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THE FLORA OF THE NEW ALBANY SHALE

PART 1. *DIICHNIA KENTUCKIENSIS*, A NEW REPRESENTATIVE OF THE CALAMOPITYEAE

BY

CHARLES B. READ

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THE FLORA OF THE NEW ALBANY SHALE

PART 1. *DIICHNIA KENTUCKIENSIS*, A NEW REPRESENTATIVE OF THE CALAMOPITYEAE

By CHARLES B. READ

ABSTRACT

A new genus of the Cycadofilicales, *Diichnia*, is described from the New Albany shale, of late Devonian age, in central Kentucky. The one known species, which is based on stem material showing internal structure, belongs in the family Calamopityeae. Foundation for the generic segregation is seen in the double leaf trace of the genotype, *D. kentuckiensis*, in contrast with the originally single trace in other known representatives of the family.

INTRODUCTION

The flora of the New Albany shale, of late Devonian age, in central Kentucky is of particular interest. First, very little is known of the older vascular plants in North America, and this flora presents a comparatively large assemblage of forms, several of which belong to genera new or meagerly known. Second, the material offers unusual opportunity to study the details of morphology of the stems and rachides, for in many specimens the internal structure is well preserved. As the methods of investigation of this flora are particularly time-consuming, however, and as the writer's duties are such that he cannot devote his undivided attention to this one project, it has been considered desirable to publish the discussion of the flora in a series of papers, of which this is the first. The others are to follow as opportunity offers.

The specimens on which this paper is based came from one locality but from several collections. Several years ago David White, while engaged in geologic work in the vicinity of Junction City, Ky., obtained a small fragment of a stem from the top of the New Albany shale. In 1930 this was placed in the writer's hands. Preliminary inspection suggested that the stem is a "*Calamopitys*," but after sections were cut it became evident that though the plant is plainly related to *Calamopitys* it is new and presents several features of great interest. In November 1932 the writer, on the advice of Charles Butts, visited the Junction City locality and spent several days collecting plant remains. Amid a wealth of valuable material additional specimens of the calamopityean form here described were obtained, so that it became possible to clear up points only vaguely shown in the original specimen.

The writer wishes to express his warmest thanks to David White, of the United States Geological Survey, who throughout the course of this work has given freely of useful advice and constructive criticism. He is likewise indebted to J. B. Reeside, Jr., and R. W. Brown, of the Geological Survey, for suggestions on certain features of the work. K. J. Murata has prepared the series of thin sections used, and his careful work is deeply appreciated.

OCCURRENCE AND PRESERVATION

The material here described came from a locality in the Harrodsburg quadrangle half a mile west of Junction City, Ky. Here a small outlier of green New Providence shale rests on black shale which is of New Albany age. Very excellent exposures are displayed at the heads of several small streams. At the most extensive of these exposures, the locality known as "Blue Licks", the following section was measured:

Section of New Providence and New Albany shales at Blue Licks, half a mile west of Junction City, Ky.

	Ft.	in.
Green clay shale weathering gray-blue; contains scattered concretions of clay-ironstone	64	
Ferruginous sandy shale containing abundant *Taonurus*		
Green clay shale weathering gray-blue	11	
Fine-grained ferruginous and slightly calcareous sandstone, the exposed surfaces showing abundant fucoidal markings	1	6
Green clay shale, nearly structureless and weathering light blue; ferruginous concretions numerous and restricted to definite layers	14	
Green New Albany shale containing kidney-shaped phosphatic nodules that bear plant remains, fish scales, bone fragments, and invertebrates	1	2
Black New Albany shale. Black thin-bedded bituminous shale containing *Sporangites*.		

The plant remains occur in the nodular layer, either as the nuclei of concretions or as impregnated masses lying directly in the clay-shale matrix. This nodular layer is referable to the top of the New Albany, rather than to the New Providence. Published reports have in the past indicated this layer as the basal member of the New Providence, however.[1] This is due to the similarity of the clay matrix carrying the nodules and the overlying clays of undisputed New Providence age. A full discussion of the stratigraphic problems is deferred until a later paper. It is from this bed that the collection described by Scott and Jeffrey [1a]

[1] Butts, Charles, The Mississippian series of eastern Kentucky: Kentucky Geol. Survey, ser. 6, vol. 7, correlation chart, 1922.

[1a] Scott, D. H., and Jeffrey, E. C., On fossil plants, showing structure, from the base of the Waverley shale of Kentucky: Roy. Soc. London Philos. Trans., ser. B, vol. 205, pp. 315-373, pls. 27-39, 1914.

in 1914 was obtained. Their material included the following species:

Calamopitys americana Scott and Jeffrey.
Calamopteris hippocrepis Scott and Jeffrey.
Periastron perforatum Scott and Jeffrey.
Stereopteris annularis Scott and Jeffrey.
Archaeopitys eastmanii Scott and Jeffrey.
Lepidostrobus fisheri Scott and Jeffrey.

The type of preservation of this material is very interesting. Analyses indicate that the petrifactions contain about 26 percent of calcium phosphate and 42 percent of ferric carbonate. Although these materials preserve the larger structures of the plants with considerable accuracy, the details of pitting are commonly obliterated, owing to a peculiar swelling of the cell walls.

PRESENT STATUS OF THE CALAMOPITYEAE

The known representatives of the Calamopityeae have been carefully studied and reviewed in recent years by several paleobotanists, including Scott and Jeffrey,[1a] Zalessky,[2] and Scott,[3] and some new types indicating a considerable diversity in structure in the group have been brought to light. It is not necessary, therefore, to dwell at any great length on the historical aspects of the investigation of the group, though it is essential to review rapidly the major morphologic features of several of the species that are more or less allied to the form described here as new.

Prior to 1901 the known species of *Calamopitys* were those originally described from Saalfeld, Thuringia, by Unger [4] and more completely elaborated by Solms-Laubach.[5] The first of these, *Calamopitys saturni* Unger, is the type of the genus, although still imperfectly known. The most significant features of this species are the narrow zone of secondary wood with numerous broad rays, the distinct, centrally mesarch xylem strands, the large pith, and the primitively monarch leaf traces dividing after their departure from the stele into several small bundles to form the *Kalymma* petiole.

From the same deposits Solms-Laubach recognized a second species, *Calamopitys annularis*, referred to *Stigmaria* by Unger.[6] This form is similar in most respects to *Calamopitys saturni* but differs in having a nearly continuous zone of eccentrically mesarch primary xylem, in the presence of medullary tracheids, and in minor features of the leaf trace.

In 1902 Scott described two species, *Calamopitys fascicularis* and *C. beinertianus* (Goeppert), which are quite distinct from those recorded from Saalfeld. Both species show a secondary wood of the typical cordaitean type with narrow medullary rays. *C. fascicularis* has a small pith surrounded by a ring of distinct mesarch xylem bundles which pass into the leaf traces after division. The leaf traces indicate a two-fifths phyllotaxy and are monarch. *C. beinertianus* has a somewhat larger sclerotic pith enclosed by partly confluent primary bundles that show a strong tendency toward endarchy, particularly in the smaller ones. The leaf trace departs as a single mesarch xylem strand.

In 1911 Zalessky [7] erected a new genus, *Eristophyton*, for these two species and suggested that the similarities seen between *Eristophyton fasciculare* and *E. beinertianum*, on the one hand, and *Calamopitys* of the original group of *C. saturni* Unger, on the other, might be analogies and that the species are far removed in their affinities. Though it has been shown that this similarity between *Eristophyton* and *Calamopitys* in the strict sense is actual, Zalessky's segregation is regarded as a valid one, although *Eristophyton* is placed by some authorities as a subgenus and by others as a genus. The latter course is preferred by the present writer.

The group of *Calamopitys* conforming to the strict definition based on *C. saturni* Unger has been segregated by Scott [8] in the subgenus *Eu-Calamopitys*. In addition to the Thuringian species there are now known *C. americana* Scott and Jeffrey and *C. radiata* Scott, the first from the top of the New Albany shale in Kentucky and the second from the Oil Shale group, Calciferous Sandstone series, Dumbartonshire, Scotland.

Calamopitys americana, it has been remarked by Scott,[9] is scarcely distinguishable from *C. annularis* (Unger) Solms-Laubach on the basis of present information. In view of their occurrence at widely separated localities they have, however, been regarded as probably distinct.

Calamopitys radiata Scott is rather distinct from any of the species so far mentioned. In the apparently mixed pith, the large exarch primary xylem strands, and the greatly dilated rays there are features which are undeniably of specific worth. No leaf traces have been observed.

In addition to these segregates in the original genus, two new genera that appear to be closely related to *Calamopitys* have been recently defined.[10] The first of these, *Endoxylon* Scott, is diagnosed as follows: [11]

[1a] See footnote 1a, p. 149.

[2] Zalessky, M. D., Étude sur l'anatomie du *Dadoxylon tchihatcheffi* Goeppert: Com. géol. [St.-Pétersbourg] Mém., pt. 58, 1911.

[3] Scott, D. H., Notes on *Calamopitys* Unger: Linnean Soc. London Jour., Botany, vol. 44, no. 297, pp. 205–232, pls. 6–8, 1918; Fossil plants of the *Calamopitys* type from the Carboniferous rocks of Scotland: Roy. Soc. Edinburgh Trans., vol. 43, pt. 3, pp. 569–598, pls. 1–6, 1924.

[4] Unger, Franz, in Richter, Reinhard, and Unger, Franz, Beitrag zur Paläontologie des Thüringer Waldes, Theil 2, Schiefer- und Sandsteinflora: K. Akad. Wiss. Wien Denkschr., Band 11, p. 81 [167], 1856.

[5] Solms-Laubach, H., Ueber die Seinerzeit von Unger beschriebenen strukturbietenden Pflanzenreste des Unterculm von Saalfeld in Thüringen: K. preuss. geol. Landesanstalt Abh., neue Folge, Heft 23, 1896.

[6] Unger, Franz, op. cit., p. 81 [167], 1856.

[7] Zalessky, M. D., Étude sur l'anatomie du *Dadoxylon tchihatcheffi* Goeppert. Com. géol. [St.-Pétersbourg] Mém., pt. 58, p. 27, 1911.

[8] Scott, D. H., Studies in fossil botany, pt. 2, pp. 108–109, 1923.

[9] Scott, D. H., Notes on *Calamopitys* Unger: Linnean Soc. London Jour., Botany, vol. 44, no. 297, pp. 205–232, pls. 6–8, 1918.

[10] Scott, D. H., Fossil plants of the *Calamopitys* type from the Carboniferous rocks of Scotland: Roy. Soc. Edinburgh Trans., vol. 43, pt. 3, pp. 569–596, pls. 1–6, 1924.

[11] Idem, p. 579.

Pith large, without medullary tracheids or sclerotic nests. Primary xylem strands large, far apart, endarch. Secondary wood dense, with narrow medullary rays, usually uniseriate and mostly only 1 cell in height; others up to about 6 cells high. Pits in 1 to 4 rows on the radial walls of the tracheids. Annual rings distinct, marked by the very narrow tracheids of the "autumn wood."

Insofar as present information goes the genus is monotypic, *Endoxylon zonatum* Scott being the only species. The type specimen came from the Carboniferous Limestone series of Ayrshire, Scotland.

The second genus is *Bilignea* (Kidston ms.) Scott.[12] Its diagnosis is as follows:

Pith replaced by a large central column of short, pitted tracheids. Leaf trace a single or bilobed strand in passing through the wood; mesarch in the upper part of its course, dwindling in size and losing its centripetal xylem as it passes down the stem. Secondary wood dense; medullary rays narrow and almost always uniseriate, from 1 to about 20 cells in height. Bordered pits of the araucarian type, in 1 to 4 rows on the radial walls of the tracheids.

Two species of *Bilignea* have been recognized, *B. solida* (Kidstone ms.) Scott and *B. resinosa* Scott,[13] the principal feature of distinction being the presence of secretory sacs in the central column of the latter and their absence in the former. Both come from Scotland, *B. solida* being derived from the Carboniferous of Ayrshire and *B. resinosa* from the Cementstone group, Calciferous Sandstone series, Dumbartonshire.

SYSTEMATIC DESCRIPTIONS

CYCADOFILICALES

CALAMOPITYEAE

Genus DIICHNIA Read, n. gen.[14]

Stems of various sizes containing a "mixed" pith. Pith distinctly angled, at least in the genotype, eccentrically mesarch xylem strands being situated at the angles and separated from the secondary wood by a few cells of parenchyma. Secondary wood very scant and traversed by wide rays; pitting not known. Cortex similar to that in *Calamopitys*. Leaf trace double, two strands from adjacent angles of the pith passing outward and dividing to form a polydesmic petiole, the exact nature of which is not definitely known.

Diichnia kentuckiensis Read, n. sp.

General features of the stem.—The general features of the stem here designated *Diichnia kentuckiensis*, n. sp., are clearly shown in figure 9, which is a diagram of a transverse section. The axis is of the less woody type characteristic of the subgenus of *Calamopitys* designated *Eu-Calamopitys* by Scott[15] and in its woody structure is quite typical of the more "herbaceous" Cycadofilices.

The central area is occupied by a large five-angled pith, the details of which are discussed beyond. Scattered in this pith are tracheids, so that the condition is of the type commonly designated "mixed." In the vicinity of each angle there are small areas of protoxylem; elsewhere such primary elements are usually absent. These protoxylem areas, as subsequently shown, are intimately connected with the leaf traces and vary somewhat in their position and configuration, which depend on their proximity to such emerging appendages.

The general features of the cylinder of secondary wood as seen in transverse section are shown in plate 30, figures 1 and 2, and as seen in longitudinal section in plate 32, figure 3. A marked similarity to *Calamopitys americana* Scott and Jeffrey [16] is at once seen. Except at the angles this secondary xylem abuts directly on the pith. The rays, it will be noted, are several cells in width.

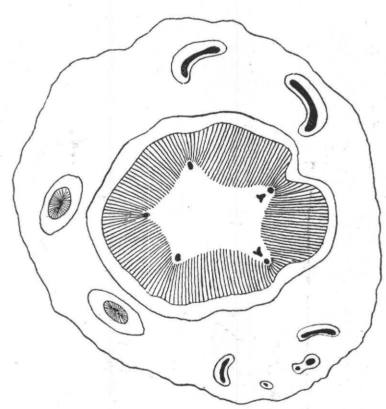


FIGURE 9.—Camera lucida sketch of a transverse section of *Diichnia kentuckiensis* showing the more obvious features of the stem. Note the large five-angled pith and the double leaf traces.

Outside of the wood is a zone of crushed and otherwise distorted and poorly preserved tissue of variable extent. The lumens are clogged, and it is impossible to determine accurately the nature of the elements. However, the logical interpretation is that this zone includes the cambium, phloem, and pericycle. On the exterior is the cortex, consisting of a thick large-celled area but slightly differentiated except near the outer surface, where occur hypodermal sclerotic strands of the type generally called "sparganum cortex." Here and there are lysigenous cavities which suggest secretory centers. At several points in text figure 9 will be noted paired lateral organs. These can be interpreted only as the vascular bundles of emerging leaf traces. These traces are double, and their divergence as indicated by successive transverse sections is 2/5.

The pith.—The general aspect of the tissue occupying the central area of the stem is clearly shown in plate 30, figures 1 and 2, and in plate 32, figure 2. This pith, if it may be called such, is large and five-angled. The groundmass is parenchymatous, consisting of nearly isodiametric cells, as is indicated by comparing the complementary sections illustrated in plate 30, figure 2, and plate 32, figure 1. The walls of these

[12] Scott, D. H., op. cit., pp. 579, 590–592.

[13] Idem, pp. 579–592.

[14] From the Greek δι, two, and ἴχνος, footstep, trace, scar, etc.

[15] Scott, D. H., Studies in fossil botany, pt. 2, p. 108, 1923.

[16] Scott, D. H., and Jeffery, E. C., On fossil plants, showing structure, from the base of the Waverley shale of Kentucky: Roy. Soc. London Philos. Trans., ser. B, vol. 205, pp. 317–330, 1914.

elements are unusually thick. This is to be regarded as a peculiarity of preservation rather than a feature indigenous to the original tissue. Occurring occasionally are canals which appear to be of secretory function and lysigenous origin. Several of these are shown in plate 30, figure 2. Also there are certain cells and aggregates of cells that are filled with a dark, gummy substance.

Rather commonly, as is indicated in plate 30, figure 4, there are "nests" of elements which resemble tracheids. In plate 32, figure 1, several of these are shown in longitudinal section, and it is at once seen that these are very elongate. A careful examination of these elements has failed to reveal any evidence of pitting, but there can be little doubt concerning the identity of these as tracheids embedded in the pith. In this respect *Diichnia kentuckiensis* resembles *Calamopitys americana* Scott and Jeffrey, which has a "mixed pith" so ligneous as to approach a typical protostelic condition.

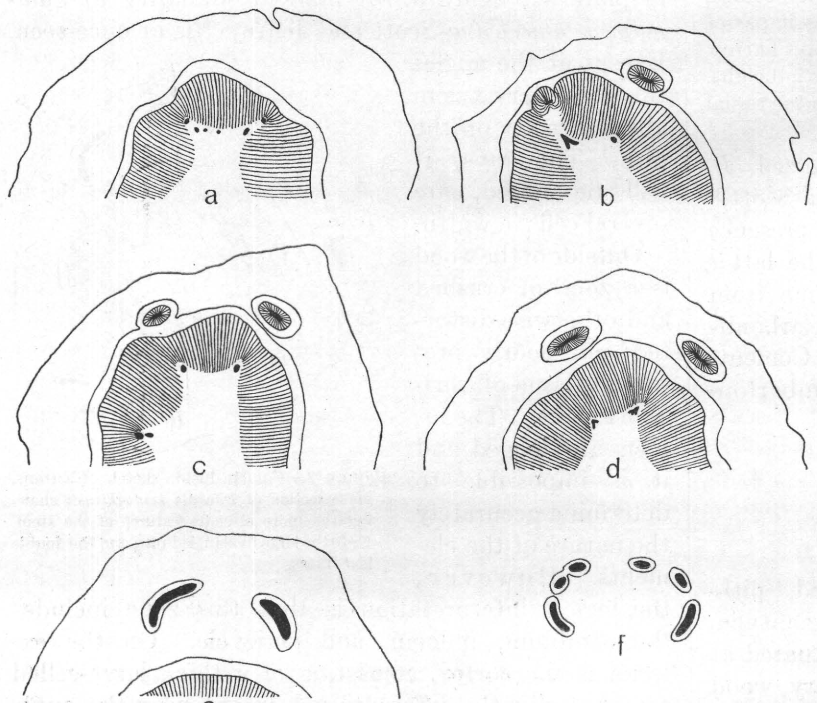


FIGURE 10.—Camera lucida sketches showing the origin and course of the leaf strands in *Diichnia kentuckiensis*. See text for explanation.

Primary xylem.—The primary xylem strands in *Diichnia kentuckiensis* are situated, as is indicated in plate 30, figures 1 and 2, and diagrammatically in text figure 9, at the angles of the pith and in consequence are well separated. (A few strands are likewise present in the body of the pith, but the present discussion is restricted to the circum-medullary ones.) Except in the vicinity of a departing leaf trace these strands are very uniform in size, eccentrically mesarch, and separated by a few cells of parenchyma from the secondary wood. However, where a strand commences to pass out to a leaf the primary bundle at the pith angle involved shifts outward to the inner margin of the secondary wood. At the same point it elongates radially, as is indicated in plate 30, figure 1, and plate 32, figures 3, 7, and 8. The protoxylem divides into two strands, and finally separate bundles of primary xylem result, the outer passing into the leaf and the inner remaining in the stem as a reparatory bundle (pl. 32, fig. 4).

Secondary wood.—The secondary xylem of *Diichnia kentuckiensis* abuts directly on the pith except at the angles, and at those points it comes into direct contact with the primary xylem only in connection with an emerging leaf trace. The general features of this cylinder are shown in plate 30, figures 1–3; plate 31, figure 3; and plate 32, figures 3, 5, and 7. The structure is very similar to that of *Calamopitys americana.* The medullary rays are numerous and vary in width from 1 to 8 cells. By far the larger number are multiseriate. As shown in plate 3, figure 1, these rays are wider in the immediate proximity of the pith. There the ray cells are nearly isodiametric or square, but farther out they become radially elongated.

Although the preservation of the material is such that the suite of longitudinal sections is very unsatisfactory to study, it has been possible to obtain some information concerning the nature of the pitting in the tracheids. In general the pits are small and multiseriate, their outline being hexagonal, owing to their alternate arrangement. This is quite in accord with the observations made by Scott and Jeffrey on *Calamopitys americana.*

Phloem and pericycle.—On the exterior of the secondary wood is a thin zone of poorly preserved parenchyma, which is shown in plate 31, figures 1 and 3, and plate 32, figure 7. Little can be said of this tissue, owing to its collapsed condition and the clogged lumens. However, it may be interpreted as being the remains of the cambium, phloem, and pericycle. Certain features of this tissue are of interest. A considerable quantity of secondary phloem was apparently developed, as is suggested by the radially arranged elements adjacent to the wood. The rays of the secondary xylem continued into the phloem for some distance, as is indicated in plate 32, figure 7.

Cortex.—The thick cortex of *Diichnia kentuckiensis* is composed chiefly of thin-walled, isodiametric cells of parenchyma (pl. 31, fig. 1; pl. 32, fig. 5). On the exterior there is a "sparganum" zone consisting of radiating strands of alternately sclerotic and thin-walled tissue, as is shown in plate 32, figures 5 and 6, and plate

31, figure 3. A hypoderm of this type is common in the less woody members of the Calamopityeae.

Here and there cavities of apparently lysigenous origin are found in the cortex. These are apparently secretory, although no evidence of gum deposits was observed. Similar "canals" lie in the parenchymatous portion of the mixed pith.

Leaf trace.—In the features so far enumerated and discussed nothing has been observed which indicates that *Diichnia kentuckiensis* is a particularly significant type. In fact, it may be safely said that apart from its organization in the vicinity of the node the structure is of little interest. However, the mode of origin and development of the leaf traces introduces several peculiarities which have not been previously recorded in the family.

To insure clarity a series of diagrammatic drawings have been prepared (fig. 10) from sections that illustrate the stages in the departure of the traces. These will be referred to in the discussion of the general features of the bundles, and the details of structure will be illustrated in the plates.

In plate 30, figure 1, are shown two primary bundles that have become tangentially elongated. These, it will be observed, are at adjacent angles of the pith. Separating them is a considerable expanse of secondary xylem in direct contact with the parenchymatous central area. Plate 32, figure 8, illustrates one of these bundles at a higher magnification. The protoxylem is clearly divided into inner and outer groups, and the inner appears to have undergone further division.

A slightly more advanced stage is represented diagrammatically in text figure 10, a. The primary xylem of each of the two strands has divided into two mesarch bundles, of which the inner ones are reparatory strands and the outer the leaf-trace strands. This stage is shown in more detail in plate 31, figure 4, plate 32, figure 4, and plate 33, figures 2 and 4. It will be noticed that the xylem of the reparatory strands is quite eccentrically mesarch, approaching endarchy. In the specimen shown in plate 32, figure 4, a further division in the reparatory strand has taken place. The primary xylem of the leaf trace is, however, centrally mesarch.

A more advanced stage in the development of the trace is shown in text figure 10, b, supplemented by plate 30, figure 2, and the intermediate stage shown in plate 30, figure 3. Before discussing these in detail one very striking feature must be brought out. There is a very noticeable lag in the anodic bundle. That is to say, the kathodic bundle is considerably in advance of the other, particularly in the early stages. This is very plainly brought out in text figure 10, b. As these two bundles, which comprise the leaf trace, pass from the stele they consist of mesarch primary xylem and a considerable amount of secondary xylem. In the earlier stages the secondary xylem is obviously restricted to the abaxial position. However, as the trace emerges from the wood, secondary xylem likewise appears on the adaxial side, so that the bundles have a radial arrangement similar to that which might be expected in a small branch, though for obvious reasons the view that they represent such a branch is untenable. The general appearance of these bundles is shown in plate 33, figures 5 and 6. It is clear that the centrally located primary xylem is mesarch. However, the protoxylem groups are several, in anticipation of further division of the bundles. These divisions may take place before the strands emerge from the secondary wood. The long axis of the primary wood is tangential.

The two bundles retain their concentric structure for some distance as they ascend and gradually pass out into the cortex. Their course is only a slight departure from that of the parent axis, as is indicated in text figure 10, c and d. They gradually become more and more tangentially flattened, however, and after they pass into the cortex the secondary xylem is lost, first on the abaxial and finally on the adaxial side. At the same time, the expanse of primary xylem increases. The tissues that are interpreted as phloem thin in the same manner, but a narrow zone is retained on the inner side and a somewhat broader one on the outer. Tangential elongation of the metaxylem continues with the development of several protoxylem groups. These stages are illustrated in text figure 10, d and e, and in plate 31, figures 1 and 3.

Leaf base.—In the later stages in the development of the leaf trace there are seen numerous divisions of the original bundles, an indeterminate number of smaller ones resulting (text fig. 10, f; pl. 33, fig. 3). The structure of these divisions is mesarch; the phloem, though thickest on the abaxial surface, appears to be present on the adaxial surface also.

These bundles retain their orientation with the long sectional axis tangential, as is clearly brought out in text figure 10, f. Unfortunately, later stages than this have not been observed in the material at hand, so it is impossible to determine accurately the nature of the actual petiole. Some suggestion of the structure that might be expected is found in the organ described by Scott and Jeffrey [17] as *Calamopteris hippocrepis* and similar ones from Thuringia referred to *C. debilis* Unger.[18] These have been interpreted as the petioles of some forms allied to *Calamopitys* but as yet unknown. They resemble *Kalymma* in their general organization but differ in the more marked collateral structure of the bundles and the tendency for these bundles to be tangentially elongated (very pronounced in *C. hippocrepis*), in contrast to the radial elongation in *Kalymma*.

[17] Scott, D. H., and Jeffrey, E. C., op. cit., pp. 330–335, 1914.

[18] Unger, Franz, op. cit., p. 53 [139], pl. 2, fig. 2; pl. 8, fig. 12, 1856.

In view of the fact that *Calamopteris* is known from the same locality and horizon as *Diichnia kentuckiensis*, it is by no means unlikely that they represent petiole and stem of the same plant. This is to be taken as no more than a suggestion, without any satisfactory proof of connection.

To summarize, the features which serve to characterize *Diichnia kentuckiensis* are these:

1. The broad five-angled pith with occasional strands of xylem and lysigenous canals.
2. The widely spaced mesarch bundles of primary xylem.
3. The broad-rayed secondary xylem abutting directly on the pith except in the vicinity of the angles.
4. The double leaf traces, the two bundles originating from adjacent primary xylem bundles at adjacent angles of the pith.
5. The tangential instead of radial elongation of the bundles after they have begun to divide in the cortex.
6. The 2/5 divergence of the leaves.

RELATIONSHIPS OF DIICHNIA

The several species referred to the genus *Calamopitys* fall naturally into two groups, which have been designated *Eu-Calamopitys*[19] and *Eristophyton*.[20] These genera or subgenera, as they are variously regarded, have been briefly contrasted above. Though differing somewhat in the structure of the primary wood, and more decidedly in the structure of the secondary wood, one feature in common is the originally monarch condition of the leaf trace. This has, in fact, been considered by some investigators a character of generic value. Clearly any tendency toward diarchy is a distinct advance of cardinal importance.

It has been shown that *Diichnia kentuckiensis* in the internodal regions shows anatomical features which unite it closely with *Eu-Calamopitys*. Minor differences exist, but they are of no more than specific worth. In the vicinity of the nodes, however, it becomes at once apparent that the stem departs widely from the definition of *Calamopitys*. The leaf traces are clearly double, the two bundles departing from adjacent angles of the five-rayed pith. Furthermore, the leaf base does not appear to conform closely with *Kalymma*, the known petiole of other species of *Calamopitys* in which that organ has been found attached. Instead it more nearly resembles *Calamopteris*.

These departures from the morphologic features typical of *Calamopitys*, to which *Diichnia kentuckiensis* shows the closest affinities, can be interpreted as a distinct and important advance. The question of the degree of separation from *Eu-Calamopitys* therefore becomes critical. As is indicated by the name already used, the writer prefers to make this separation generic. As the genus cannot be placed in any of the segregates that have so far been proposed, it becomes necessary to erect a new group. For this genus the name *Diichnia* is proposed, and the type is to be regarded as *D. kentuckiensis*. The characters to be used in delimiting the segregation have been pointed out in the description of the species. Of particular importance is the diarch leaf trace. Likewise the pattern of the leaf base, which is similar to that described as *Calamopteris*, may afford a criterion for separation from *Eu-Calamopitys*, which shows the *Kalymma* structure in the petiole.

The question of relationships is one which the writer hesitates to discuss at any great length, for obvious reasons. A few generalizations based on the more significant features of *Diichnia kentuckiensis* may, however, be stated with a fair degree of accuracy. In *Eu-Calamopitys* there is a definite trend in the direction of a diarch leaf trace. This is very well illustrated in the two species, *Calamopitys saturni* Unger and *C. americana* Scott and Jeffrey.[21] It has been pointed out that in the first of these the leaf trace passes through the wood as a single bundle and divides only after it has reached the cortex. In *C. americana* the strand of xylem divides as it passes through the secondary wood, the two bundles being quite distinct by the time the cortex is reached.

It is not out of place at this point to mention the exactly parallel case found in the family Lyginopterideae, genus *Heterangium*. In *Heterangium grievii*, from Pettycur, Scotland, the leaf trace is at first monarch, but the protoxylem divides into two after leaving the stele. Division of the bundle does not take place, however, until the vicinity of the rachis is reached. In certain other species segregated by Scott in *Eu-Heterangium* there is a somewhat earlier division of the trace, but it remains primitively monarch. In the other segregate, *Polyangium*, the leaf trace is double where it leaves the stele and undergoes numerous divisions while in the cortex.[22]

The situation which has just been outlined in *Heterangium* is exactly analgous to that in the Calamopityeae, where *Diichnia kentuckiensis* shows a double leaf trace and apparently occupies the same position relative to *Eu-Calamopitys* that *Polyangium* occupies relative to *Eu-Heterangium*.

Another feature which *Diichnia kentuckiensis* exhibits and which is suggestive of anatomical advance over most species of *Eu-Calamopitys* is the unusually slight amount of primary xylem grouped in very discrete bundles. *Calamopitys americana* and *C. annularis* are characterized by nearly or quite contin-

[19] Scott, D. H., Studies in fossil botany, pt. 2, pp. 108–109, 1923.

[20] Zalessky, M. D., op. cit., p. 27, 1911.

[21] Scott, D. H., Notes on *Calamopitys* Unger: Linnean Soc. London Jour., Botany, vol. 44, no. 297, pp. 205–232, 1918.

[22] Scott, D. H., The Heterangiums of the British Coal Measures: Linnean Soc. London Jour., Botany, vol. 44, no. 295, pp. 91–92, 1917.

uous primary xylem. *Calamopitys saturni* resembles *Diichnia kentuckiensis* closely in the meager quantity of primary xylem.

The structure of the petioles, if it is accepted that *Calamopteris* is that organ in *Diichnia kentuckiensis,* is of negative value in speculating on the relationships of the species. Clearly the two types are distinct, but whether *Calamopteris* shows structural advances over *Kalymma* is a question that cannot be answered by the writer.

CONCLUSIONS

The observations that have been made on *Diichnia kentuckiensis* may be summarized as follows:

1. *Diichnia kentuckiensis* is a stem from the late Devonian strata of Kentucky presenting numerous features which ally it with species grouped in *Eu-Calamopitys* by Scott.

2. The double leaf trace, which is a conspicuous feature of the plant, is a structure that renders *Diichnia kentuckiensis* distinct from any previously described form.

3. The leaf trace exhibits characters which suggest that *Calamopteris* may have been the petiole.

4. On the basis of the diarch traces a new genus, *Diichnia,* is proposed for stems conforming to *Diichnia kentuckiensis.* The definition of *Eu-Calamopitys* describes the leaf trace as single at the point of origin.

5. The guarded opinion is expressed that through diarchy and reduction of primary xylem *Diichnia kentuckiensis* shows distinct advances over the related species of *Calamopitys* (*Eu-Calamopitys*).

PLATES 30–33

PLATE 30

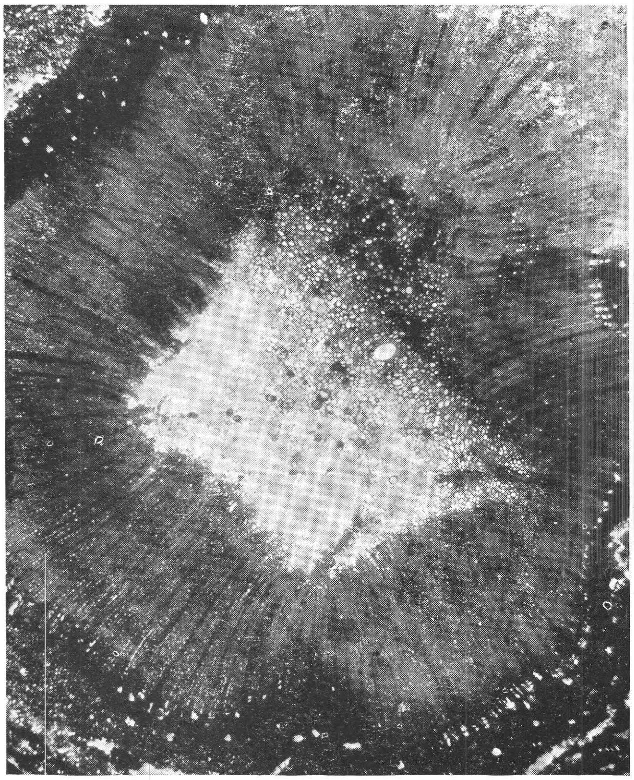
Diichnia kentuckiensis, n. gen. and n. sp.

FIGURES 1, 2. General view of the central axis of a stem showing the five-angled "mixed" pith and the position of the primary wood. Note the secretory canals occurring in the parenchymatous portion of the pith. × 7.

FIGURE 3. A portion of a transverse section showing the departure of the double leaf trace. × 7.

FIGURE 4. A portion of the central mixed pith showing the tracheids, which are scattered throughout the mass. × 60.

FIGURE 5. A single primary xylem bundle in a position indicating close proximity to an emerging leaf trace. Note that the primary xylem, which normally is separated from the secondary wood by a few cells of parenchyma, is here directly in contact with those elements. × 60.



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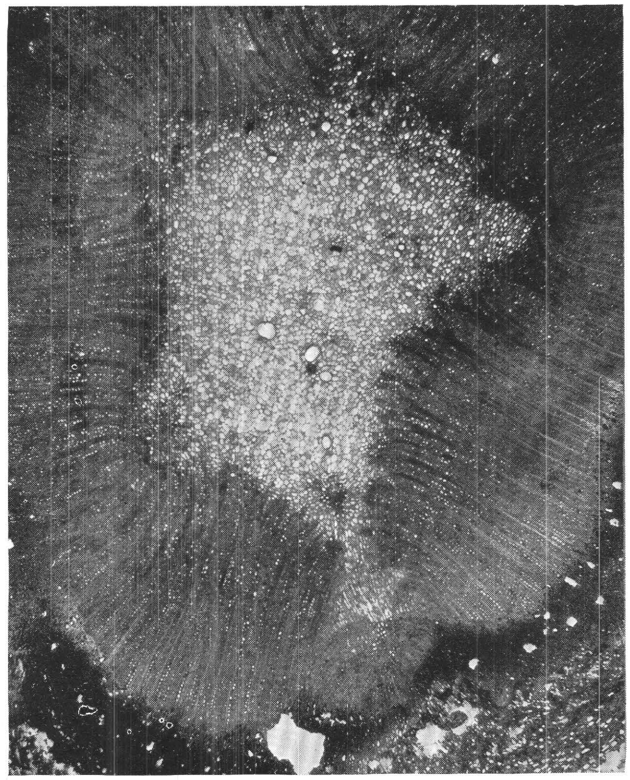

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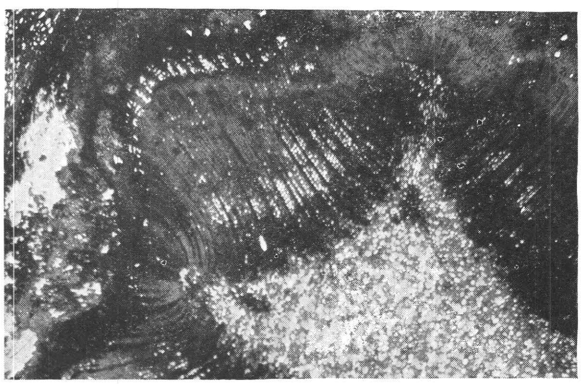

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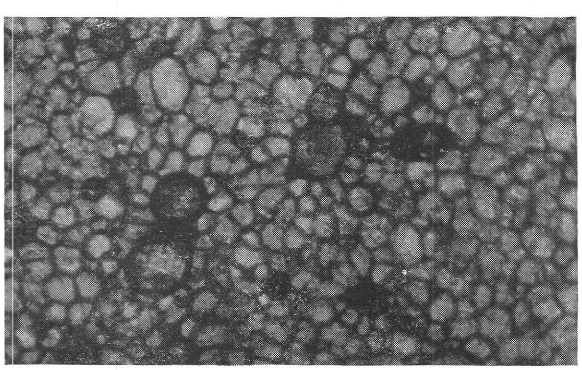

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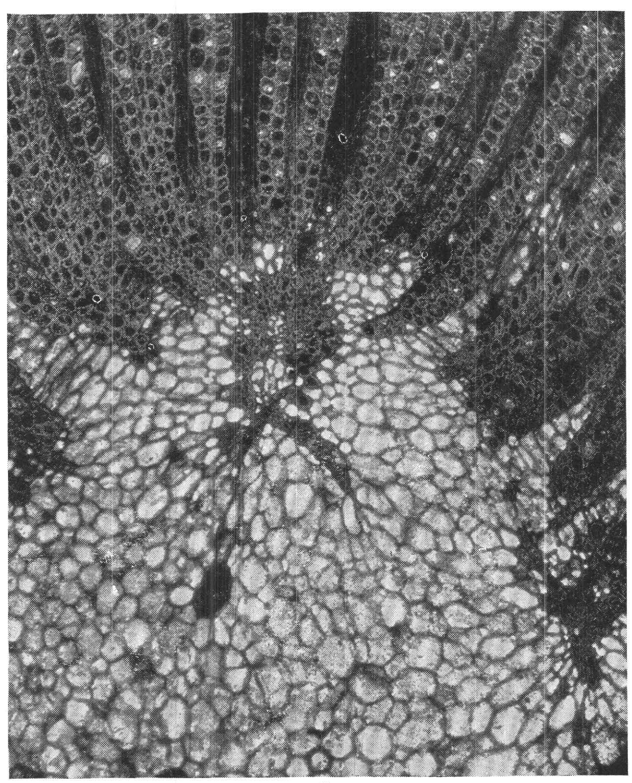

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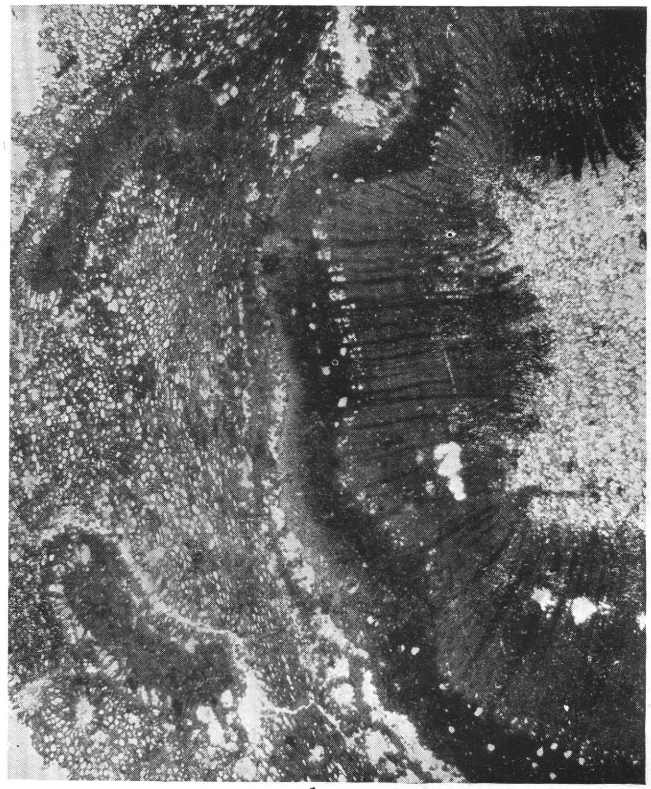
DIICHNIA KENTUCKIENSIS READ.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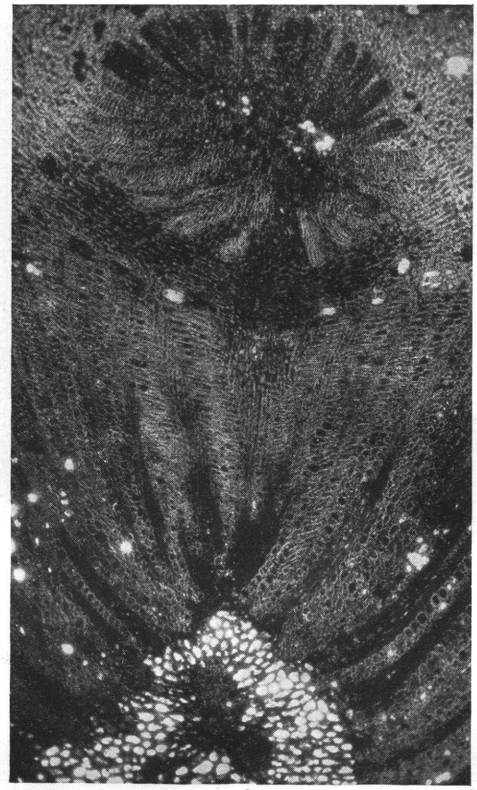
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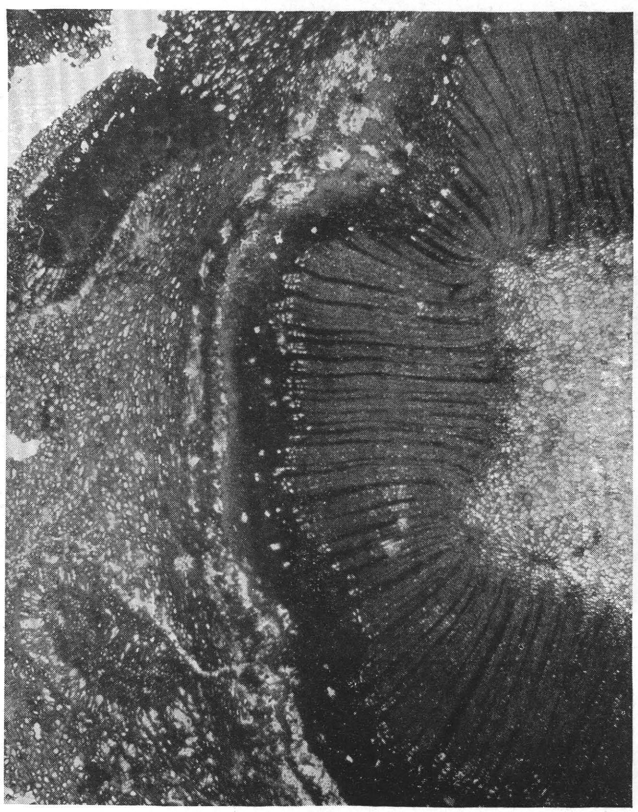
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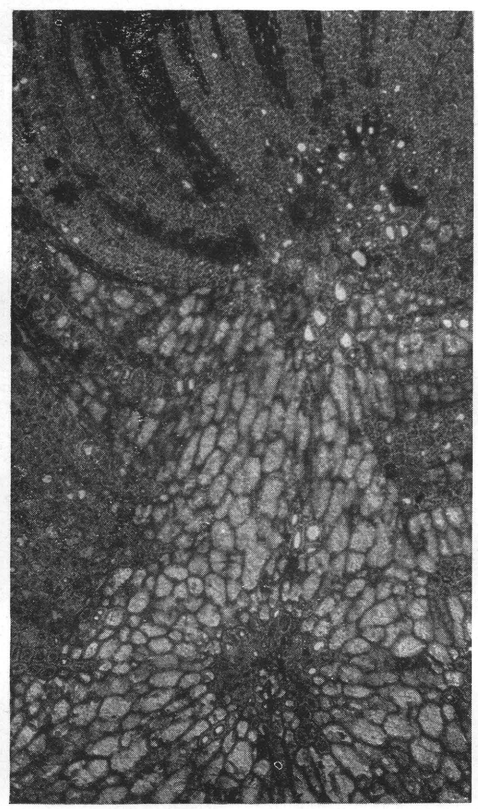
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DIICHNIA KENTUCKIENSIS READ.

PLATE 31

Diichnia kentuckiensis, n. gen. and n. sp.

FIGURES 1, 3. A portion of a stem in transverse section showing the stele from which two bundles of a single leaf trace have departed from adjacent angles of the pith occupied by bundles of primary wood. Note the tangentially elongate leaf-trace bundles in the cortex. × 7.

FIGURE 2. Transverse section showing one bundle of the double leaf trace directly after it has emerged from the secondary wood. Note the reparatory strand in the pith and the nearly perfect radial symmetry of the leaf-trace bundle. × 24.

FIGURE 4. Transverse section of a portion of the primary and secondary wood and adjacent tissues showing the departure of a leaf-trace strand. Note the isolated reparatory bundle. × 35.

PLATE 32

Diichnia kentuckiensis, n. gen. and n. sp.

FIGURE 1. Radial section of the "mixed" pith showing the occurrence of medullary tracheids. Note the nature of the parenchymatous tissue. × 30.

FIGURE 2. Radial section of the whole stem. × 7.

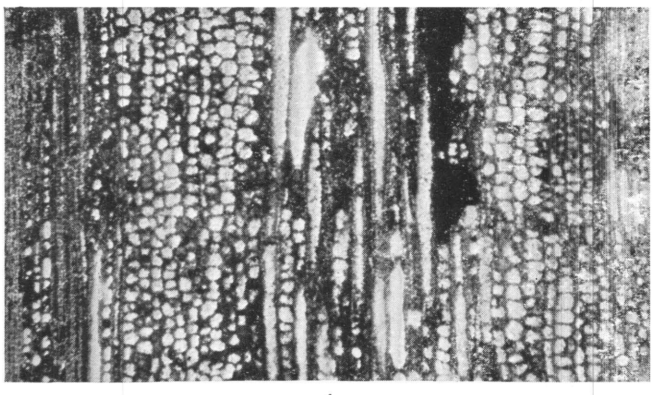
FIGURE 3. Transverse section showing division of primary bundle into a leaf-trace strand and a reparatory strand. × 35.

FIGURE 4. Transverse section showing the leaf trace and reparatory strands separate in the immediate vicinity of a node. × 35.

FIGURE 5. General view of a transverse section of *Diichnia kentuckiensis* showing the characteristic five-angled pith, the woody cylinder, the broad cortex with radial hypodermal strands, and the leaf traces embedded in the cortex. × 7.

FIGURE 6. Tangential section of the hypodermis showing the alternation of sclerenchyma and parenchyma. × 30.

FIGURES 7, 8. Transverse sections of primary bundles and adjacent tissues at the origin of leaf-trace strands. × 24.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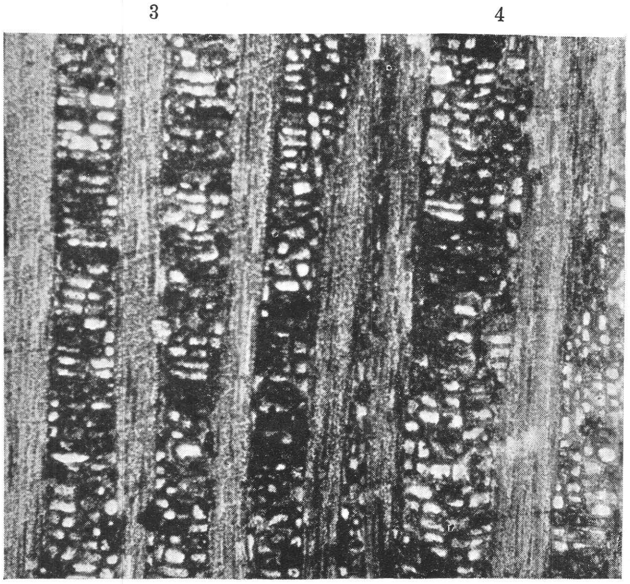
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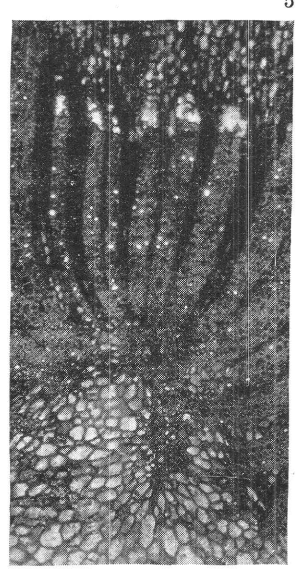
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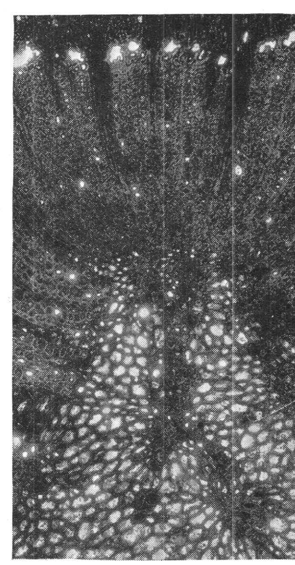
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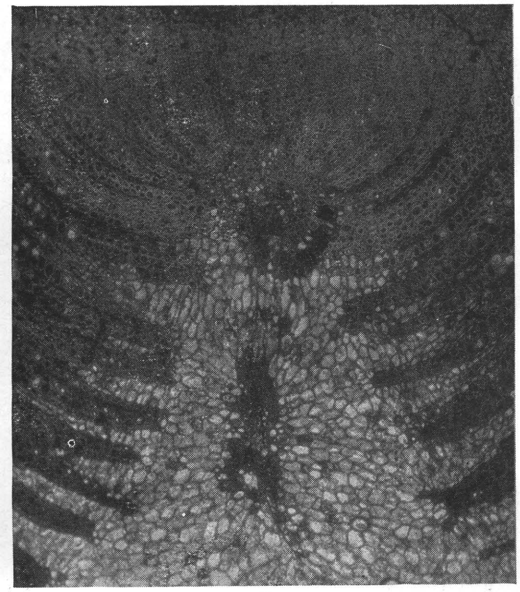

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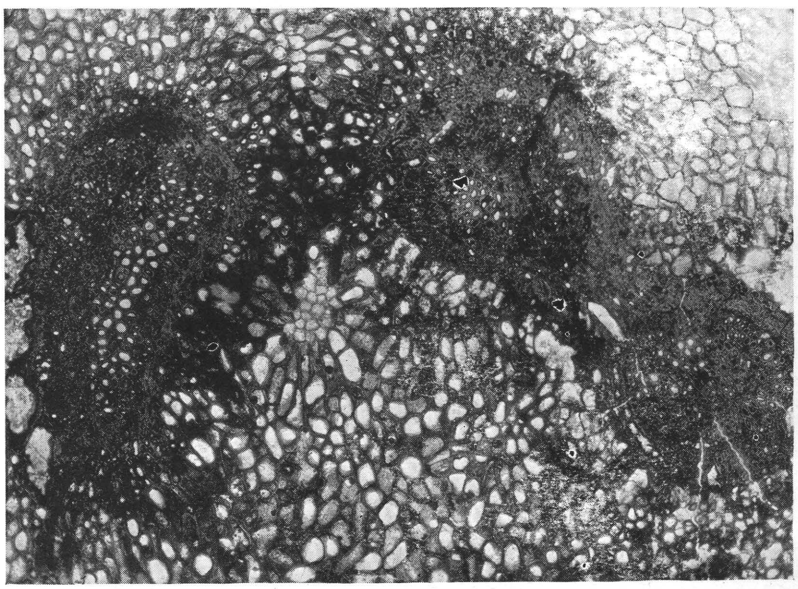

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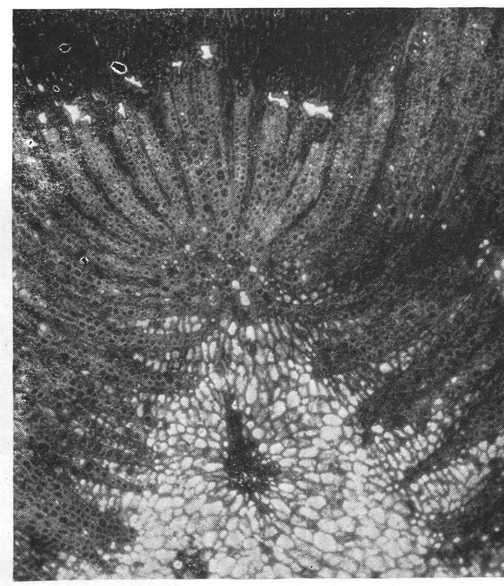

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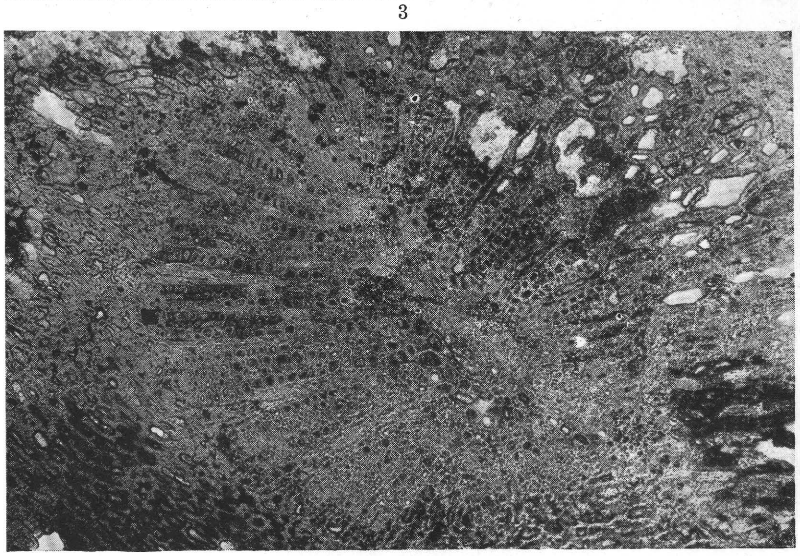

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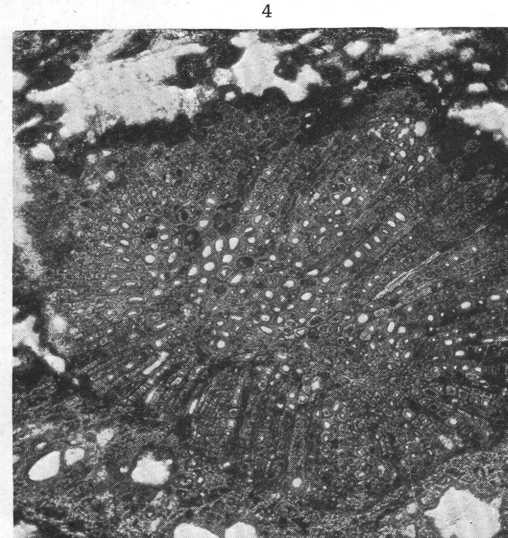

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DIICHNIA KENTUCKIENSIS READ.

PLATE 33

Diichnia kentuckiensis, n. gen. and n. sp.

FIGURE 1. A single bundle of the leaf trace as it appears in the middle cortex before division. × 24.

FIGURES 2, 4. Transverse sections of departing leaf-trace strands. Observe the reparatory bundles embedded in the outer pith. × 24.

FIGURE 3. A portion of a leaf trace in the cortex after division has taken place. × 24.

FIGURES 5, 6. Transverse sections of leaf-trace bundles as they appear just after emerging from the secondary xylem. Note the concentric structure. × 24.