchyma. Two leaf traces are shown. The internal periderm at this place lies outside the upper limit of the photograph. $\times 100$.

