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### CONTRIBUTIONS TO OUR KNOWLEDGE OF AMERICAN CARBONIFEROUS FLORAS<sup>1</sup>

#### IV. A NEW SPECIES OF *LEPIDODENDRON*

ELOISE PANNELL

*Formerly Graduate Assistant, Henry Shaw School of Botany of Washington University*

Previous investigations have established *Lepidodendron* as one of the most abundant and widely distributed genera during the Carboniferous period, and the results of the present study indicate that it was the dominant element of the southern Illinois flora in middle Pennsylvanian times.

Lycopod remains are present in almost every specimen of the hundreds of coal-balls collected during the past two years from the Pyramid mine of the Binkley Coal Company in Perry County, Illinois.<sup>2</sup> Over 100 stems referable to *Lepidodendron* have been found thus far. This study is based chiefly on a selection of about 25 of the best-preserved specimens exhibiting a representative picture of the structural variations found in the various orders of branching. Associated with the stems are leaves, roots, and reproductive organs. Some of these have already been described (Andrews and Pannell, '42) while others will be considered here and in later studies.

#### ***Lepidodendron scleroticum* sp. nov.**

The designation of a new species of this supposedly well-known genus probably needs a few words of explanation. Since Sternberg's

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<sup>2</sup> A detailed description of the occurrence of coal-balls at this locality has been given in the first of this series of contributions (Ann. Mo. Bot. Gard. **29**: 1-18. 1942).



account of the type species in 1823, more than 100 others have been described from compression material and over 20 from petrified specimens. There is little doubt that a considerable amount of synonymy exists in this long list of names. It is equally obvious to any investigator who has studied the Carboniferous Lycopods at all carefully that we are only beginning to understand the morphological boundaries of the group. Very notable contributions relative to their reproductive organs have been made during the past few years (Arnold, '40; Hoskins and Cross, '41; Schopf, '38; Andrews and Pannell, '42). It is hoped that future studies will shed more light on the relationships between the cones and isolated vegetative remains.

*Lepidodendron* stems constitute the dominant element of our Pyramid Mine collections, and the genus is abundantly represented in the roof shales of certain southern Illinois mines. The large number of specimens at hand makes possible a much more complete description of the stem structure of the plant as a whole than do most of the previously described species, many of which are based on a single specimen. It will also be shown that *L. scleroticum* presents highly distinctive cortical characters which in themselves adequately justify the new specific name.

The stems range from 3 mm. to 9 cm. in diameter, while larger stelar fragments or portions of bark were found indicating stems as large as 30 cm. in diameter. Two specimens with abundant secondary growth have been selected to show the typical organization of the tissues and the distinctive features of the species (pl. 18, figs. 1 and 2). They are numbers WCB55 and WCB56 respectively, in the Washington University fossil plant collection. A description of these specimens is followed by a shorter consideration of certain others in order to present a composite picture of the shoot system as a whole.

The pith, which is present in all of the larger stems, is surrounded by the xylem cylinder of primary and secondary origin, which is in turn surrounded by the phloem. The cortex may be divided into three zones, although these are not always distinct. The inner cortex immediately exterior to the phloem is composed of delicate parenchymatous and small sclerotic cells. The parenchyma cells are often poorly preserved and the sclerotic cells crushed. The highly distinctive middle cortex consists of sclereids grouped into nests and surrounded by parenchyma. The outer cortex presents a dicty-



oxylon arrangement of slightly elongate thickened cells and parenchyma.

The periderm forms a large portion of the stem. It is composed of compactly arranged cells that were intimately connected with the mechanical support of the tree. The cork cambium is well preserved in some of the smaller stems.

*Development of the Primary Xylem.*—

In *Lepidodendron scleroticum* there is a marked relationship between stem size and primary xylem development. In small twigs from 3 to 10 mm. in over-all diameter, the xylem cylinder is typically protostelic, measuring from .26 to .78 mm. (pl. 19, fig. 6). The protoxylem is exarch and unevenly distributed around the periphery. Branches with steles as small as this never exhibit any secondary xylem. Stems from 10 to 22 mm. show a mixed protostele varying from 1.04 to 1.56 mm. in diameter (pl. 19, fig. 3). When the cylinder of the primary xylem attains a diameter of 1.5–2 mm. secondary wood begins to form. In older stems from 3 to 5 cm. in diameter the

TABLE I

SHOWING THE RELATIONSHIPS BETWEEN DIMENSIONS OF PITH AND PRIMARY AND SECONDARY XYLEM IN THE VARIOUS BRANCH ORDERS

Stem No.	Total diameter of stele	Radius of the primary body	Radius of the primary xylem ( $X_1$ )	Radius of the secondary xylem ( $X_2$ )
	mm.	mm.	mm.	mm.
WCB16 (2)	.26	.13	.13	None
WCB55A (2)	.39	.18	.18	None
WCB54 (2)	.45	.23	.20	None
WCB265 (2)	.52	.26	.24	None
WCB16B (3)	.52	.26	.24	None
WCB54 (3)	1.04	.53	.31	None
WCB55A (2)	1.10	.55	.45	None
WCB124A (1)	1.30	.65	.55	None
WCB54C (7)	1.56	.78	.52	None
WCB16B (3)	1.69	.64	.58	None
WCB54A (8)	1.69	.84	.71	$X_2$ beginning
WCB58A (2)	1.88	.94	.78	$X_2$ beginning
WCB106A (1)	2.08	1.04	.80	None
WCB124A (1)	2.08	.84	.62	.19
WCB19C (1)	4.81	1.23	.65	1.17
WCB135A (2)	5.20	1.69	.91	1.04
WCB180A (2)	5.72	1.30	.84	1.56
WCB57A (2)	5.98	1.69	.91	1.43
WCB56B (7)	6.24	1.82	.97	1.30
WCB148A (2)	6.76	1.82	1.04	1.52
WCB55A (10)	6.86	1.56	1.04	1.82
WCB61B (1)	7.80	1.82	1.77	2.08
WCB18A (2)	7.87	1.95	1.77	2.21
WCB20X (5)	8.12	2.04	1.04	2.20



xylem cylinder averages 6.7 mm., of which 3.1 is primary and 3.6 is secondary. The pith is now well developed, forming about one-half the total diameter of the primary body. Figure 6 is a photograph of the largest stele found, the secondary xylem measuring 22 mm. in radius and the primary xylem 6-7 mm. Table 1 presents a more detailed compilation of the dimensions of 24 well-preserved stems.

The sequence of development shown in the table is uniform, and since only stems with well-preserved cortical tissues were used there is no reason to believe that they are not all referable to *L. scleroticum*.

A study of this series not only clearly illustrates the intra-stelar origin of the pith, but it presents evidence that the whole primary body increases in size even after the initiation of secondary wood. The evidence is based on the three following points: (1) no secondary wood around a protostele or a small primary cylinder was observed; (2) all the larger stems showed a siphonostele which probably developed from the smaller mixed protostele during the formation of the first few mm. of secondary growth; (3) wedge-shaped gaps exist between the secondary tracheids along the contact zone between the primary and secondary xylem (fig. 8) which are constant in all stems of any appreciable secondary growth. The gaps may be due either to pressure exerted by the increased circumference of the primary cylinder or to the decay of parenchymatous tissue laid down during the early stages of cambial activity. The rather fine preservation of the immediately adjoining parenchyma cells in both primary and secondary wood leaves little doubt that the first explanation is the correct one. The increase in size of the metaxylem was probably accomplished both by the maturation of the individual tracheids (cf. figs. 3, 6) as well as by the division of parenchyma cells associated with the tracheids.

Bower ('30) has been the most active investigator of the development of the primary body of vascular cryptogams. His research attempted to determine the physiological relationships between tracheids and living parenchyma cells which seemingly govern the ontogeny of the primary stelar body. He dealt largely with the different types of steles exhibited in the various species of Lycopods and concluded that the primitive xylic column in the fossil forms may undergo one or more of four types of progressive changes in order to maintain a more or less constant tracheid-parenchyma relationship. These may be briefly summarized as:



1. A "fluting" of the periphery of the primary body is noted in certain species (*L. Harcourtii* Witham, and *L. selaginoides* Binney). This fluting resulted in a series of concave crenulations which increased the surface area.

2. Medullation occurs in most *Lepidodendrons*, but some are reported as protostelic while others develop a mixed protostele or siphonostele. Bower described branches of *Lepidophloios Wunschianus* Carruthers which show a general relationship of stem size to pith development, but he made no observations on the beginning of secondary growth in the various twigs.

3. In species which developed secondary xylem the wood rays apparently served to retain a more or less constant tracheid-parenchyma relationship. Secondary wood may occur in both protostelic and medullated species although in some it is reported as absent.

4. Segregation of the primary xylem into separate strands occurs in certain *Lepidostrobus* cones (*L. Brownii*).

These four tendencies apparently helped maintain a nearly constant ratio of living to dead cells in the progressive evolution of the vascular tissue in the fossil Lycopods.

#### *The Secondary Xylem.*—

The fossil Lycopods produced little secondary wood in comparison with the size of the trunk. In most of the *Lepidodendron scleroticum* stems studied, which were about 4 cm. in diameter, the ring of secondary xylem measured from 1 to 2 mm. in width. Isolated fragments in which the secondary wood reached a radial dimension of 5 cm. were found, but it cannot be said definitely that they belong to *L. scleroticum*, since the outer parts of the stem were not preserved. However, the specimen previously discussed (pl. 19, fig. 4), which developed secondary wood 3 cm. in thickness, possessed enough fragments of the characteristic cortical sclerotic nests to be assigned to this species.

At first, secondary growth is slight and develops frequently only on one side, with gaps between the active cambial cells. In such specimens the cambial development is closely comparable to that found in *Lepidodendron fuliginosum* Williamson, *L. intermedium* Williamson, and *L. obovatum* Sternberg. This peculiar type of cambial activity is described by Scott ('20, p. 137), for the above three species as follows:



"The cambium was an anomalous one, arising in various parts of the phloem zone and pericycle. It produced a good deal of the secondary parenchyma, among which there are usually scattered groups of wood; the secondary tracheids have a very sinuous and irregular course. We may regard these species as exhibiting either a primitive and rudimentary or reduced form of secondary wood."

*Lepidodendron scleroticum* shows this supposed primitive character only at the beginning of the growth of secondary wood, for after 10 to 20 xylem cells have been formed in an irregular manner the tracheids around the entire primary stele develop actively. There is frequently unequal growth of secondary wood on one side of the cylinder, probably due to some environmental condition.

The first few secondary tracheids formed average 52  $\mu$  in width; but after 10 to 20 cells have developed, the tracheids range from 88 to 104  $\mu$ . None of the secondary tracheids reached the robust size of the primary ones which average 130  $\mu$ , some even 195  $\mu$ . Although the length of the tracheids is difficult to follow, due to their frequent distortion by rays and traces, approximately 30 cells were followed in their entirety. These were found to average 12 mm., some reaching 15 mm. Near the ends, the tracheids gradually tapered to a point.

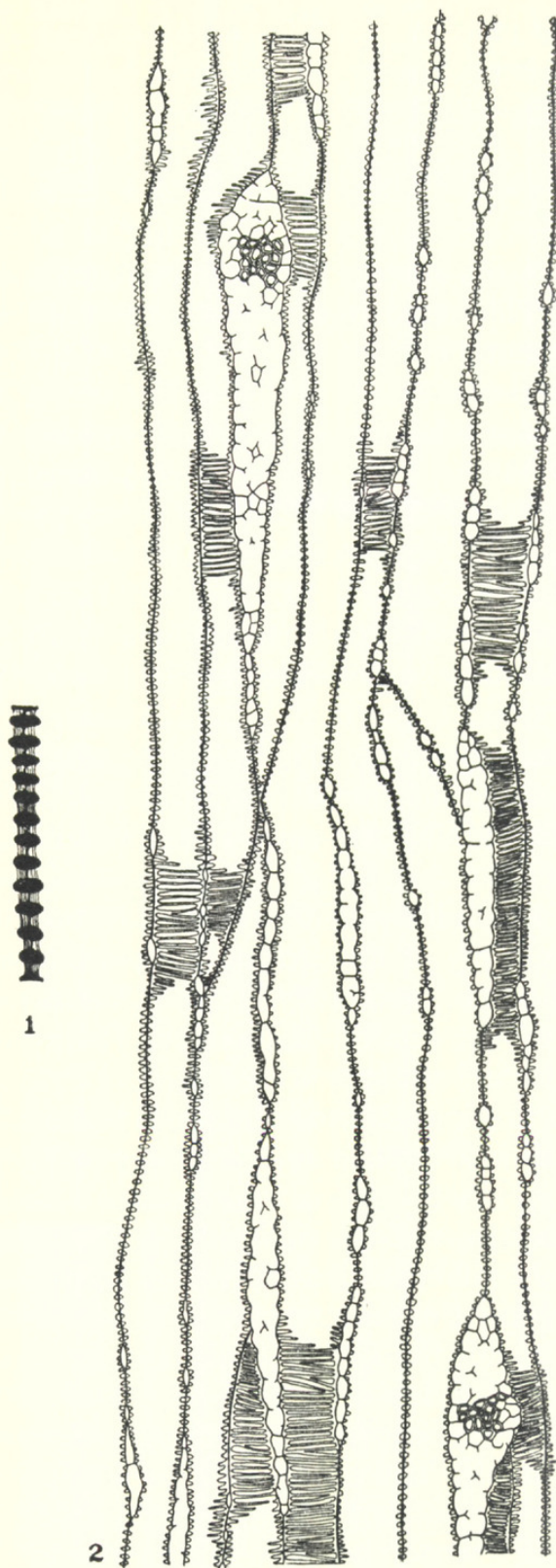
Using the maceration technique, the pronounced scalariform sculpturing of the secondary walls of the primary and secondary tracheids was studied in detail (fig. 5). The transverse bars are about 5.3  $\mu$  in width and are spaced at a slightly greater distance. They extend completely across the wall face and at the corners merge into a continuous layer. The bars frequently dichotomize but with no regularity. Extending across the openings between the bars is a series of numerous fine threads which have been described in several other species of *Lepidodendron* as well as in *Lepidostrobus Bertrandi* Zalesky, *Sigillaria Boblayi* Brongn. and *Stigmaria ficoides* Brongn. Three interpretations of their morphology have been recorded:

1. Seward and Hill ('00) describe them as post-mortem changes in the primary wall which made the pit-closing membrane torn and fragmentary.

2. Calder ('32) considers them, in *Lepidodendron Brownii* Unger, as tertiary thickenings laid down in a thin layer around the bars of the scalariform thickenings, with the fine threads connecting the layers.

3. Arnold ('40), in his description of *Lepidodendron Johnsonii*, regards them as part of the secondary thickenings which lay against the primary wall and bridged the pit cavity on the inside.





Text-figs. 1-2.—*Lepidodendron scleroticum*: fig. 1, longitudinal section of scalariform thickenings,  $\times 100$ ; fig. 2, tangential section of wood,  $\times 50$ .



A study of the macerated tracheids of *L. scleroticum* presents strong evidence supporting their secondary nature as described by Arnold. The threads show definite connection with the secondary thickenings (text-fig. 1). They are also too evenly spaced to be torn fragments of the primary thickenings as Seward and Hill regarded them. Their structure appears similar to the outgrowths of the secondary walls in the vested pits of the Angiosperms described by Bailey ('33). The scalariform thickenings and the threads seem to be of the same material with no outer layer of the bars or tertiary thickenings as reported by Calder. The fine strands are, as far as it is possible to determine, secondary thickenings of the same material as the scalariform bands lying next to the primary wall connecting adjoining bars.

The wood rays vary from a single row of cells to many cells high and several cells wide (text-fig. 2). The cells range from 15 to 30  $\mu$  in diameter and are about three times as long (radially). The walls of all the ray cells are characterized by delicate scalariform thickenings although these never become as pronounced as in the tracheids or leaf trace elements. There is no reason to believe, however, that they were not living cells, and they present the only possibility of maintaining the ratio of living to dead cells in the secondary xylem.

On the basis of studies in other plant groups the rays of *L. scleroticum* are clearly of an exceedingly primitive nature. This is suggested both in the variability in size of the rays as a whole, as well as the wide range in individual cell size. A less specialized ray structure would be difficult to conceive.

The leaf trace originated from the protoxylem cells at the periphery of the primary xylem and followed a horizontal course through the entire extent of secondary wood in all the specimens studied. This feature is of considerable interest since the largest stems had certainly shed their leaves before any appreciable amount of secondary growth. Both the tangential sections of the leaf bases and the impressions of the *Lepidodendron* stems in the shale indicate that only small twigs actually bore leaves. This persistent growth of the leaf trace has been noted in certain species of *Araucaria*, living and fossil. The character is probably present in other species of *Lepidodendron*, but it has not been studied in detail.

Near the primary wood the trace is surrounded by only a few ray cells, but as it progressed through the secondary wood the surrounding ray tissue increased in height and breadth. Text-fig. 2



was drawn from a tangential peel taken about 3 mm. from the periphery of the primary wood. The amount of xylem cells remains relatively constant in all the traces, as well as within the same trace as it progresses through the secondary wood. The protoxylem, if such were differentiated, is not distinguishable.

The leaf trace follows an upward course through the cortex and then resumes a horizontal course through the extensive periderm tissue. This will be considered in more detail in the discussion of the extra-stelar tissues.

#### *Branching.*—

An excellent specimen showing monopodial branching is included in our collections (No. WCB254). The block was sectioned into nine parts and the stele studied at the various stages of development. The progressive origin and departure of the branch trace, with the closing of the gap, are illustrated in pl. 21, figs. 13–16. In fig. 13 the stele is seen before the departure of the branch, while fig. 14, which is 5 mm. above, represents the beginning of the trace. In fig. 15 the branch trace has progressed in its upward course 10 mm., and in fig. 16 about 20 mm., from the point of origin. The new stele is at first crescent-shaped, and as it departs, some secondary wood is carried with the primary tracheids (fig. 15). The branch gap is then bridged and the stele of the branch becomes circular, losing the secondary wood. Shortly above the last stage figured, the specimen becomes poorly preserved and the newly formed branch is completely lost.

In fig. 16 at *p* a band of tissue, secondary in origin and presumably periderm, may be noted. In all probability this represents the junction of the stem and branch cork but it was not possible to follow it up high enough to observe the actual separation of the branch.

Most of the stem compressions observed in the roof shales in southern Illinois mines indicate that dichotomy was of more frequent occurrence than monopodial branching, and only a few poorly preserved specimens branching dichotomously have been found in the coal-balls. Although a reconstruction of *L. scleroticum* probably compares closer to Hirmer's for *L. obovatum* (Hirmer, '27) than it does to Scott's for *L. elegans* (Scott, '20) the types of branching undoubtedly varied considerably in different species.

#### *Cambium and Phloem.*—

The delicate nature of the cambium and phloem prevents good preservation in fossil plants. In *L. scleroticum*, these tissues are



partially preserved only in the better specimens. The cambium appears to have been composed of several layers of cells, and the surrounding phloem area is very small when compared with the large amount of secondary wood. These cells are represented in fig. 11. There have been two interpretations of the structure of the phloem cells in *Lepidodendron*: one, supported by Weiss ('01), states that sieve cells are present; the other view, that of Seward ('02), holds that the phloem cells were not morphologically sieve cells but a type of secretory cell. It is only possible to say that the phloem in *L. scleroticum* probably consisted of very primitive undifferentiated parenchymatous cells not great in extent and little of secondary origin.

*The Cortex.*—

The cortical tissue is composed of three zones which are distinct even in young twigs. The inner cortex directly adjoining the phloem consists of delicate parenchymatous cells and small heavily thickened sclerotic cells. The parenchymatous cells are usually poorly preserved and the sclerotic cells crushed. The disorganized tissue forms a band next to the xylem in most of the stems (fig. 21).

The remaining cortical cells, separated from the inner cortex by a cavity caused by the decay of that tissue, are well preserved. The middle cortex is composed of heavily thickened sclerotic cells grouped into nests and surrounded by parenchymatous cells most abundantly associated with the leaf traces which follow a gradual upward course through the cortex. The position, arrangement, and size of these cells may be noted in figs. 17, 18, and 19.

The outer cortex consists of parenchymatous and sclerenchymatous cells which are less thickened and more elongated than the sclerotic ones of the middle cortex. At first there are only a few small elongate sclerenchymatous cells among the sclerotic nests, but in the outer portions of the cortical region a reticulate network is formed from the decayed parenchymatous cells surrounding the leaf trace and the fibrous sclerenchyma (fig. 20).

The composition and arrangement of the cortical tissue present the most distinctive characters of *Lepidodendron scleroticum*. The sclerotic nests, which have never been reported in a species of *Lepidodendron*, make possible specific recognition when only fragments of the stems are preserved. The reticulate network of the outer portions of the cortex has been described in *L. esnostense* and *L. rhodumnense* Renault ('79). These species differ from *L. sclerot-*



*icum* not only in cortical tissue, for they have no sclerotic nests, but they were protostelic with no secondary xylem.

*The Periderm.*—

The periderm of the fossil Lycopods is one of their most characteristic features, since it was not primarily a protective tissue, but served as the main support of the stem. The early English paleobotanists regarded it as vascular tissue or “pseudo-wood” (Binney, 1862, Witham, 1833). Williamson (1872) was the first investigator to dispel this erroneous concept. Since that date our knowledge of this tissue has rapidly increased, terminating in the thorough study by Kisch ('13).

In *Lepidodendron scleroticum*, the cork cambium arises early in the growth of the twig, often before the mixed stele has developed an active vascular cambium. The phellogen originates 5–10 cells within the epidermis and divides rapidly. As in other species of *Lepidodendron*, the division is the exact reverse of the phellogen activity in modern trees, for the cambium lays down the great bulk of the tissue centripetally with only a small portion of phellem. A young twig shows little cellular differentiation of the cork (fig. 23) until after 2 to 3 mm. of growth. Its cells near the leaf bases divide radially, which increases the circumference of the stem and keeps the leaf bases intact. Most of the periderm cells are 6–10 times longer than broad and are sharply pointed at the ends. They vary from thick and heavy to fragmentary and thin (fig. 22). The transition occurs in frequent succession and the partial decay of the thin-walled cells produces a series of holes. Such a periderm structure has been described in *Lepidodendron selaginoides* and *Lepidophloios Wunschianus*, but the degree of thickening of the preserved cell walls in those species is more constant. These gaps in the periderm have been described by Hovelacque ('92), in *Lepidodendron selaginoides*, as less-resistant layers formed at periods of sluggish growth, but recently they have been interpreted in another species as secretory strands (Arnold, '40). Although some of the cells surrounding the cavities show horizontal septa in tangential section, there are no other indications that the gaps were anything but decayed cells of less-resistant structure.

The leaf trace follows a horizontal course through the great mass of periderm. Small sclerotic cells of the cortex may follow the trace for a distance into the cork, but the parenchyma cells associated with the trace have greatly decreased in mass.



*The Leaf Bases.*—

The structurally preserved leaf bases of *L. scleroticum* were studied by peels made tangential to both young and old stems and were found to have the characteristic shape shown in fig. 26. The general appearance of the leaf cushions is a spiral arrangement of rhomboid structures separated by a narrow groove where the stem surface was exposed. A small ligule, sunken in a pit, appears near the apex of the cushion. Beneath the ligule is the vascular bundle surrounded by a cavity of decayed parenchyma and phloem. In most species, parichnos strands are present on either side of the vein. Young twigs of *L. scleroticum* show parichnos composed of 10–15 parenchyma cells, but in older cushions the parenchyma cells and phloem have decayed, leaving a cavity surrounding the lower parts of the xylem cells of the trace.

Several isolated fragments of leaf bases referable to *Lepidophloios* were also found in the Pyramid Mine coal-balls (fig. 24). Judging from the relatively few specimens found, however, this genus constituted but a minor element in the flora. A considerable number of well-preserved supposed *Lepidodendron* stems have been checked by means of sections taken through the leaf cushions to insure their correct identification. It is hoped that future collections may shed additional light on this *Lepidophloios* species.

An attempt has been made to correlate *Lepidodendron scleroticum* with certain of the large Lycopod trunk compressions occurring above the same coal seam in adjacent parts of Illinois. Approximately 25 specimens of stem compressions of various sizes were collected from the shale above coal #6 at the Old Ben Mine #11, Franklin County, Illinois. Exact specific determinations of impressions and compressions is difficult due to the varying degrees of preservation. It was possible, however, to separate the collection with reasonable accuracy into two species of *Lepidodendron* and one of *Lepidophloios*. The impressions of the leaf bases of *Lepidophloios laricinus* Sternberg closely resemble those of the petrified *Lepidophloios* figured. Of the two *Lepidodendrons*, *L. Volkmannianum* Sternberg ('25) compares more favorably with leaf bases of *L. scleroticum*. The other *Lepidodendron* impressions are probably *L. rimosum* Sternberg, for the leaf bases are slender. *Lepidodendron Volkmannianum* (fig. 26) has been reported a number of times from the southern Illinois area, although it was described under different specific names (Lesquereux, '66, '70; Noé, '25).



The size of the impression specimens of *L. Volkmannianum* on the shale above the coal shaft makes a probable reconstruction possible. Figure 26 is one of the smaller stems, about  $1\frac{1}{2}$  inches in diameter. It was selected as an illustration because its size is comparable to the majority of the *Lepidodendron scleroticum* specimens, and although the trace and parichnos cannot be clearly observed the leaf scar is easily recognized. The stem branches dichotomously at the top, but the preservation of one branch is poor. Other specimens show leaf bases from  $\frac{1}{2}$  to  $\frac{3}{4}$  inches wide. Judging from the size relationship of leaf bases and stem in the completely preserved impressions, these larger specimens would probably have measured 1–2 feet in diameter.

*Economic Importance.*—

In view of the fact that *Lepidodendron* stem remains are by far the most frequently encountered fossils in the Pyramid Mine coal-balls it is of interest, economically, to note that the coal itself is in all probability composed very largely of the stems and leaves of this plant. Since the periderm constitutes the greater part of the stems it is that tissue which is largely responsible for this rich deposit of coal.

*Diagnosis:* Primary body protostelic to siphonostelic depending on stem size; secondary xylem present, abundantly so only around fully developed siphonosteles; inner cortex characterized by prominent sclerotic nests, outer cortex a reticulate sclerotic net in tangential section; massive periderm irregularly zoned by decay of less-resistant cells; leaf cushions resembling closely those of *L. Volkmannianum*.

*Locality and Horizon:* Pyramid Mine of the Binkley Coal Company, Perry County, Illinois; coal #6, Carbondale formation, middle Pennsylvanian.

*Type specimens:* WCB55 and WCB56, Washington University (St. Louis).

*Lycopod Organs Associated with L. scleroticum.*—

*Leaves:* Many Lycopod leaves were found preserved near the petrified *Lepidodendron* stems. Although the evidence strongly suggests their affinity with *L. scleroticum*, no stems were found actually connected with the Lycopod leaves. The leaves vary from 1



to 5 mm. in width. Although their shape is frequently distorted, all their internal tissues show the same general arrangement. The length of the leaves is impossible to determine accurately since they were curved and broken before petrification. Several could be measured from 2 to 3 cm. in length without any appreciable change in thickness.

The xylem occurs in a single horizontally elongated strand composed of 40–50 tracheids, the amount of xylem varying with the leaf size. The protoxylem cells are difficult to distinguish, but they probably occur along the abaxial margin of the bundle. The metaxylem consists of scalariform tracheids. The phloem is concentrated on the abaxial side of the xylem and in some cases may enclose the entire xylem strand. A bundle sheath of thick-walled sclerenchyma cells surrounds the vein but is especially concentrated near the phloem. Around the bundle sheath, but more pronounced on the lower side, is an additional sheath of transfusion cells from 4 to 6 layers thick. Their diameter is equal to or greater than the xylem tracheids. Parenchymatous cells of about the same size but without the thickenings are mingled with the transfusion cells.

The hypodermal layers, from 4 to 6 cells in thickness, add another unique character to the leaf structure. The tissue is composed of elongate sclerenchyma with transverse end walls, and presents a uniform transition from small, heavily thickened cells immediately beneath the epidermal layer, to larger, less-thickened ones composing the last few rows.

The stomatal grooves appear on either side of the thickened portion of the blade surrounding the vein. The sub-stomatal area consists of modified hypodermal cells with air passages between the groups of small rectangular cells.

The mesophyll is poorly-preserved but, as far as can be determined, it consists of more or less isodiametric cells closely packed together. There appear to be no air spaces between cells in the blade itself, but there are large ones in the stomatal chamber. No evidence of differentiation into palisade and spongy tissue exists. The mesophyll, which was probably the only chlorophyllous tissue, constitutes a relatively small portion of the leaf.

Lycopod leaves have been described in this country by Graham ('35) and Reed ('41) under the generic name *Lepidophyllum*. These leaves, associated with *Lepidodendron scleroticum*, compare closely with *Lepidophyllum Thomasi* Graham.



*Associated Fructifications:* Several Lycopod microsporangiate cones and many seeds, one containing a well-preserved gametophyte, were found in the coal-balls. A complete description of these fossils has been presented under the name *Lepidocarpon magnificum* (Andrews and Pannell, '42). Although the evidence is incomplete it seems likely, on the basis of association, that these fructifications belong to *Lepidodendron scleroticum*.

*Discussion.*—

An observer of the abundant Lycopod remains of the Carboniferous period cannot help postulating an explanation for the extinction of that great flora. The climatic conditions of that era have been considered as producing a swampy habitat similar to the present-day great Dismal Swamp in Virginia. This belief is substantiated by the associated fern and horsetail remains occurring with the Lycopod fossils. The great abundance of Lycopod organs and the excellent preservation of the external surface of the stems give considerable evidence for the "in situ" origin and fossilization of the material.

A study of the petrified *Lepidodendrons* presents a striking variation from the usual concept of hydrophytic characters. The evolutionary tendency in these Lycopods was towards extreme bulk of dead cortical tissue. This tendency expressed itself in the stem by the bulky periderm and the small xylem and phloem cylinder, and in the leaves the hypodermal layer decreased the photosynthetic area. The apparent xerophytic modification of the leaves may have come about to prevent evaporation, not because of the scarcity of water but *because the small stele was unable to conduct rapidly enough*. The tree would be efficient under moist conditions as the seeds were probably quick to germinate and growth was apparently regular and rapid. But with the increasing dryness of the Permian period, the tree with its excessive modification in bulk and poor conducting and photosynthetic abilities rapidly became extinct.

*Acknowledgement.*—

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## EXPLANATION OF PLATE

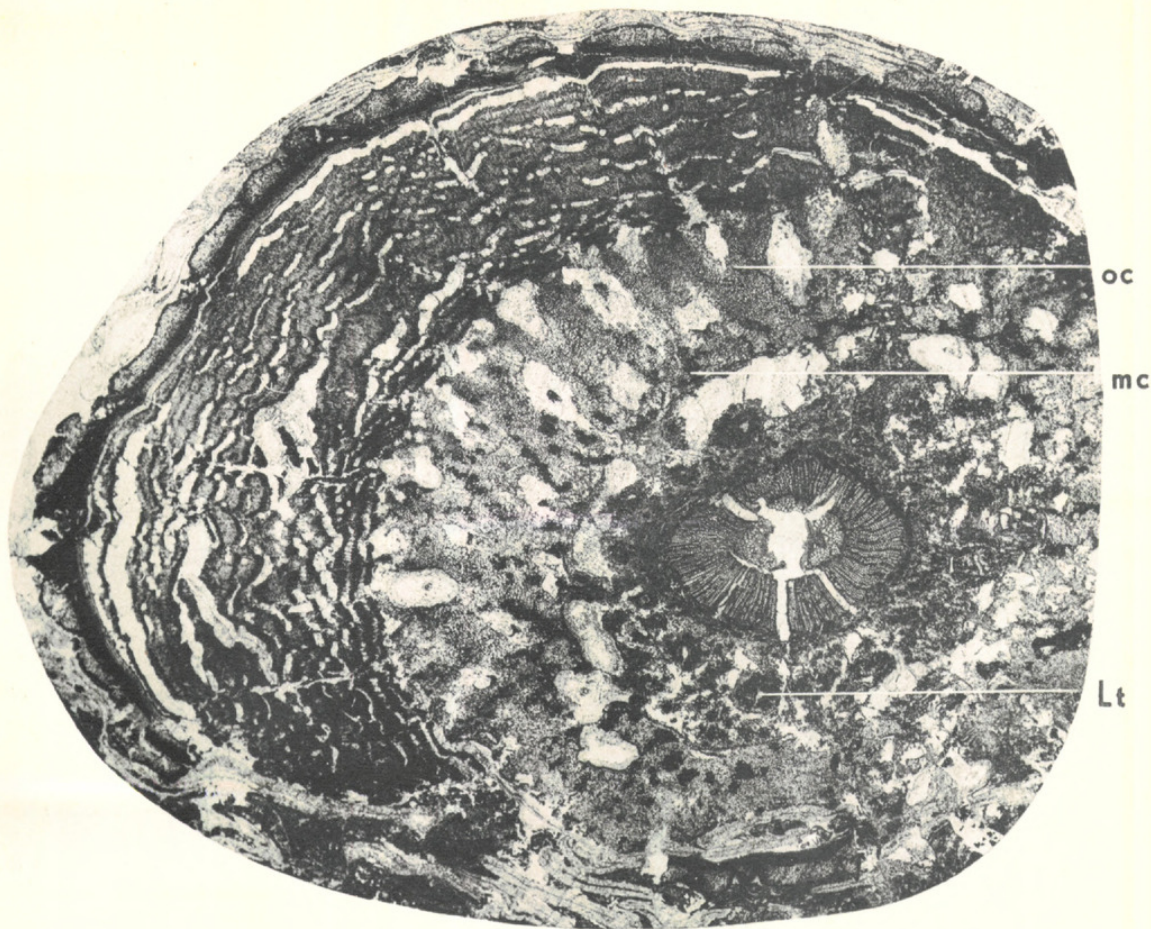
## PLATE 18

*Lepidodendron scleroticum*

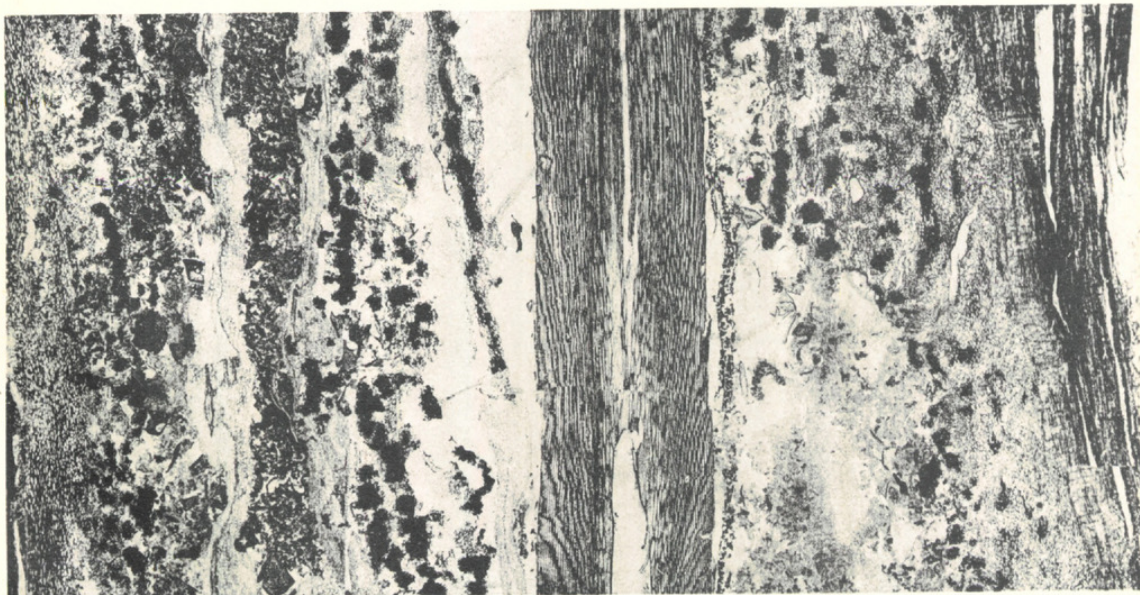
Fig. 1. Transverse section of stem: oc, outer cortex; mc, middle cortex; Lt, leaf trace.  
WCB55A.7,  $\times 3$ .

Fig. 2. Longitudinal section of stem. WCB56I.20,  $\times 3$ .





1



2

PANNELL—AMERICAN CARBONIFEROUS FLORAS. IV



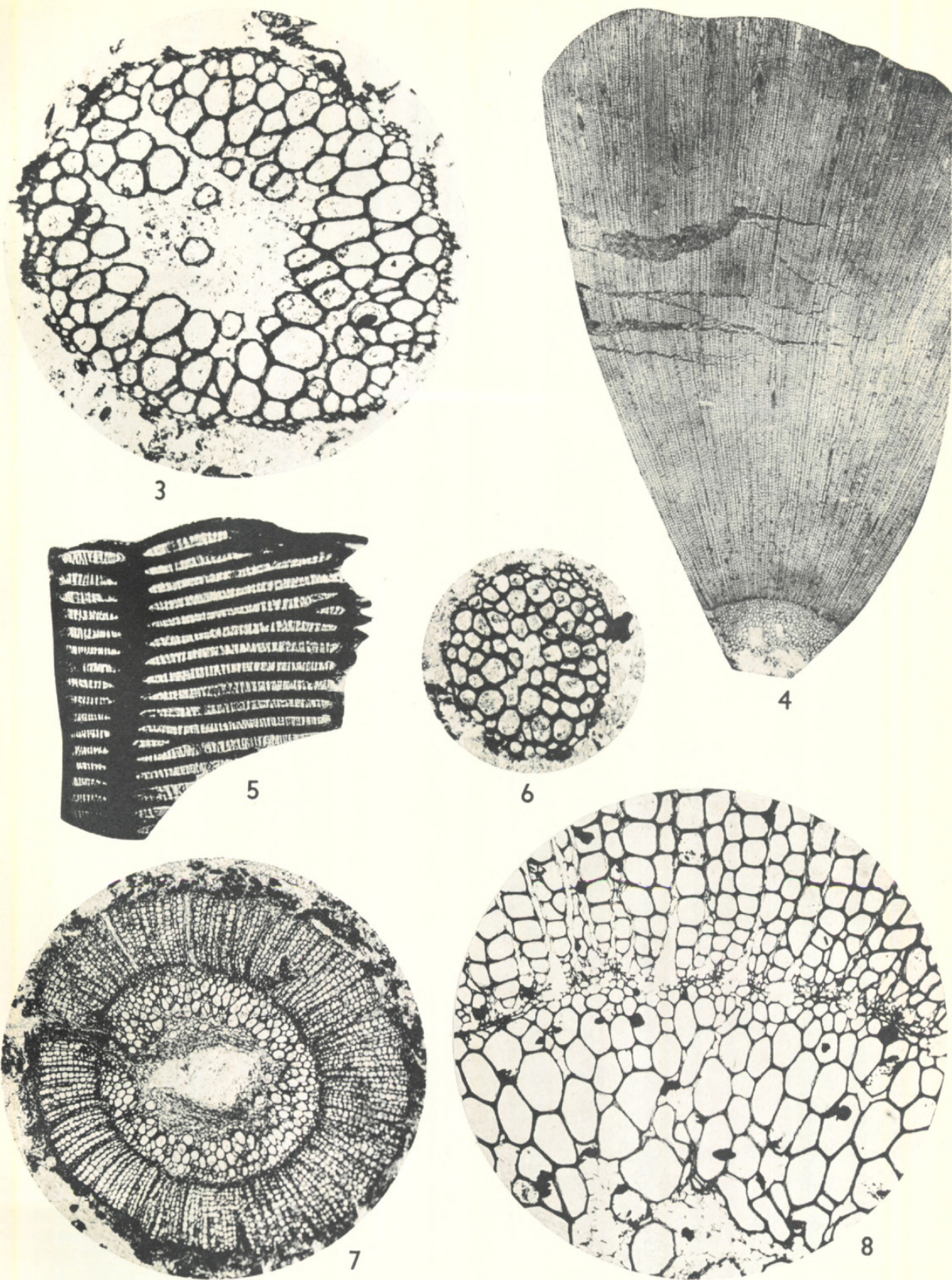
## EXPLANATION OF PLATE

## PLATE 19

*Lepidodendron scleroticum*

- Fig. 3. Transverse section of mixed protostele. MCB54.3,  $\times 57$ .  
Fig. 4. Transverse section through a portion of a large stele. WCB42.2,  $\times 3.6$ .  
Fig. 5. Macerated tracheids showing "vestured pits." Slide 1213,  $\times 290$ .  
Fig. 6. Transverse section of protostele. WCB54.3,  $\times 57$ .  
Fig. 7. Transverse section of siphonostele. WCB253E.B1,  $\times 14$ .  
Fig. 8. Transverse section through contact zone of primary and secondary xylem.  
WCB56B.7,  $\times 57$ .





PANNELL—AMERICAN CARBONIFEROUS FLORAS. IV



## EXPLANATION OF PLATE

## PLATE 20

*Lepidodendron scleroticum*

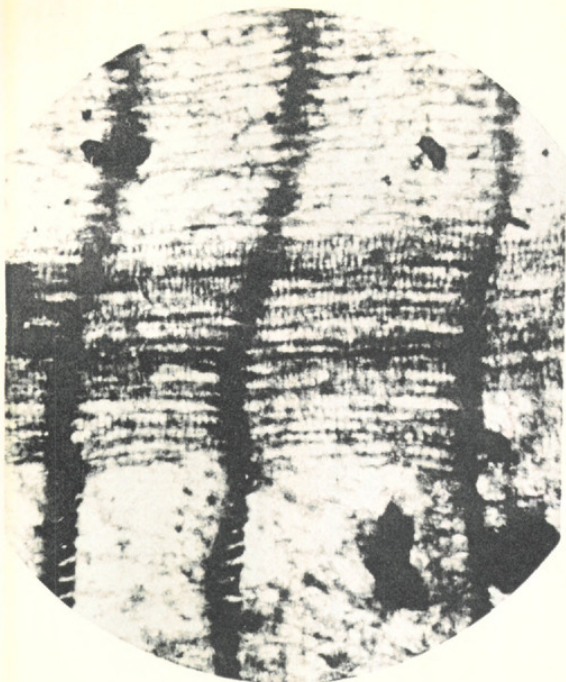
Fig. 9. Leaf trace passing through secondary xylem, in radial section. WCB82B.S3,  $\times 100$ .

Fig. 10. Wood-ray cells in radial section. WCB90B.1,  $\times 200$ .

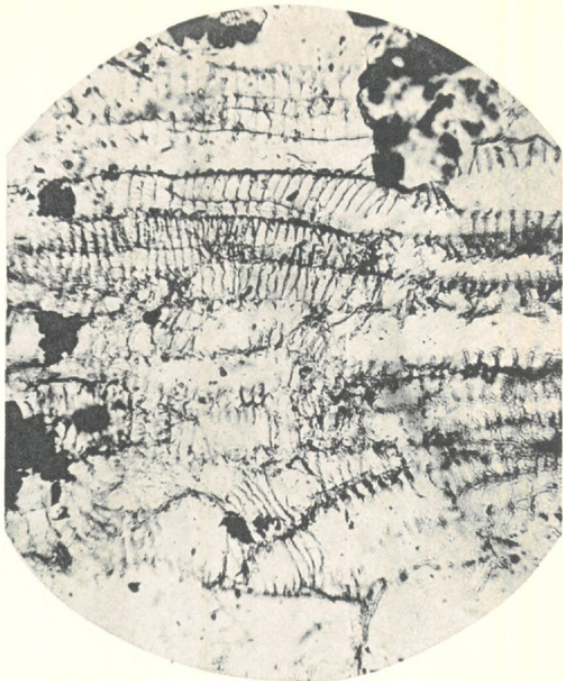
Fig. 11. Transverse section through outer part of secondary xylem and phloem. WCB55A.10,  $\times 75$ .

Fig. 12. Showing course of leaf trace from primary into secondary xylem. WCB56I.2,  $\times 80$ .

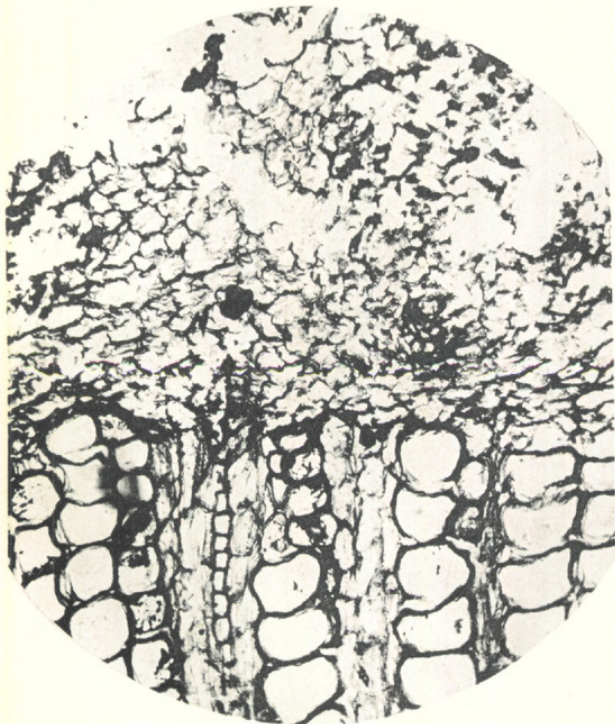




9



10



11



12



## EXPLANATION OF PLATE

## PLATE 21

*Lepidodendron scleroticum*

Figs. 13-16. Part of a series of peels tracing the origin and departure of a branch stele: p, periderm. All figures  $\times 8$ .

Fig. 13. WCB253A.1.

Fig. 14. WCB253C.T2.

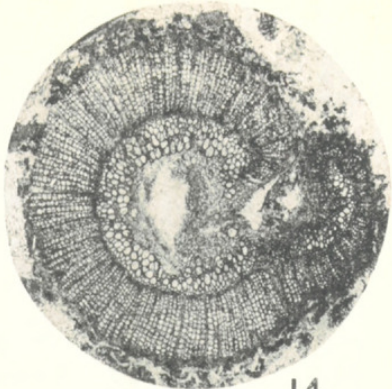
Fig. 15. WCB253D.T1.

Fig. 16. WCB253F.T2.

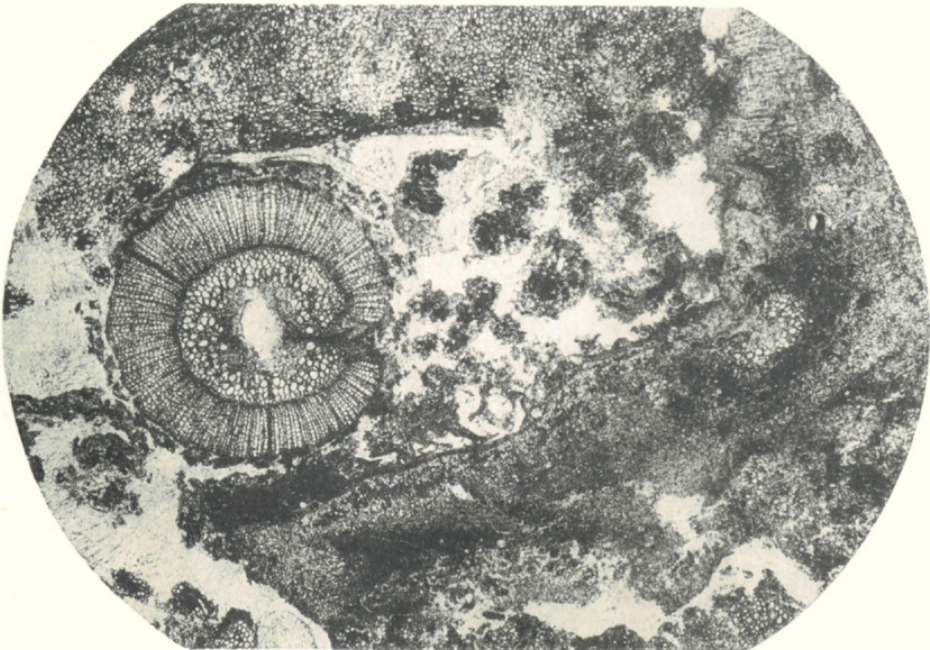




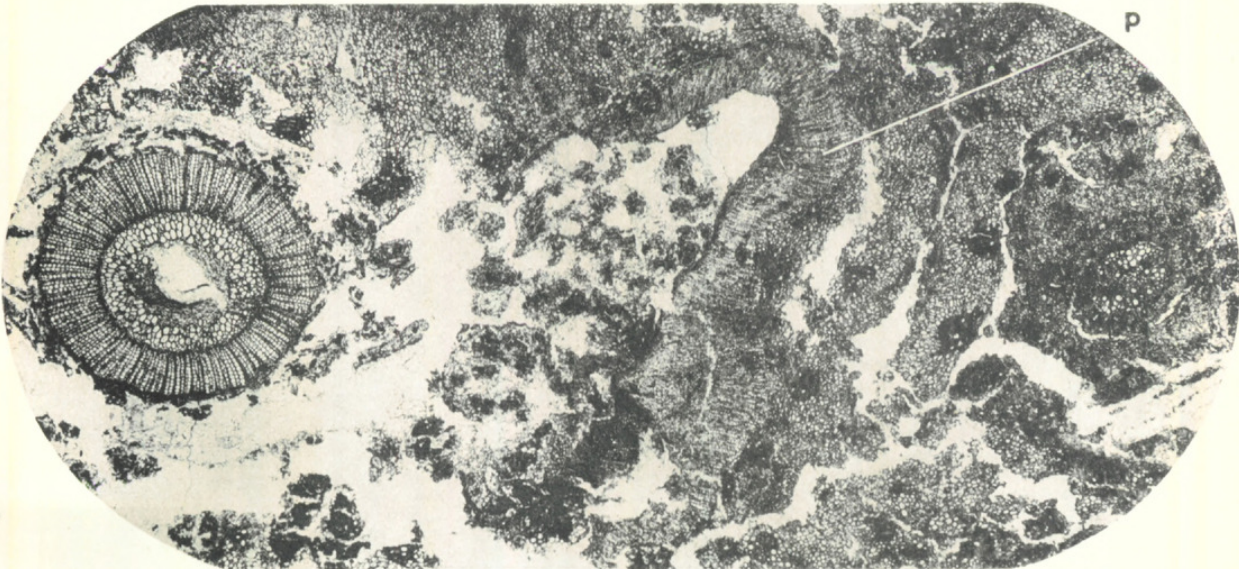
13



14



15



P

16



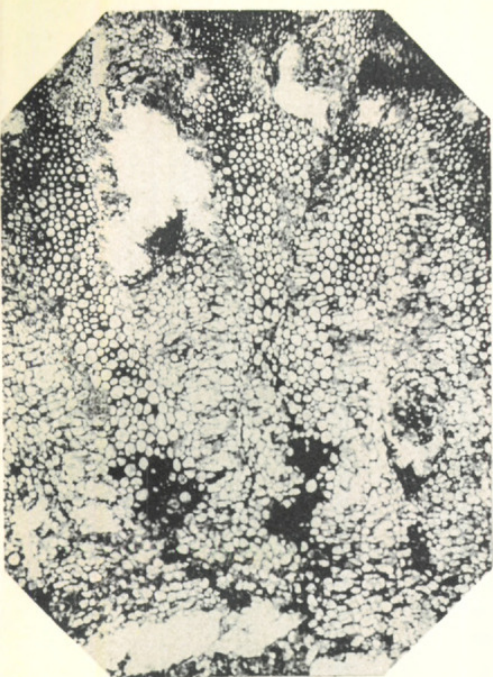
## EXPLANATION OF PLATE

## PLATE 22

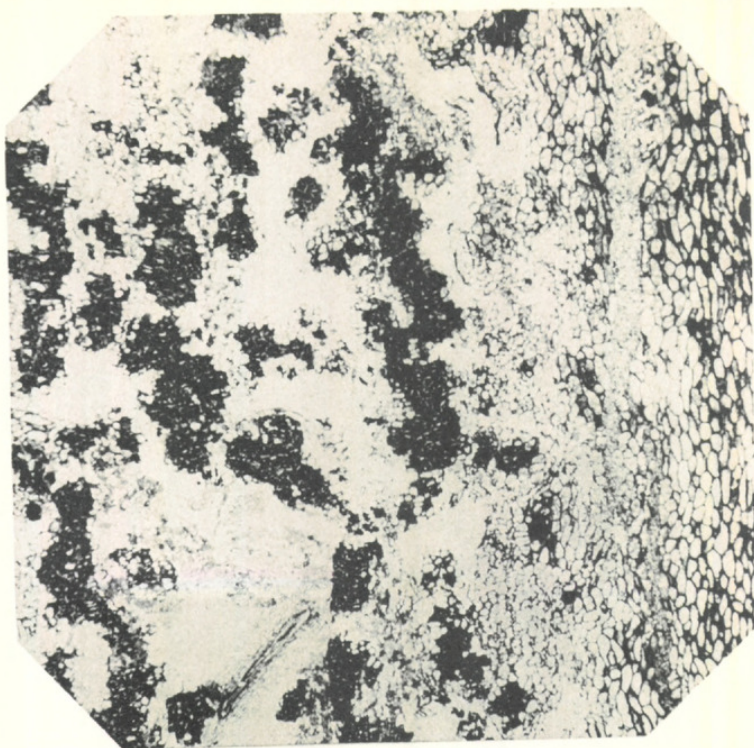
*Lepidodendron scleroticum*

- Fig. 17. Transverse section of cortex. WCB55A.7,  $\times 8$ .  
Fig. 18. Radial section of cortex. WCB56I.20,  $\times 8$ .  
Fig. 19. Tangential section through central region of cortex. WCB55III.515,  $\times 7$ .  
Fig. 20. Tangential section through outer region of cortex. WCB56I.B2,  $\times 5$ . See text for detailed explanation.





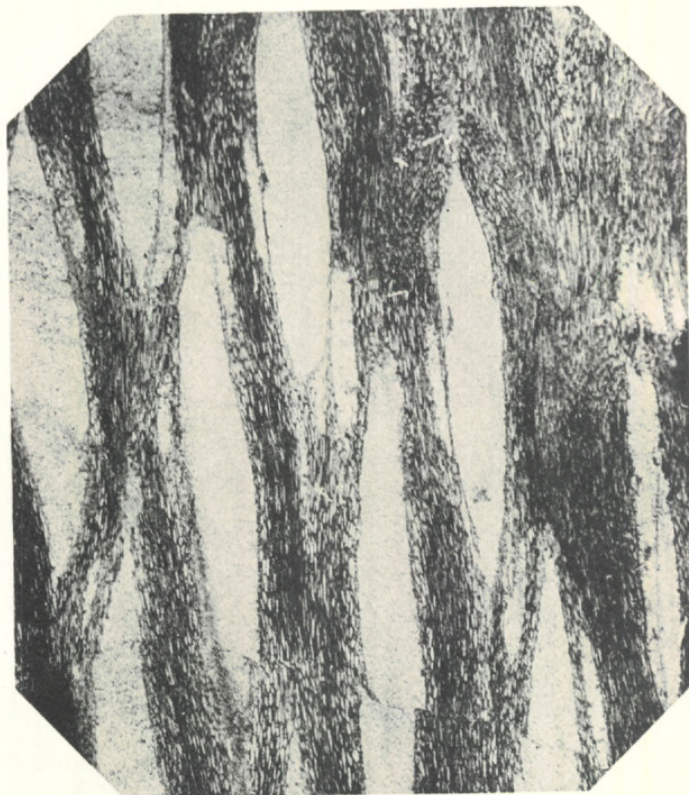
17



18



19



20



## EXPLANATION OF PLATE

## PLATE 23

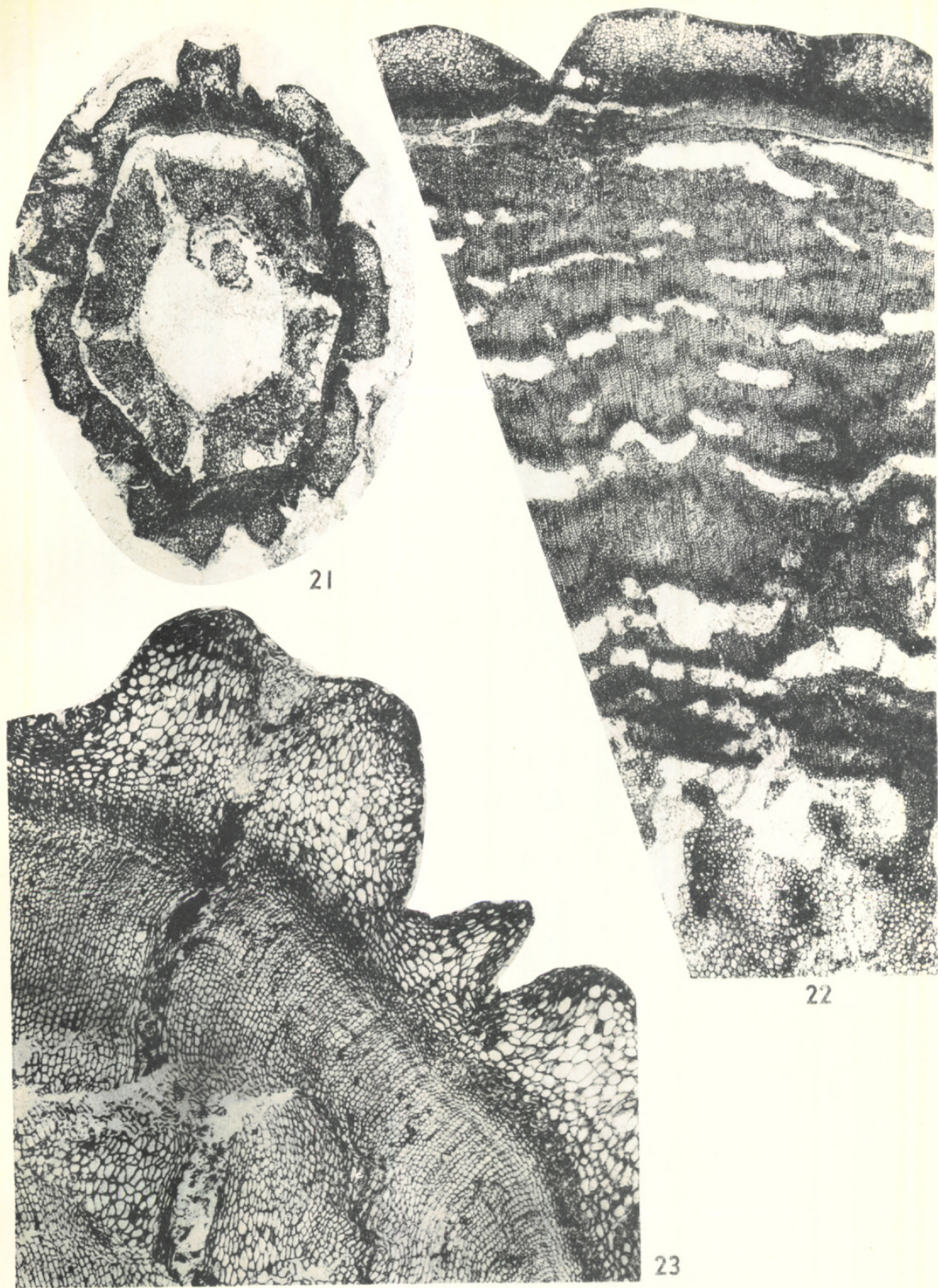
*Lepidodendron scleroticum*

Fig. 21. Transverse section through young stem. WCB16C,  $\times 10$ .

Fig. 22. Transverse section through periderm and leaf bases of a comparatively old stem. WCB55A.7,  $\times 10$ .

Fig. 23. Transverse section through periderm and leaf bases of a young twig. WCB54A.8,  $\times 40$ .





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## EXPLANATION OF PLATE

## PLATE 24

Fig. 24. *Lepidophloios* sp. from the Pyramid mine, Perry County, Illinois. WCB58B.9,  
× 5.

Fig. 25. *Lepidodendron scleroticum*, tangential section through leaf cushions. WCB91.6,  
× 5.

Fig. 26. *Lepidodendron Volkmannianum* (?) from Franklin County, Illinois. No. 1447,  
× 1.





Pannell, Eloise. 1942. "Contributions to Our Knowledge of American Carboniferous Floras. IV. A New Species of *Lepidodendron*." *Annals of the Missouri Botanical Garden* 29, 245–274. <https://doi.org/10.2307/2394321>.

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