THE FLORA OF THE NEW ALBANY SHALE

Part 2. THE CALAMOPITYEAE AND THEIR RELATIONSHIPS

By Charles B. Read

ABSTRACT

Material referable to *Calamopitys americana*, *Calamopitys foerstei*, *Stenomyelon muratum*, *Kalymma lirata*, *Kalymma resinosa*, and *Kalymma auriculata*, from the upper portion of the New Albany shale in central Kentucky, is described. All these species are based on the internal structure of stems and petioles. The suggestion is made that the genus *Stenomyelon* should be included in the family Calamopityeae rather than in a separate family. Relationships of the several species and genera belonging to the Calamopityeae are discussed, and it is recommended that the name *Calamopitys* be restricted to manoxylic forms (*C. saturni* Unger, etc.), that *Eristophyton* be used for the pycnoxylic species which have in the past been placed in *Calamopitys*, and that *Sphenoxylon* be adopted for the American species which has been called *Calamopitys eupunctata*. It is pointed out that the Calamopityeae may be divided, naturally, into two major groups—a manoxylic, protostelic group and a pycnoxylic, medullated group. *Stenomyelon* is probably in the lineage of the more primitive Calamopityeae, and *Endoxylon* is presumably the most advanced type now known.

INTRODUCTION

In the first paper of this series the writer described in detail the morphology of a particularly interesting member of the Calamopityeae. The continued study of the New Albany shale and its flora, both in the field and in the laboratory, has resulted in the making of large collections of new or heretofore imperfectly known plants. The present report summarizes the results of the examination of the calamopityean forms and includes accounts of the species of *Calamopitys*, *Stenomyelon*, and *Kalymma*, all from the New Albany shale in the vicinity of Junction City, Ky.

The writer wishes to express his gratitude to Mr. Guy Campbell, of New Albany, Ind., with whom he spent several weeks in the field in 1934 and 1935, for his interest and aid in making the collections. The thin sections have been prepared by K. J. Murata, of the Geological Survey, and his interest, both in the preparation and in the study of the flora, is appreciated.

SYSTEMATIC DESCRIPTIONS

CYCADOFILICALES

CALAMOPITYEAE

Genus CALAMOPITYS Unger 1856

1856. Unger, Franz, in Richter, Reinhard, and Unger, K. Akad. Wiss. Wien Denkschr., Band 11, p. 73 [159].

The genotype of *Calamopitys* is *C. saturni* Unger, from the *Cypridina* shales of uppermost Devonian or lowest Carboniferous age in the vicinity of Saalfeld, Thuringia. This species is of the type designated *Eu-Calamopitys* by Scott.[1] It is similar to both *C. americana* and *C. annularis*, differing only in the more nearly centrally mesarch position of the protoxylem, in the apparent absence of medullary tracheids, and in the details of leaf-trace emission.

In the writer's opinion, the name *Calamopitys* should be restricted to the manoxylic species—that is, the eu-calamopityean forms—and the pycnoxylic species should, as suggested by Zalessky,[2] be segregated in the genus *Eristophyton*. This course is adopted in the present paper.

Calamopitys americana Scott and Jeffrey

Plate 16, figures 1, 2; plate 17, figures 1–4; plate 18, figures 1–4; plate 25, figure 1; plate 26, figures 2, 5

1914. Scott, D. H., and Jeffrey, E. C., Royal Soc. London Philos. Trans., ser. B, vol. 250, pp. 317–330, pl. 27, figs. 1–7; pl. 28, figs. 8–14; pl. 29, fig. 22; pl. 30, figs. 23–29; pl. 31, fig. 30; pl. 34, figs. 49–51; pl. 35, figs. 1–4; pl. 36, figs. 5–8.

1918. Scott, D. H., Linnean Soc. London Jour., Botany, vol. 44, no. 297, pp. 206–209, 218, pl. 6, figs. 1–10.

1923. Scott, D. H., Studies in fossil botany, 3d ed., pt. 2, pp. 109–116, figs. 49–51.

1936. Read, C. B., Jour. Paleontology, vol. 10, no. 3, pp. 218–219, pl. 27, fig. 1.

According to Scott,[3] *Calamopitys americana* is characterized by

> Primary xylem strands eccentrically mesarch, with the centrifugal portion smaller and smaller-celled than the centripetal. Strands united laterally to form an almost closed xylem-ring.
>
> Pith "mixed", containing a varying proportion of medullary tracheids.
>
> Leaf trace dividing into two as it passes through the secondary wood. Each leaf-trace bundle, where it leaves the wood, surrounded by a zone of secondary thickening.
>
> Secondary wood with high, multiseriate medullary rays, not enlarged outward. Tracheids with several series of alternating bordered pits on the radial walls.
>
> Leaf base with the structure of *Kalymma*, containing a number of mesarch bundles, each with from 2 to 5 protoxylem groups.

Primary structure and pith.—To go into more detail regarding the anatomy of *Calamopitys americana*, the pith, as has been stated, is "mixed", so that with only a slight departure from the commonly accepted defini-

[1] Scott, D. H., Studies in fossil botany, 3d ed., pt. 2, pp. 108–109, 1923.

[2] Zalessky, M. D., Étude sur l'anatomie du *Dadoxylon tchihatcheffi* Goeppert: Com. géol. [St.-Pétersbourg] Mém., nouv. sér., livr. 58, p. 27, 1911.

[3] Scott, D. H., Notes on *Calamopitys* Unger: Linnean Soc. London Jour., Botany, vol. 44, no. 297, p. 218, 1918.

tion the structure may be regarded as protostelic. Some idea of the situation may be grasped from an examination of plate 17, figures 1–4. The central area of the stem is at once seen to be occupied by a heterogeneous mass of tissue consisting of a groundmass of parenchyma containing isolated and connected groups or "nests" of few to many thick-walled cells, which have been identified as tracheids. Toward the periphery these aggregations of tracheids become more regularly disposed and finally form an almost continuous primary xylem. Figures 1–4, plate 18, illustrate a portion of this tissue more highly magnified, and it becomes evident that the primary structure is mesarch, the protoxylem being immersed but nearer the outer margin of the bundle than the inner.

Secondary wood.—Abutting this almost continuous ring of mesarch primary xylem on the exterior is a considerable thickness of secondary wood. This tissue is homogeneous, consisting of radially arranged tracheids except for the numerous multiseriate parenchymatous rays. The general aspect of the secondary wood in transverse section is shown in plate 18, figures 1 and 2, and in longitudinal section in plate 16, figure 2. The rays range in width from 1 to 11 cells and are, of course, widest close to the inner margin of the wood. They may be high, as is shown by the longitudinal tangential section.

It is impossible to demonstrate satisfactorily the pitting of the tracheids. It appears, both from the observations of Scott and Jeffrey and from those of the writer, that the pits are small, multiseriate, and alternate.

Phloem and pericycle.—Beyond the secondary wood there is a zone of more or less crushed and partly decomposed tissue, which is largely parenchymatous in nature. Its general appearance is shown in plate 18, figures 1 and 4. A similar tissue is commonly present in *Diichnia kentuckiensis*, where, as in the present species, it is interpreted as the remains of cambium, phloem, and pericycle.

Cortex.—The cortex of *Calamopitys americana* is a very broad zone of parenchymatous tissue. Its general aspect is shown in plate 16, figure 1. The cells are nearly isodiametric in transverse section and rather short. On the exterior is a zone of parenchyma in which are embedded radial plates of sclerenchyma to form a hypodermis of the familiar "*Sparganum*" type. The vascular bundles of the leaf traces that traverse the cortex are considered below.

Leaf trace.—The description up to this point has developed the fact that *Calamopitys* is a stem of modified protostelic type producing secondary wood and exhibiting a broad cortex. In these respects it resembles the stems of several species of *Heterangium*, and it is not until the leaf traces are examined that features are observed which serve to establish definitely the generic identity of *Calamopitys americana*.

The series of photographic illustrations in plate 17, figures 1–4, serve to show rather diagrammatically the stages in the origin and development of the leaf trace.

An early stage in the development of the foliar trace is shown in plate 17, figure 1. It will be recalled that the primary xylem is nearly continuous around the "mixed" pith. The first indication of a departing leaf trace is the formation of a prominent angle in the "mixed" pith at the point of emission (pl. 17, fig. 1). As this angle develops, the adjacent primary bundle moves outward and becomes radially elongated. The protoxylem, which at first lies as a single group near the outer margin of the bundle, begins to elongate radially (pl. 18, fig. 1) and finally separates into two radially alined groups surrounded by metaxylem (pl. 18, fig. 2). The outer of these is the primary bundle of the leaf trace; the inner is known as a reparatory strand and remains in the stem as an integral part of the primary wood. As the angle of emission becomes more and more prominent and the subtending fan of secondary wood thins, the leaf-trace bundle becomes tangentially flattened and finally divides into two strands, each with its own protoxylem (pl. 18, figs. 3, 4). These strands remain close together at first but become more widely separated as they pass farther out. In the course of this passage a fan of secondary wood is seen on the outer side. As the double bundle emerges from the secondary wood of the stem a centripetal zone of secondary wood is developed, so that the leaf trace at this point has a concentric structure, which is, however, eccentric by reason of the position of the protoxylem and the smaller amount of centripetal secondary wood.

As the trace passes through the zone of phloem and pericycle the secondary xylem lessens in amount, and at the same time the two protoxylems become more widely separated, so that finally the two bundles are developed. As these pass into the inner cortex they diverge gradually and slowly lose all traces of secondary wood. As a result each bundle consists of primary xylem with an eccentrically mesarch protoxylem and is completely ensheathed by phloem and pericycle.

Leaf base.—In the collection made by the writer in 1932 there are several stems in which the cortex is well preserved. In view of the fact that Scott and Jeffrey apparently had only fragmentary material of the cortex showing leaf bases, an attempt is here made to record detailed observations on this feature.

As has already been indicated, the cortex is a rather homogeneous zone consisting of parenchyma except at the outer border, where a "*Sparganum*" hypodermis is present. The course of the leaf trace from its origin in the primary wood through the secondary wood, phloem, and pericycle has so far been followed, and it has been observed that the trace, originally single, divided into two bundles, which draw apart as the pericycle is traversed. As these bundles enter the inner cortex the situation is that shown in plate 18, figure 4, and described in a previous paragraph.

These bundles gradually diverge as they continue outward and become radially elongate, with the development of two or more protoxylems. At the same time the last vestiges of secondary wood are lost, first on the inner side and later on the outer.

Soon, by a process of medial longitudinal constriction, each of these bundles divides into two. Successive divisions of these bundles finally result in a structure of the type illustrated in plate 16, figure 1. It will be noted that the bundles tend to be radially elongated, but where several protoxylems are present the long axis may be tangential.

Affinities of Calamopitys americana.—*Calamopitys americana* is a member of the group which has been designated by Scott [4] *Eu-Calamopitys*. This subgenus is characterized by the generally manoxylic secondary wood, large, uniform, mesarch primary xylem strands, and a marked tendency toward the development of a "mixed pith." In addition, all these forms give off *Kalymma*-like petioles.

Contrasted with *Eu-Calamopitys* is the group variously assigned to a genus or subgenus under the name *Eristophyton* Zalessky.[5] In this segregation the secondary wood is pycnoxylic, the primary bundles large and mesarch above, and small with a tendency to become endarch below. To the writer it appears that this group is a logical generic segregate, and he suggests that *Eristophyton* be regarded as a distinct genus. It then follows that *Eu-Calamopitys* may be discarded, because the whole of the group falling in the genus *Calamopitys* Unger likewise falls in *Eu-Calamopitys*. In other words, the generic recognition of *Eristophyton* establishes *Calamopitys* and *Eu-Calamopitys* as synonymous.

Calamopitys americana is very closely related to *Calamopitys annularis* Unger, if one may judge from Scott's recent account.[6] This species carries what appears to be a "mixed pith"—exarch-mesarch primary xylem strands, forming a nearly continuous ring, and manoxylic secondary wood. However, there are no details on record concerning the nodal morphology, which is of great importance in delimiting the species. In consequence, the two forms must remain separate for the present, although it is not improbable that they may be combined in time.

Calamopitys americana is quite distinct from the other known species of the genus. Comparisons are made in the general summation of the group elsewhere in this paper.

[4] Scott, D. H., Studies in fossil botany, 3d ed., pt. 2, p. 108, 1923.

[5] Zalessky, M. D., Étude sur l'anatomie du *Dadoxylon tchihatcheffi* Goeppert: Com. géol. Mém., nouv. sér., livr. 58, p. 23, 1911.

[6] Scott, D. H., Notes on *Calamopitys* Unger: Linnean Soc. London Jour., Botany, vol. 44, no. 297, pp. 210–215, 1918.

Calamopitys foerstei Read

Plate 19, figures 1–3

1936. Read, C. B., Jour. Paleontology, vol. 10, no. 3, p. 219, text fig. 6.

In the Junction City material there are several specimens of a species of *Calamopitys* which has been, with some hesitation, described as new. This species was named in honor of Dr. August Foerste, the eminent American geologist who named the Linietta clays, the basal part of which is the source of the material described in this paper.

As the material in hand consists of decorticated specimens, the following remarks are of necessity confined to the woody cylinder. A series of sections has been prepared, and these show the essential features of leaf-trace emission, a feature upon which this species is primarily based.

General morphology.—In plate 19, figure 1, a transverse section of a specimen of *Calamopitys foerstei* is shown at a low magnification. The more obvious features are the five-angled pith of rather large size and the woody cylinder traversed by multiseriate rays. Situated on the edge of the pith, but not usually in direct contact with the secondary wood, are numerous discrete bundles of mesarch primary xylem. Scattered through the pith are a few isolated or grouped tracheids. It is therefore evident that the central portion of the plant is a "mixed" pith comparable to that in *Diichnia kentuckiensis* and *Calamopitys americana*. At one angle (pl. 19, fig. 1, *rs*) of this "mixed" pith it is evident that there is an interruption in the continuity of the tissues, owing to the departure of a leaf trace. At the other angles are to be seen other leaf traces in less advanced stages of emergence.

These traces, it is evident, are mesarch in structure and are developed in the fashion which is typical of the *Calamopitys*—that is, through the division of medullary xylem bundles into inner reparatory strands and outward-passing leaf-trace strands.

Details of leaf-trace emergence.—Owing to the insufficient and incomplete material available the nodal morphology can at present be only outlined in a general way. At an angle from which a leaf trace is to depart there is a gradual confluence of two strands of primary xylem lying on each side of the angle and embedded in the "mixed pith." These strands appear to remain separate while the protoxylem divides to form an outward-passing leaf-trace bundle from each and a continuing reparatory strand from each. The situation at this stage is seen in plate 19, figure 2, where the protoxylem groups of the reparatory and leaf-trace strands are separated, yet the metaxylem remains a continuous strand. An interesting feature here is that these two leaf-trace bundles, though initially separate, tend to fuse so far as the metaxylem is concerned, thus forming a single leaf-trace bundle incorporating two protoxylems. As this bundle emerges through the secondary wood it carries with it a fan of secondary xylem, presumably into the cortex, so that the general aspect on the outer face of the stele is probably similar to that in *Calamopitys americana*, and as the reparatory strand is finally separated from the leaf trace a broadly inverted U-shaped strand is seen resting in the angle of the pith. At later stages this bundle, which still carries two protoxylems, one in each lobe, divides, and thus two distinct bundles are formed. These diverge slightly but remain adjacent to the prominent pith angle.

Relationships of Calamopitys foerstei.—*Calamopitys foerstei* is a rather unusual form apparently intermediate in many respects between *Diichnia kentuckiensis* and *Calamopitys americana*. In fact, it is questionable whether this species should be referred to *Diichnia* or *Calamopitys*. In view of the departure of the leaf trace as a single bundle with two protoxylems, the designation as *Calamopitys* seems preferable. As this species now stands it is rather unsatisfactory, however, and it is to be hoped that more complete material will be found illustrating morphologic features that are now unknown or imperfectly understood.

Genus STENOMYELON Kidston and Gwynne-Vaughan, 1912

1912. Kidston, Robert, and Gwynne-Vaughan, D. T., Royal Soc. Edinburgh Trans., vol. 48, pt. 2, pp. 263–271.

Stenomyelon muratum Read

Plate 20, figures 1–4; plate 21, figures 1–4; plate 22, figures 1–4; plate 23, figures 4, 5; plate 26, figures 1, 3, 6

1936. Read, C. B., Jour. Paleontology, vol. 10, no. 3, p. 220, pl. 29, fig. 1.

A single specimen collected in 1932 from Junction City is referable to the genus *Stenomyelon* Kidston.[7] A diagnosis of the type species, *Stenomyelon tuedianum* Kidston, is as follows:

> Stem monostelic, primary xylem without xylem parenchyma, divided more or less distinctly into three lobes by as many radiating and interrupted bands of parenchyma. Primary tracheae porose on all walls. The protoxylems of the leaf trace decurrent as exarch strands on the extremities of the lobes. Secondary thickening occurs. Secondary tracheae with porose pits on the radial walls only. Medullary rays numerous. Stele closely invested by a zone of sclerotic periderm. Leaf traces depart successively from the extremities of the lobes and repeatedly divide in the cortex. Leaf-trace protoxylems become immersed. Outer cortex of the "*Sparganum*" type.[8]

With this diagnosis in mind, attention may now be turned to the new Kentucky material. In plate 23, figures 4, 5, thin sections of *Stenomyelon muratum* are seen. Examination of these sections shows that the more obvious features are (1) a large triangular "pith", which in reality is a "mixed" pith or parenchymatous protostele; (2) a surrounding zone of secondary growth, marked by the occurrence of prominent rays; (3) a one-third phyllotaxy; (4) a broad, rather parenchymatous cortex; (5) leaf traces which originate from an angle of the "mixed" pith and which emerge slowly.

DETAILS OF MORPHOLOGY OF THE STEM

"Mixed" pith.—The features of the central column, or so-called pith, are well exhibited in plate 20, figures 1–4. Figure 1 shows that the triangular column is made up principally of sclerotic elements, which are beyond any doubt primary tracheids. Interspersed with this mass of xylem are scattered cells and groups of cells of parenchyma, and around the periphery, except at the angles, there is an almost continuous zone of parenchyma. One of the most marked features of this primary wood is the very slight differentiation of protoxylem except in the vicinity of emerging leaf traces, a feature which *Stenomyelon muratum* shows with *S. tuedianum* Kidston. In the latter species "there appear to be no protoxylem strands proper to the stem itself, but in the neighborhood of the departing leaf traces a pair of definite exarch protoxylem strands are usually to be seen."[9]

Secondary wood.—Most of the details of secondary-wood structure that are discernible in the material may be seen in plate 21, figures 1–4. It is of the manoxylic type, with rather large tracheids and numerous multiseriate rays, which are broadest where they abut on the "mixed" pith. As is true of most of the Kentucky material, the preservation is such that few finer details of structure may be seen in longitudinal section. It appears, however, that the pitting is crowded on the walls of the cells and probably restricted to the radial surfaces.

Outer stelar tissues.—On the exterior of the secondary wood may be seen in some sections the fragmentary remains of probable cambium, phloem, and parenchyma. Examples of preservation of these tissues are seen in plate 21, figure 2, and plate 22, figures 1 and 2. These tissues are poorly preserved and somewhat crushed; they exhibit few features of more than casual interest.

Cortex.—The bulk of parenchymatous tissue that sheaths the woody cylinder is clearly referable to the cortex. This zone is for the most part a homogeneous one, consisting of large-lumened, more or less isodiametric cells. The walls are in places somewhat thickened, but this may be a function of preservation.

A well-differentiated and extensive hypoderma is present and consists of sinuous yet radiating strands of sclerenchyma, which frequently anastomose. The

[7] Kidston, Robert, and Gwynne-Vaughan, D. T., On the Carboniferous flora of Berwickshire, pt. 1, *Stenomyelon tuedianum* Kidston: Royal Soc. Edinburgh Trans., vol. 48, pt. 2, pp. 263–271, pls. 1–4, 1912.

[8] Idem, p. 270.

[9] Idem, p. 265.

general aspect of this tissue is clearly shown in plate 22, figure 4.

Leaf trace.—In order to clarify the discussion of the leaf trace during the course of its development and emission, a series of photographs has been prepared from serial thin sections. These are shown in plate 20, figures 1–4; plate 21, figures 1–4; and plate 22, figures 1–2. The central column of admixed primary xylem and parenchyma is triangular in cross section and shows a development of protoxylem only at the three angles in connection with the emission of leaf traces. A very early stage in the development of the leaf-trace bundle is shown in plate 20, figure 3. An angle of the primary xylem has developed a slight bulge outward, and protoxylem has been differentiated. At this stage the bundle is mesarch. Somewhat later stages in the development of this trace are seen in plate 20, figure 4, and plate 21, figure 1, and as the bundle passes slowly outward (pl. 21, figs. 1–2) there is a gradual diminution in the amount of subtending secondary growth. It is obvious that the protoxylem, while it remains mesarch, is very eccentric (pl. 21, fig. 2), being just within the outer edge of the metaxylem.

In plate 21, figure 2, the protoxylem is evidently eccentrically mesarch and is enclosed in a large bundle of metaxylem, which has developed a centripetal constriction prior to its separation from the primary xylem of the main axis. The protoxylem is elongated tangentially, and the full significance of this feature is seen in plate 21, figure 3. At this stage the secondary cylinder has been completely broken by the leaf trace that has separated from the main mass of primary xylem. This trace has now assumed an oval outline, with the long axis tangential to the main axis. The protoxylem, which continues to lie near the outer edge of the bundle, has divided into two distinct groups.

As the trace passes upward and outward it assumes the appearance shown in plate 22, figure 1. The protoxylems have become more widely separate, and the bundle, now clearly double, becomes more elongate tangentially. It is now evident that the trace will divide into two bundles, as is shown in plate 22, figure 2. At this point the trace has emerged into the phloem and pericycle, and the two bundles have diverged considerably. The protoxylem occupies an immersed position near the outer edge of each bundle.

As these two strands pass into the cortex further division takes place, so that the leaf base is polydesmic. Owing to the fragmentary condition of the specimens at hand it is impossible to define accurately the bundle pattern of the petiole or leaf base. However, some observations of slight value have been made. The bundle structure remains eccentric by reason of the position of the protoxylem and is also concentric, consisting of an immersed protoxylem (one to several) near the outer edge of the wood, encased in metaxylem and completely surrounded by tissues which are regarded as phloem and pericycle. This structure is shown in detail in plate 22, figure 3.

In the early stages of development the several bundles are arranged in a horseshoe outline and lie in the homogeneous cortex. The cross-sectional outline of the bundles in which only one protoxylem is present is nearly circular or only slightly oval. Where more than one protoxylem is present, these usually have a tangential alinement. In consequence the general aspect of the leaf base and of the individual bundles is somewhat different from that recorded for *Kalymma*, in which many of the bundles are elongated radially.

In the material at hand later stages of the leaf base are very imperfect. It appears, however, that numerous bundles exist, and that these are arranged in a ring.

The hypodermis, which is the outermost tissue preserved in the leaf base, is very characteristic. It consists of curving and frequently anastomosing strands of sclerenchyma and parenchyma and forms a zone of considerable width, as is shown in plate 22, figure 4.

Affinities of Stenomyelon muratum.—It has been shown in the preceding paragraphs that *Stenomyelon muratum* is characterized by (1) a mixed three-angled pith in which the protoxylem is imperfectly differentiated except in the advent of an emerging strand to supply the leaf; (2) a rather broad zone of secondary growth characterized by numerous multiseriate rays, some of which may be very broad; (3) a narrow zone of poorly preserved phloem and pericycle; (4) a broad zone of cortex; and (5) leaf traces passing outward from the angles of the mixed pith in a one-third divergence. A protoxylem develops at the angle, occupying an eccentrically mesarch position, and gaps the stele widely as it emerges. At the same time it divides into two bundles in the course of its passage through the secondary wood and further divides to form a polydesmic trace.

These facts immediately establish *Stenomyelon muratum* as a member of the Cycadofilicales, which were a dominant element of the Paleozoic floras. A comparative treatment of several of these with specimens in hand is now necessary to determine the affinities of the new form. In the writer's judgment the most valuable criteria in this comparison are data relating to the mixed pith, the morphology of the primary xylem, the leaf trace, and the leaf base. Of secondary importance is the structure of the secondary wood, phloem, pericycle, and cortex.

Although *Stenomyelon muratum* departs in certain features from the concept of the genus as it was defined by Kidston and Gwynne-Vaughan, nevertheless it seems to fit closely enough to make generic segregation unwise. The American form is characterized by a more parenchymatous central column, the "mixed pith", than the English *S. tuedianum* Kidston and *S. triparti-*

tum Kidston.[10] In both these English species there is simply a roughly tripartite division of the protostelic central column by narrow strands of parenchyma. However, this feature may be regarded as one that may vary considerably between species of the same genus.

The poorly characterized protoxylem, except in the vicinity of a leaf trace, is likewise a point in common, as is the method of leaf-trace emission. According to Kidston and Gwynne-Vaughan the leaf trace in *Stenomyelon tuedianum* "departs from the ends of the lobes of the primary xylem in a perfectly protostelic manner." [11] A comparison of Kidston and Gwynne-Vaughan's illustrations with those in this paper demonstrates a general similarity in the mode of leaf-trace departure. It is true that the leaf trace in the English material shows a more marked development of secondary xylem than that of *S. muratum*. Likewise the protoxylem is exarch, becoming immersed, in *S. tuedianum*, whereas in *S. muratum* the protoxylem is mesarch, tending slightly toward exarchy. Similar bundles are likewise developed in the petiole bases of both species, and these bases are polydesmic. Thus it would appear that although *Stenomyelon muratum* varies in detail from *S. tuedianum* and *S. tripartitum* Kidston it may be definitely assigned to the genus.

Probably the closest affinities of *Stenomyelon muratum* and, in consequence, of the other species of the genus are with the Calamopityeae, the family in which the writer suggests that *Stenomyelon* be placed. It would seem that except for the apparent absence of protoxylem in the cauline axis and, in consequence, of reparatory strands in connection with an emerging leaf trace, *Stenomyelon* might readily be admitted as an offshoot of the *Calamopitys* type in which secondary xylem is but slightly manifested in the leaf-trace bundles. Moreover, in view of the fact that there is some differentiation of protoxylem in *S. tripartitum* Kidston, it would appear that this feature is one of but doubtful value. The leaf base, both in the Calamopityeae and in *Stenomyelon*, is polydesmic, and the bundles are similar.

In summary, it is the writer's opinion that *Stenomyelon* is closely related to various calamopityean genera and should be assigned to the family Calamopityeae. It parallels some of the Lyginopterideae, but whether it has any direct relationship to that family is doubtful.

Genus KALYMMA Unger

1856. Unger, Franz, K. Akad. Wiss. Wien, Math.-nat. Klasse, Denkschr., Band 11, p. 157.

The generic name *Kalymma* is used for detached petioles referable to *Calamopitys* and related genera. As defined by Unger and as now understood, it refers particularly to petiolar organs characterized by a ring of polydesmic bundles, each bundle concentric in structure. This ring of bundles is embedded in a groundmass of parenchyma. Externally the petioles are characterized by a sheathing zone of alternating soft and sclerotic strands, the "*Sparganum*" cortex, and this is, of course, limited by the epidermis.

Unger originally described two species of *Kalymma*, *K. grandis* and *K. striata*. It is probable that these are identical, however. Scott and Jeffrey [12] in 1914 recognized *Kalymma grandis* Unger from the plant beds that yielded the material here under discussion. They likewise described *Calamopteris hippocrepis* from the same deposits, and, while admitting the relationship of this form and *Kalymma grandis*, they suggested generic segregation.

Calamopteris is a genus likewise established by Unger [13] and similar to *Kalymma* except for the tangential rather than radial elongation of the vascular bundles. It was suggested by Scott and Jeffrey [14] that these two genera might be grouped together, although they did not adopt that procedure. In this paper the writer suggests that the several species assigned to the two genera be placed in the genus *Kalymma*, which is preferable, owing to its more common usage.

The reasons for this generic synonymy are several:

1. A transition may be seen in a large series of specimens of *Kalymma* from the type defined as *Kalymma* with radially elongated bundles to the type defined as *Calamopteris* with tangentially elongated bundles.
2. The prominent invaginations mentioned by Scott and Jeffrey in the rim of bundles of *Calamopteris hippocrepis* and *C. debilis* Unger are characteristic of *Kalymma lirata* and cannot be taken as features of value in generic segregation. Such invaginations are common in other species in proximity to a dichotomy of the petiole.
3. The structure of the individual bundles appears to be identical in *Kalymma* and *Calamopteris*.
4. The parenchymatous groundmass and the "*Sparganum*" cortex are identical in both genera.

As regards the ramification of these petioles there is evidence at hand indicative of proximal dichotomy and distal lateral branching—that is, the fronds were probably bipartite. In the large specimens of *Kalymma* a deep groove marks both the abaxial and adaxial faces of the ring of vascular bundles. Certain fragments show these furrows strongly developed, with a tendency toward the formation of two equal rings of bundles. It is thus obvious that a dichotomy took place a short distance above.

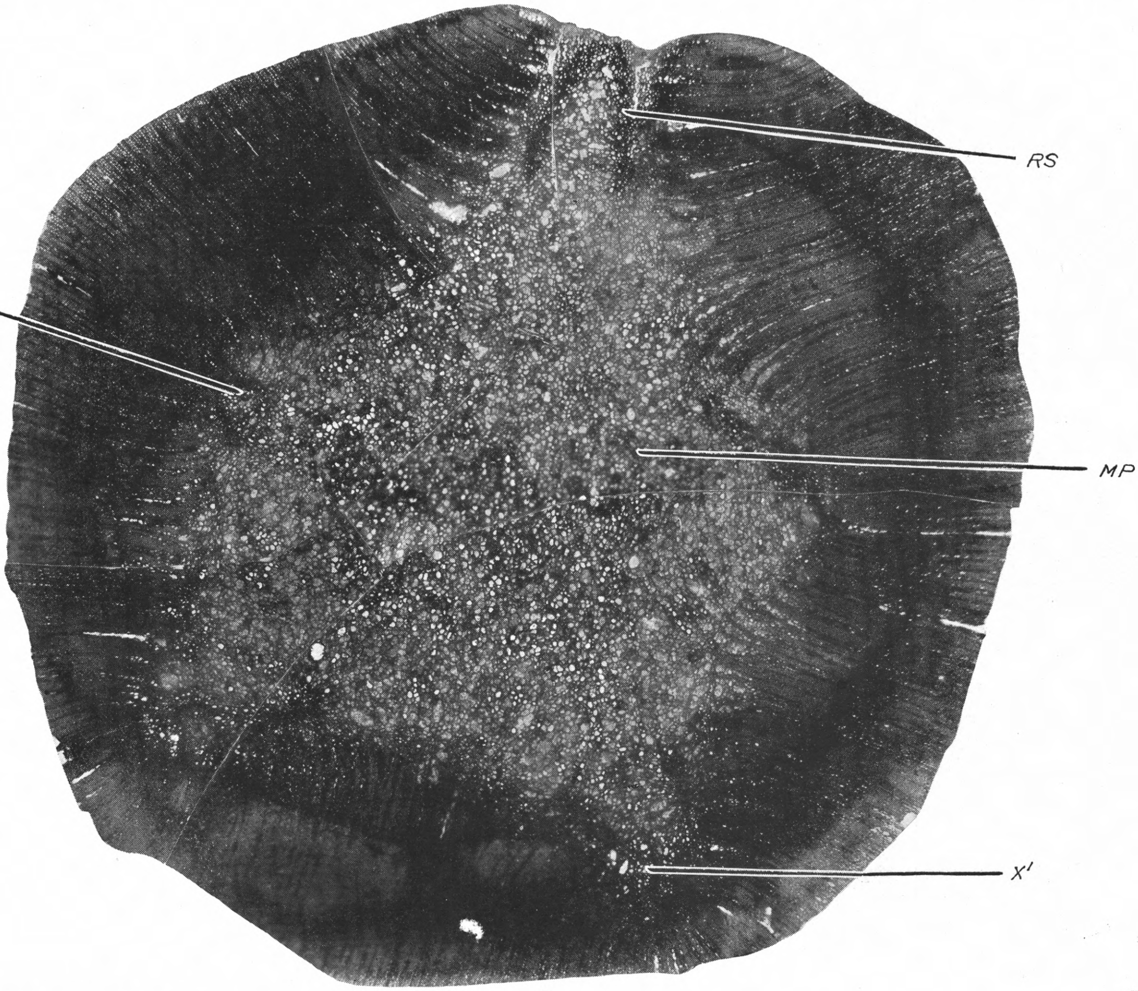
[10] For a description of this form see Scott, D. H., Studies in fossil botany, 3d ed., pt. 2, pp. 141–143, 1923.

[11] Kidston, Robert, and Gwynne-Vaughan, D. T., op. cit., p. 266.

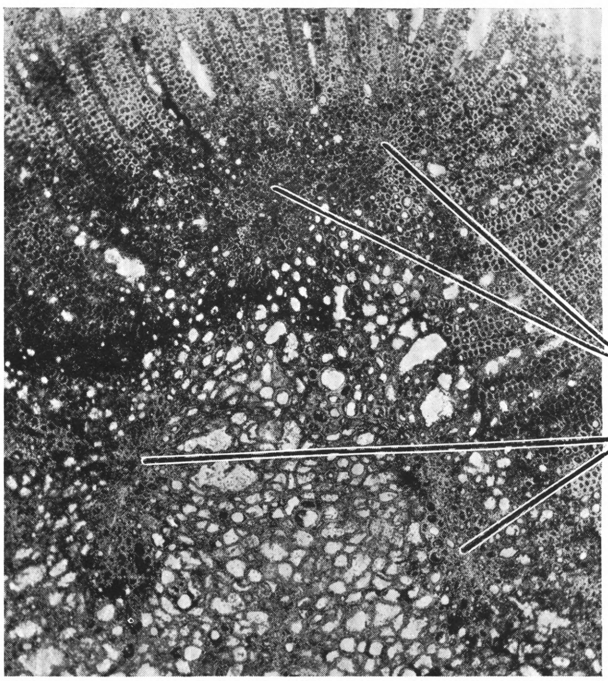
[12] Scott, D. H., and Jeffrey E. C., On fossil plants showing structure from the base of the Waverly shale of Kentucky: Royal Soc. London Philos. Trans., ser. B, vol. 205, pp. 327–330, 1914.

[13] Unger, Franz, op. cit., p. 158.

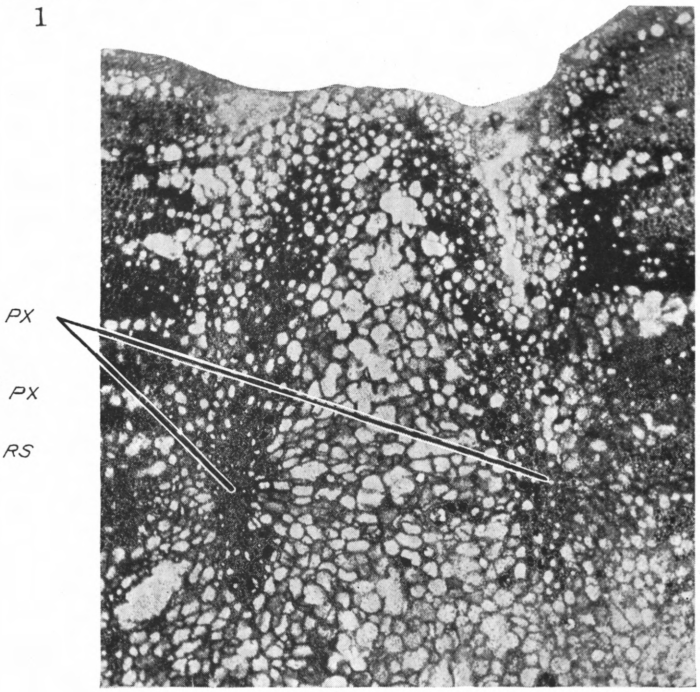
[14] Scott, D. H., and Jeffrey, E. C., op. cit., pp. 334–335.



1



2



3

CALAMOPITYEAE OF THE NEW ALBANY SHALE.

PLATE 19

Calamopitys foerstei Read

FIGURE 1. A mosaic of photographs of a transverse section of the stem showing the "mixed" pith (MP), the primary bundles (X^1), and a reparatory strand (RS). Enlarged 7 diameters.

FIGURE 2. A more detailed view of one angle of the "mixed" pith showing the two bundles involved in leaf-trace emission (RS), and the single leaf-trace bundle with two protoxylem groups which results (PX). Enlarged 24 diameters.

FIGURE 3. A more detailed view of another angle of the "mixed" pith showing the double reparatory strand with protoxylem at PX. Enlarged 24 diameters.

PLATE 20

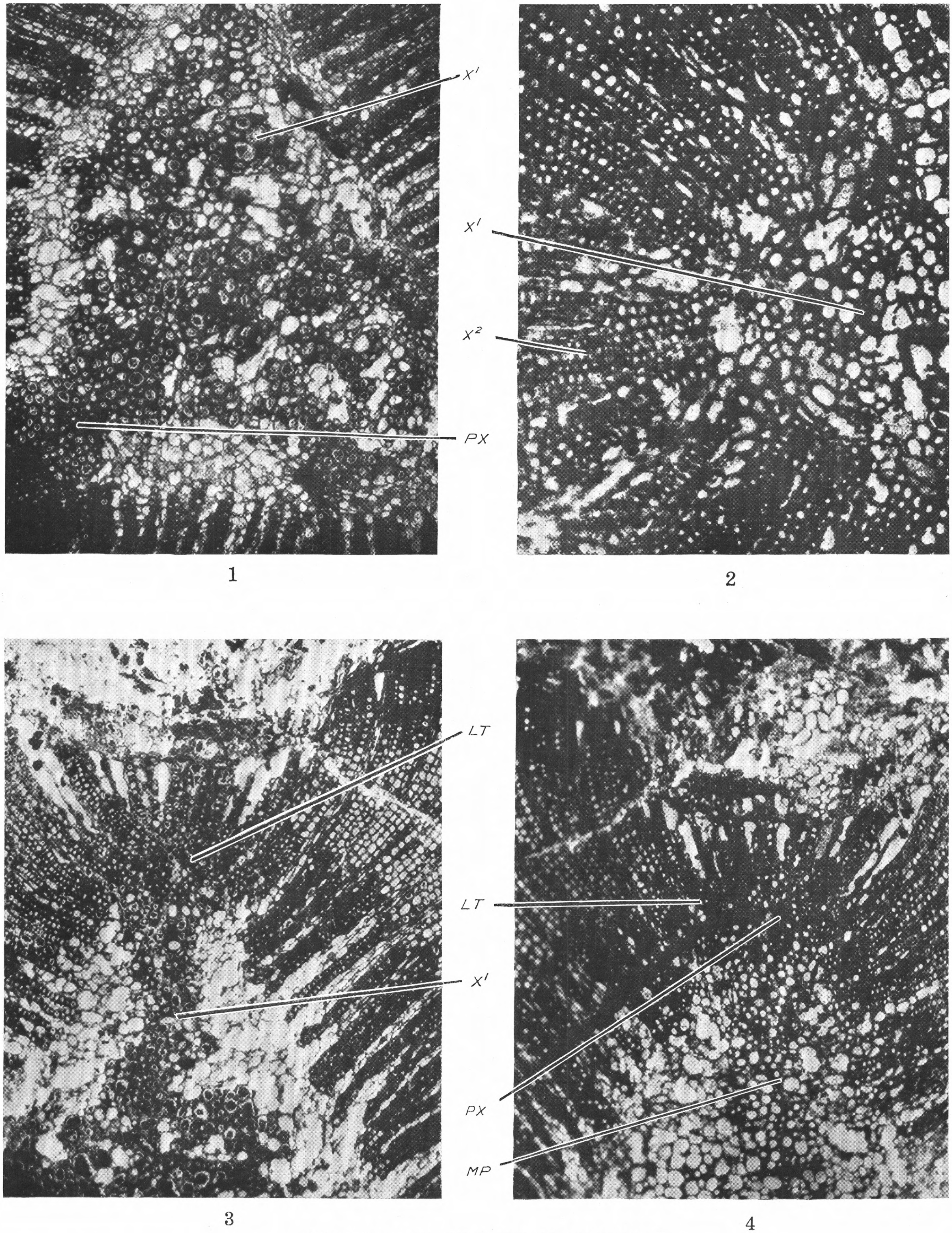
Stenomyelon muratum Read

FIGURE 1. A photograph showing a transverse section of the protostele or so-called "mixed" pith. Note the admixture of parenchyma. The protoxylem of an emerging leaf trace is seen at PX. Enlarged 24 diameters.

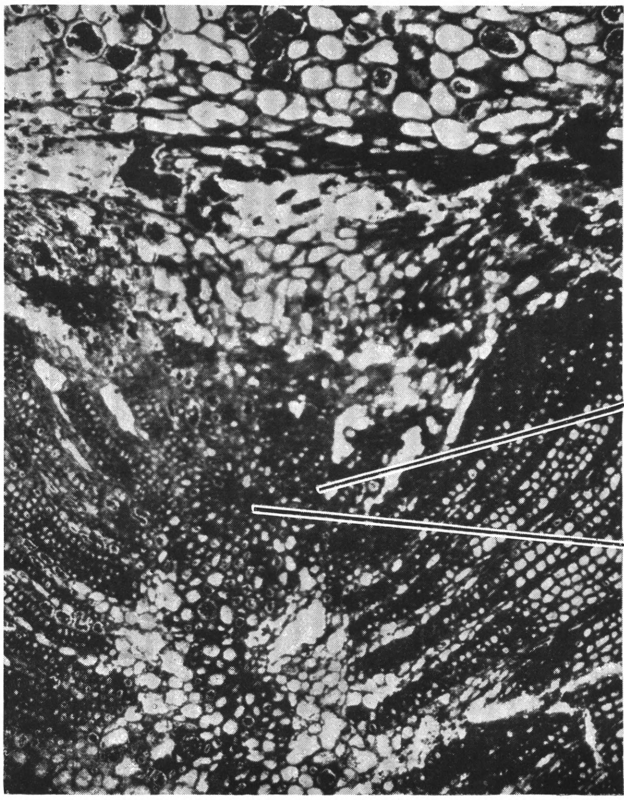
FIGURE 2. A photograph of a portion of the "mixed" pith and adjacent secondary xylem. Note the absence of a definite protoxylem. X^1, Primary xylem; X^2, secondary xylem. Enlarged 50 diameters.

FIGURE 3. A photograph of a transverse section of the stem showing an early stage in leaf-trace emission. A protoxylem has been differentiated, and the leaf trace is passing outward through the secondary xylem. X^1, Primary xylem; LT, leaf-trace protoxylem. Enlarged 24 diameters.

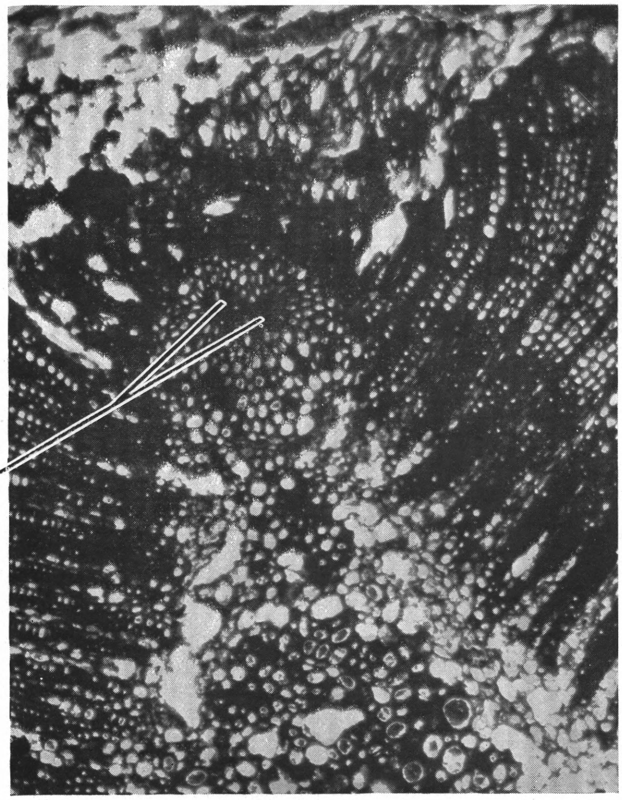
FIGURE 4. A photograph of a slightly later stage in the emission of a leaf trace. The protoxylem is apparently dividing. MP, "Mixed" pith; PX, protoxylem; LT, leaf trace. Enlarged 24 diameters.



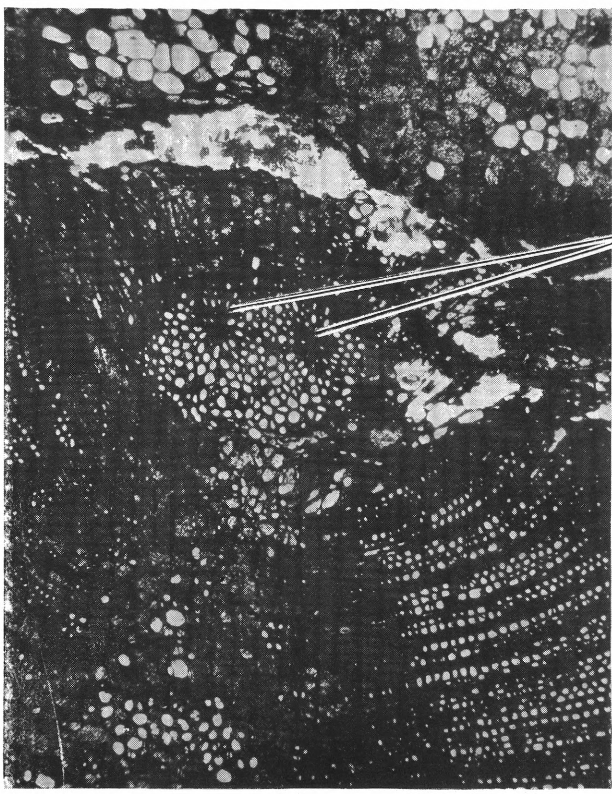
CALAMOPITYEAE OF THE NEW ALBANY SHALE.



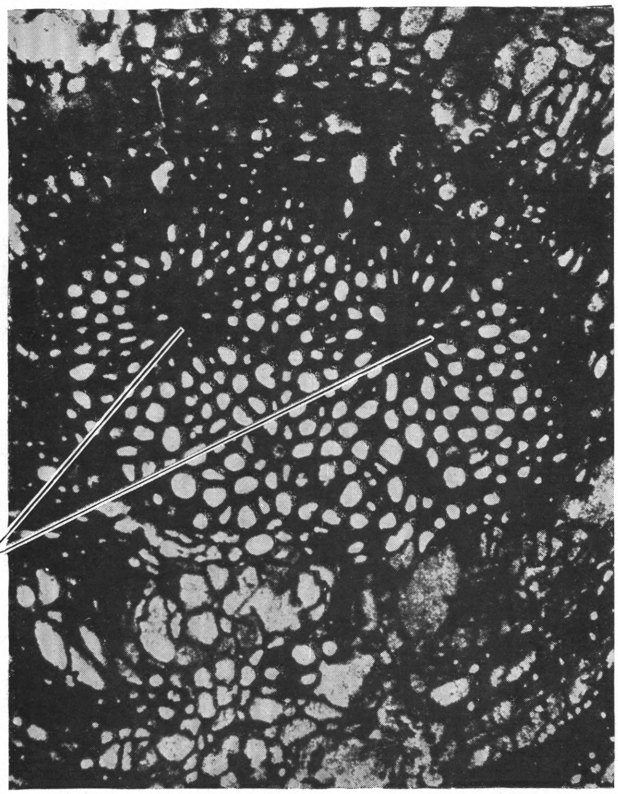
1



2



3



4

CALAMOPITYEAE OF THE NEW ALBANY SHALE.

PLATE 21

Stenomyelon muratum Read

FIGURE 1. Photograph of a transverse section of *Stenomyelon muratum* showing an early stage in the emission of the leaf trace. It will be noted that the protoxylem is divided into two. LT, Leaf trace; PX, protoxylem. Enlarged 24 diameters.

FIGURE 2. A photograph of a stage slightly later than figure 1, showing leaf-trace emission. Note that the protoxylems are separated. Enlarged 24 diameters.

FIGURE 3. A still later stage in leaf-trace emission. The trace here shows two definite protoxylems and is tangentially elongate. Enlarged 24 diameters.

FIGURE 4. A photograph at a higher magnification of the leaf trace shown in figure 3. Note the two mesarch protoxylems. Enlarged 50 diameters.

PLATE 22

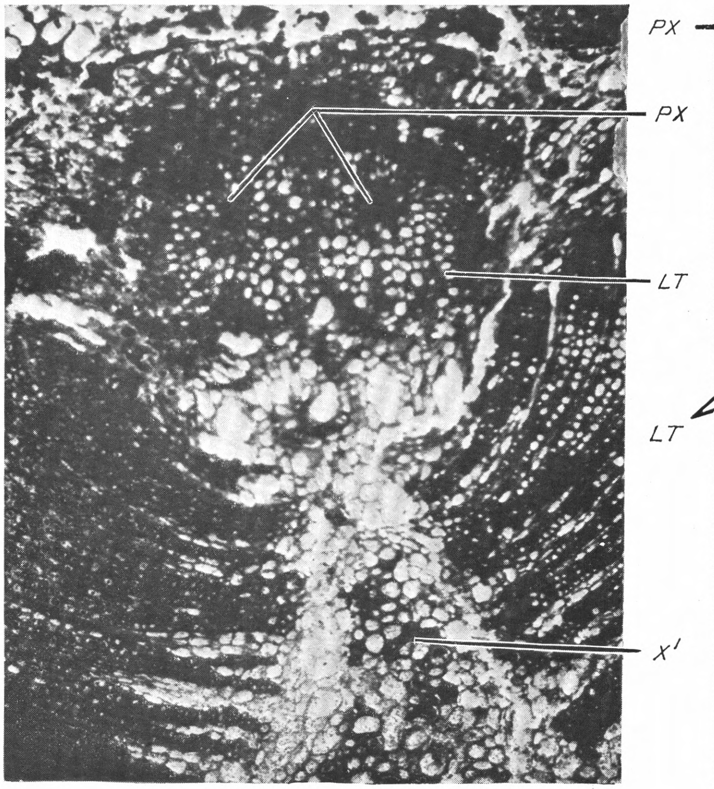
***Stenomyelon muratum* Read**

FIGURE 1. A transverse section of the stem showing the bilobed leaf trace in the outer stelar tissues. PX, Protoxylem; LT, leaf trace; X^1, primary xylem. Enlarged 24 diameters.

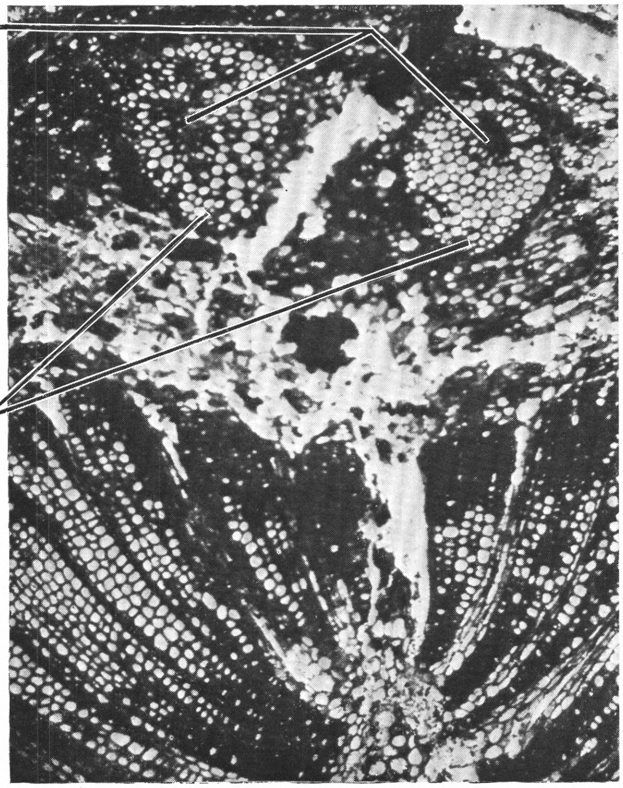
FIGURE 2. A somewhat later stage than figure 1, showing the two bundles of the leaf trace in the inner cortex. These are the result of division of the single strand shown in figure 1. Continued division results in the formation of a polydesmic petiole of the *Kalymma* type. Enlarged 30 diameters.

FIGURE 3. A portion of the cortex of the stem showing two vascular bundles of a polydesmic leaf base. Note the mesarch protoxylem. Enlarged 50 diameters.

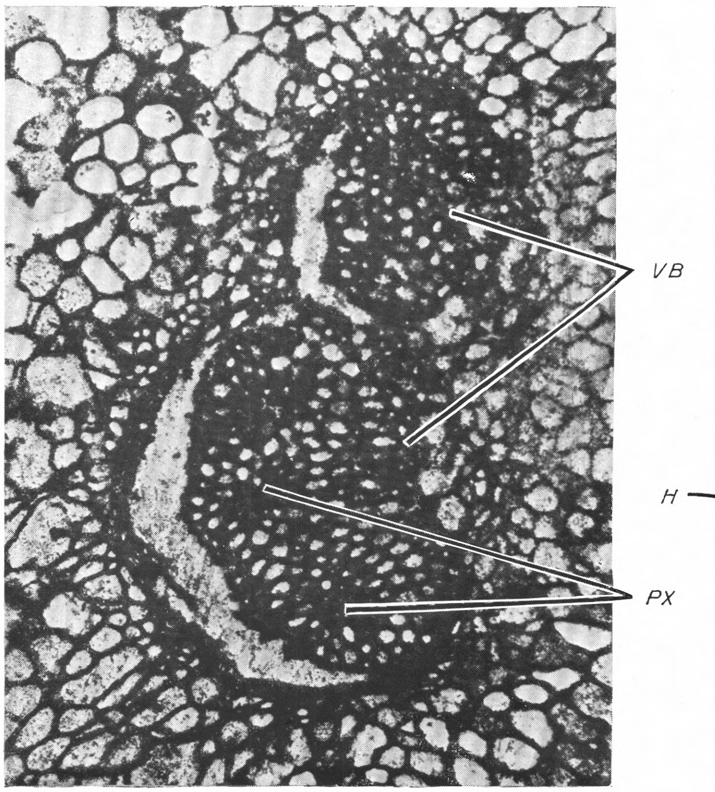
FIGURE 4. A photograph illustrating the hypodermal strands in the outer cortex. Above a partly decomposed vascular bundle is seen. H, Sclerotic strands of the hypodermis. Enlarged 24 diameters.



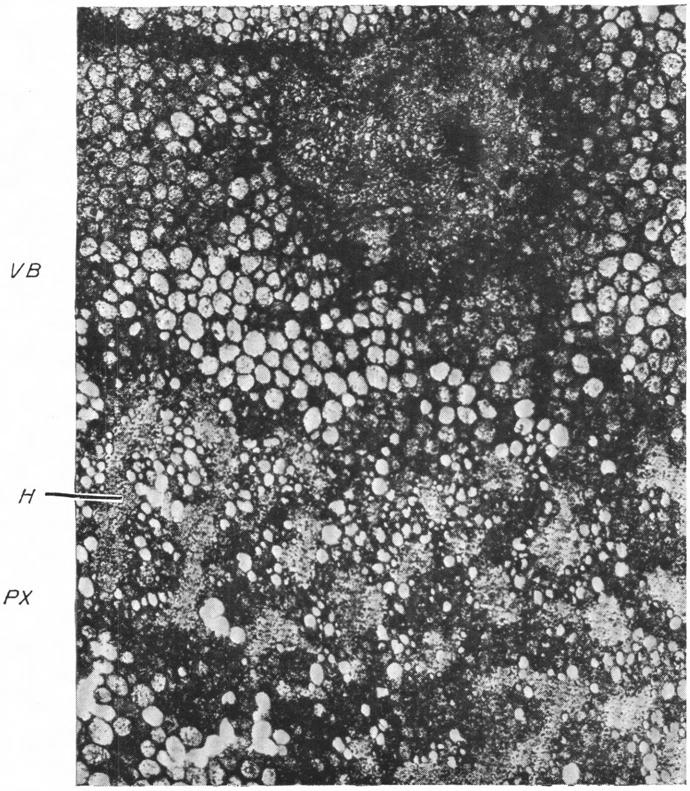
1



2



3



4

CALAMOPITYEAE OF THE NEW ALBANY SHALE.

CALAMOPITYEAE OF THE NEW ALBANY SHALE.

PLATE 23

Kalymma lirata Read

FIGURE 1. A photograph of a portion of the petiole, showing the prominent abaxial and adaxial furrows in the ring of vascular bundles. Enlarged 6 diameters.

FIGURE 2. A petiole of the *Kalymma lirata* type cut a short distance below a dichotomy, showing the ring of vascular bundles, the very pronounced furrows, and a fragment of the "*Sparganum*" cortex. Enlarged 6 diameters.

Kalymma resinosa Read

FIGURE 3. A petiole showing the vascular bundles forming an open U and the lysigenous secretory ducts. Enlarged 6 diameters.

Stenomyelon muratum Read

FIGURES 4, 5. Photographs of two transverse sections showing the general aspect of the stem at a low magnification. Enlarged 6 diameters.

Kalymma auriculata Read

FIGURE 6. A photograph of a transverse section showing the general aspects. Note the prominent abaxial projections of the vascular bundles. Enlarged 6 diameters.

PLATE 24

***Kalymma lirata* Read**

FIGURE 1. A photograph of a transverse section showing the ring of vascular bundles (VB), the abaxial (ABVB) and adaxial (ADVB) furrows in the ring, the parenchymatous groundmass (C), and the "*Sparganum*" hypodermis (H). Enlarged 15 diameters.

PLATE 25

Kalymma lirata Read

FIGURE 1. A leaf base of the *Kalymma lirata* type (LB) shown attached to the stem of *Calamopitys americana* Scott and Jeffrey. ST, Stele of *C. americana;* H, "*Sparganum*" hypodermis. Enlarged 7 diameters.

FIGURE 2. A photograph of a portion of a section of *Kalymma lirata* showing the vascular bundles (VB), embedded in the parenchymotous groundmass. Enlarged 15 diameters.

Kalymma resinosa Read

FIGURE 3. A transverse section of *Kalymma resinosa* showing the vascular bundles, the secretory canals (SC), and portions of the "*Sparganum*" cortex. Enlarged 6 diameters.

FIGURE 4. A portion of a transverse section of *Kalymma resinosa* illustrating the secretory canals (SC) and the vascular bundles (VB). Enlarged 24 diameters.

PLATE 26

Stenomyelon muratum Read

FIGURE 1. A portion of the "mixed" pith and adjacent secondary xylem in a somewhat tangentially cut longitudinal section. Note the admixture of parenchyma and tracheids in the "mixed" pith. Enlarged 25 diameters.

FIGURE 3. A more detailed view of a portion of the photograph shown in figure 1. Enlarged 40 diameters.

FIGURE 6. A tangential longitudinal section showing two sclerotic strands in the cortex. Enlarged 30 diameters.

Calamopitys americana Scott and Jeffrey

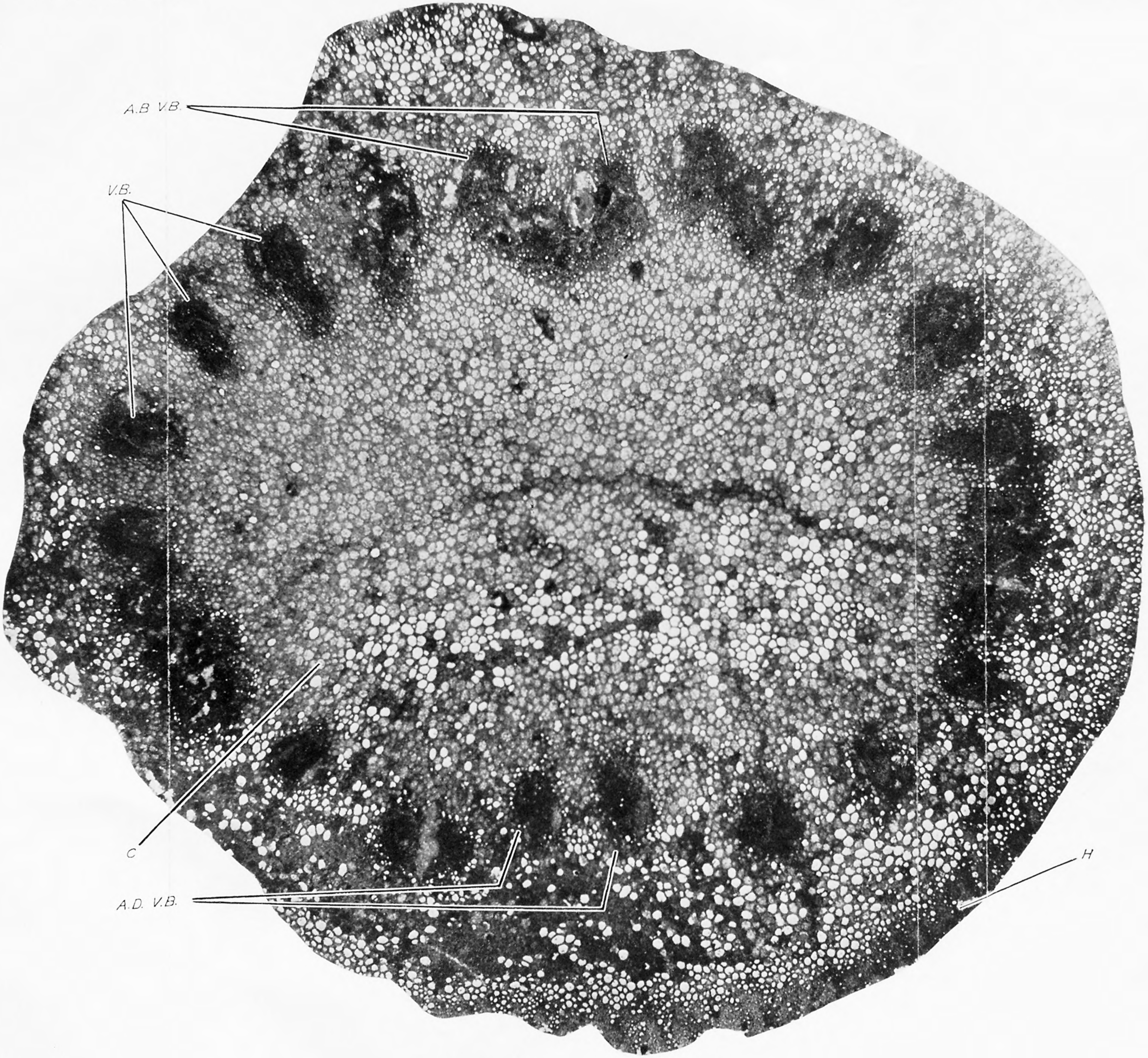
FIGURE 2. A leaf trace as seen on the outer face of the stele. Note the bilobed trace and the fan of secondary xylem, which is quickly lost as the trace passes through the cortex. Enlarged 20 diameters.

Kalymma lirata Read

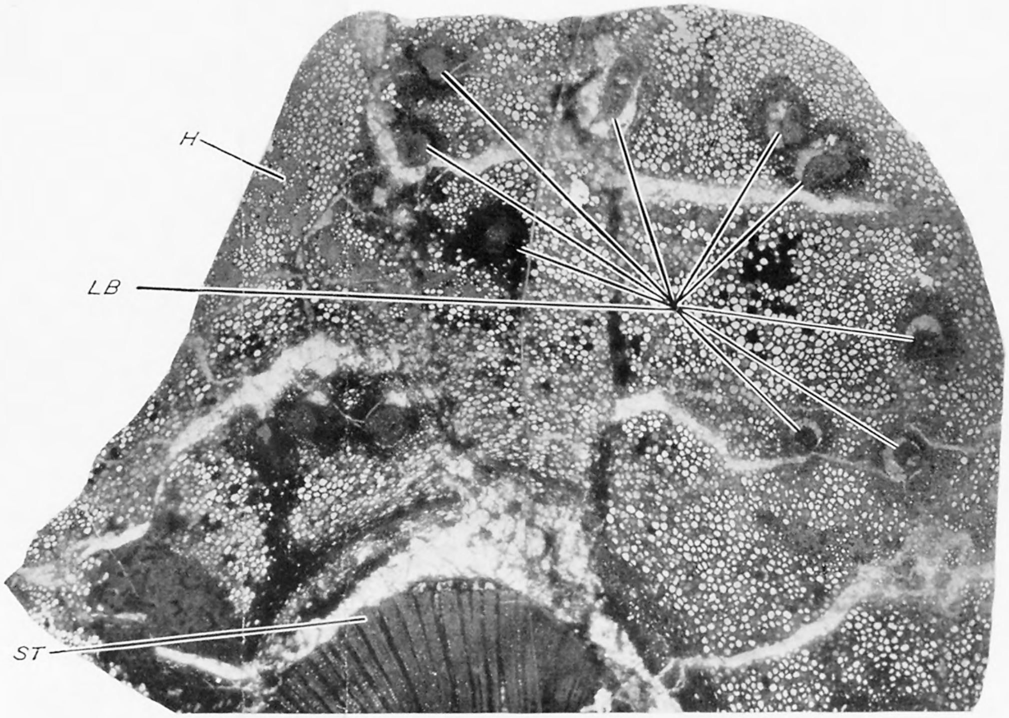
FIGURE 4. A single vascular bundle showing the concentric structure. Enlarged 24 diameters.

Calamopitys americana Scott and Jeffrey

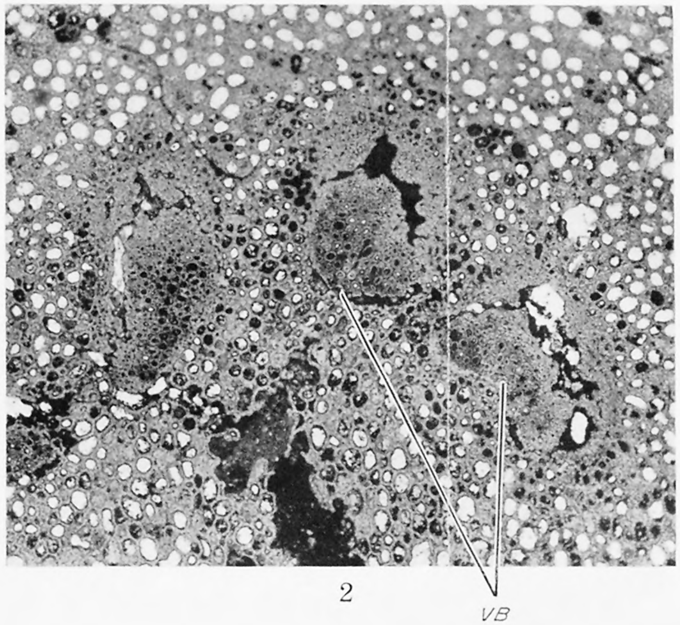
FIGURE 5. A portion of the "mixed" pith as seen in longitudinal section. Enlarged 30 diameters.



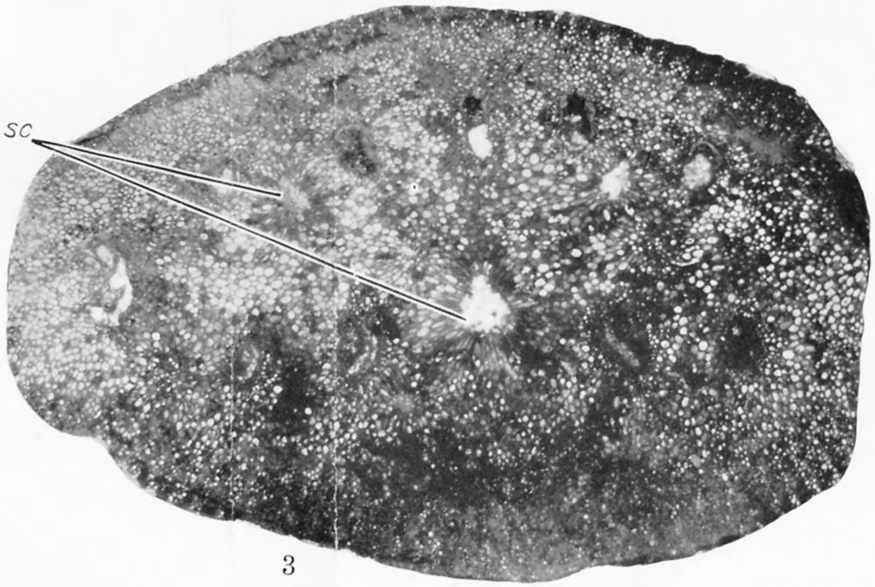
CALAMOPITYEAE OF THE NEW ALBANY SHALE.



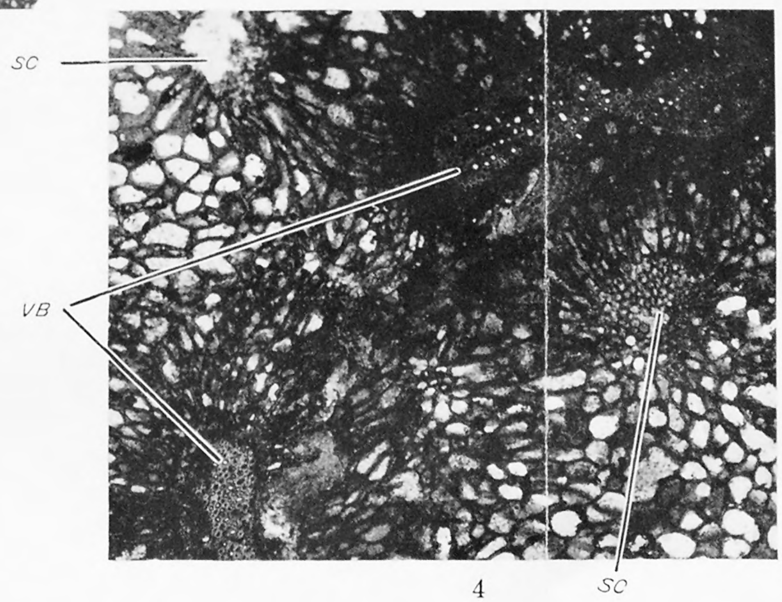
1



2

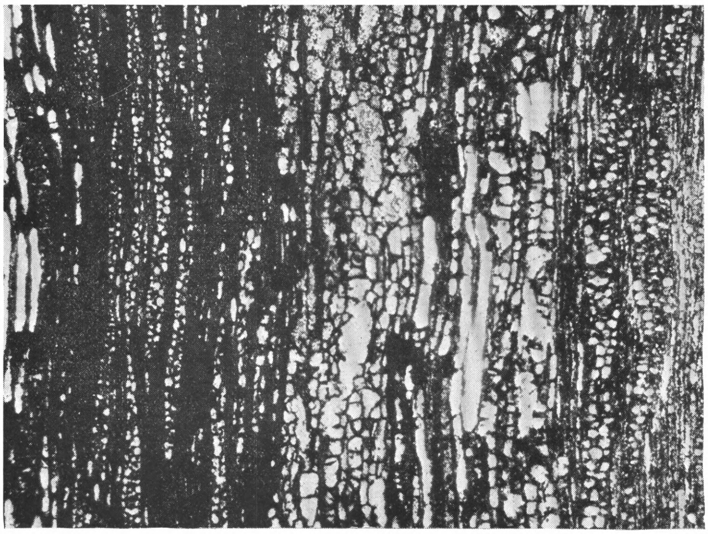


3

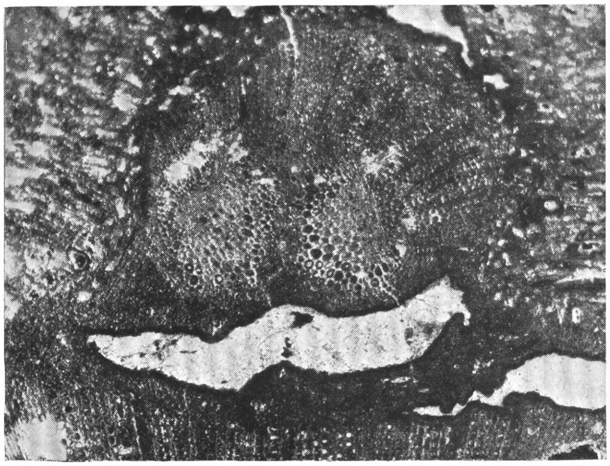


4

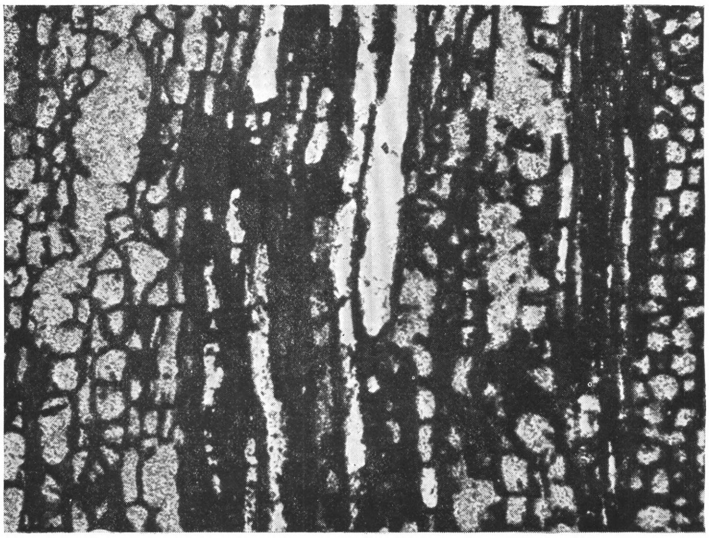
CALAMOPITYEAE OF THE NEW ALBANY SHALE.



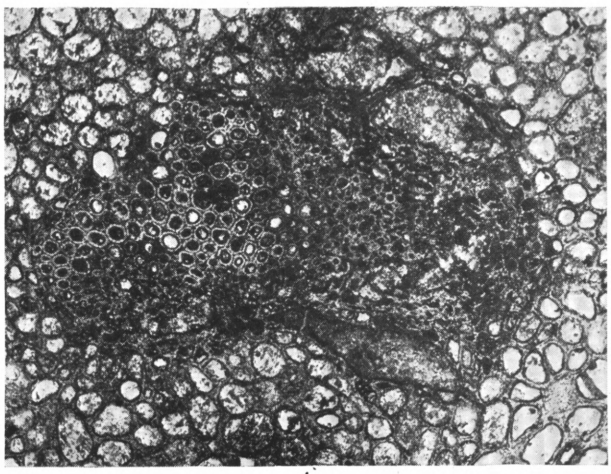
1



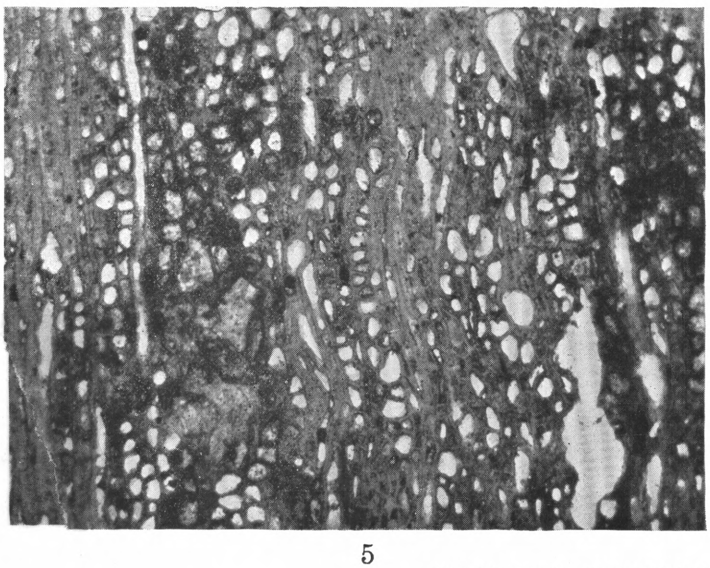
2



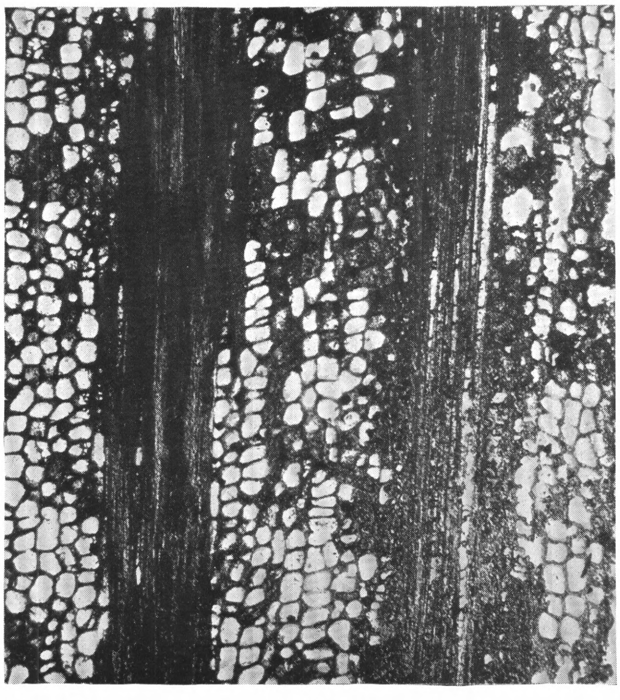
3



4



5



6

CALAMOPITYEAE OF THE NEW ALBANY SHALE.