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PETRIFIED CONES OF THE GENUS *CALAMOSTACHYS* FROM THE CARBONIFEROUS OF ILLINOIS

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VOLUME XIV

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CONTENTS

INTRODUCTION

CALAMITEAN cones are rather common fossils in Pennsylvanian plant-bearing rocks, but the different kinds cannot always be recognized with certainty unless the preservation reveals the relation of the spore-bearing organs to the other parts. Compressions, which make up the great majority of Carboniferous plant fossils, seldom show this feature clearly. Consequently, most of our knowledge of the morphology of calamitean fructifications has been derived from coal ball material in which both the relation of the parts and the tissue structure can be observed to some extent.

Most petrified calamitean fructifications have been found to belong to either *Calamostachys* or *Palaeostachya,* which differ mainly in the position of the sporangiophores on the cone axis. Several species of both genera have been found in coal balls from Great Britain and continental Europe, but this is, as far as I know, the first account of a structurally preserved *Calamostachys* from North America. It is true that Andrews (1951) listed "*Calamostachys* sp." as an American coal ball plant, but I have not found any accounts of cones definitely attributable to this genus. The only other references to *Calamostachys* are descriptions of compressed material in the works of Lesquereux, White, Bell, and others. The situation is different with respect to the similar and related genus *Palaeostachya*. This genus has two American species, *Palaeostachya andrewsii* of Baxter (1955) and *P. decacnema* of Delevoryas (1955). A third form, which Anderson (1954) called *Palaeostachya multifolia,* is a *Calamostachys* instead. Material that had been identified with Anderson's species constitutes the subject of this account.

Material

The following discussion is concerned with four cones from the well-known coal ball locality near Berryville in southern Illinois. Three of the cones (Pls. I–XI), all from one coal ball, are very similar, and are here designated as syntypes of the new species *Calamostachys americana.* A fourth cone (Pl. XII), which shows some differences believed to be correlated with its smaller size, is also placed in the new species.

All specimens illustrated are catalogued and deposited in the Museum of Paleontology of the University of Michigan.

Locality

The Berryville locality is near the western edge of Lawrence County in southern Illinois, and is on the farm of Ralph Brian, two miles north and one mile east of the town of Berryville. The coal ball stratum is exposed in the bed of a small creek, and belongs to the Calhoun coal horizon of the McLeansboro group of the Pennsylvanian system. A fairly large and interesting flora has been described from this locality in contributions by Andrews, Mamay, Stewart, Delevoryas, Morgan, and others.

Acknowledgments

I am especially obliged to Professor Wilson N. Stewart of the University of Illinois for the privilege of describing the new material. Although Professor Stewart himself has a primary interest in the Berryville plants, he insisted that I undertake this particular study. I am also grateful to Professor Henry N. Andrews of Washington University for making available the set of more than 100 collodion peel sections that Anderson prepared of his *Palaeostachya multifolia.* It has thereby been possible to establish that our cones and those which Anderson described are the same species.

Anderson intended his combination *Palaeostachya multifolia* to embrace the *Calamites multifolia* (Reed, 1938) and some poorly preserved cone fragments from the Berryville locality and from Booneville, Indiana, which were discovered after 1938. In naming the new material it is necessary to refer it to another genus (*Calamostachys*), and I have decided against continued use of the trivial epithet *multifolia*.[1] Through the cooperation of Dr. R. M. Kosanke I have been privileged to examine the type specimen of *Calamites multifolia* Reed which is in the collection of the State Geological Survey Division of Illinois. The specimen is probably a portion of a calamitean cone. Details of the structure of the axis are obscure, and sporangiophores, sporangia, and spores are absent. It is too poorly preserved to serve as the basis for identification of other material.

Distinctions between Palaeostachya and Calamostachys

The most important difference between *Palaeostachya* and *Calamostachys* is in the position of the sporangiophores. In both genera the central axis bears regularly spaced whorls of bracts which are united into discs in some species. In *Palaeostachya* the sporangiophores stand obliquely in the bract axils, but in *Calamostachys* they are attached to the cone axis about midway between successive bract whorls. Because the bract and sporangiophore whorls in *Calamostachys* alternate on the cone axis and are about equally spaced, this genus is sometimes referred to as having fertile and sterile nodes. This is correct if the nodes are merely regarded as the places of attachment of appendage whorls, but in *Calamostochys* the bract and sporangiophore traces appear to form at the same node, and it seems doubtful whether it is correct to refer to two kinds of nodes.

Anderson referred his cone fragments to *Palaeostachya* because he thought that the sporangiophores arose obliquely in the bract axils. His description is accompanied by a reconstruction of the cone (Anderson, 1953, p. 411) which shows this feature. However, his preparations, especially those which he illustrated, show no axillary sporangiophores. These organs are, in fact, absent in his material and the oblique position of any part is the result of crushing. As far as I can determine, Anderson's cones reveal no diagnostic characters of *Palaeostachya*. They show some of the general features of sphenopsid cones but nothing more. In the newly discovered specimens the bases of the sporangiophores stand out distinctly

[1]It would probably be necessary to retain *multifolia* had Anderson proposed it for a new species of *Palaeostachya*, but because he used it merely to make a new combination it can be rejected.

between the bract discs on the cone axis (Pl. I, Fig. 2; Pl. V, Figs. 1 and 3; Pl. VII) and identity with *Calamostachys* is positive.

Another difference commonly supposed to distinguish *Palaeostachya* from *Calamostachys* is the course of the sporangiophore trace. In *Palaeostachya* it is described as ascending about halfway up the internode, then bending abruptly downward and entering the sporangiophore base in the axil below. Although Hickling (1907), who described *Palaeostachya vera* in detail, formally added the flexed trace to the generic diagnosis, it cannot be retained as a distinguishing character because (1) it is not always present in *Palaeostachya* and (2) it has been found in *Calamostachys*. Delevoryas (1955) observed a trace in *P. decacnema* which takes a direct course from the node to the sporangiophore base. That a situation fundamentally the same as that which Hickling described also exists in *Calamostachys* has been known for a long time but seems to have escaped general notice. Renault (1896) first saw it in some French material. Even more pertinent is that fact that Hickling (1910) described a flexed trace in *Calamostachys binneyana* only three years after he had emphasized its presence in the other genus, although for some unexplained reason he attached no special significance to it in *Calamostachys*.

GENERAL FEATURES

The three syntypes of *Calamostachys americana* are larger than most calamitean strobili, ranging from 3 to 4 cm. in diameter. Two of them are compressed to one-half or less than one-half of their original diameters (Pl. II, Figs. 1 and 2). The other syntype which is 12 cm. long but incomplete, is slightly less flattened (Pl. I, Fig. 1).

The noded axis bears bracts and sporangiophores in alternating whorls. The bract whorls, which are spaced at intervals of about 4 mm., contain about 45 laterally fused bracts which form horizontally expanded discs having radii of about 1 cm. The fusion is so complete that the individual units have virtually lost their identities except for the small vascular strand in each one. The discs turn upward at the margin, and immediately above the upturn the bracts separate and extend upward as free terminal laminae which overlap the next two discs above (Pl. VI, Fig. 1).

The sporangiophore whorls each contain about 30 sporangiophores. They are located on the cone axis about midway between the bract whorls (Pl. V, Fig. 1; Pl. VII).

The sporangia were peltately borne and were originally elongated in the same direction as the sporangiophore stalks (Pl. IX, Fig. 4). They were about 8 mm. long and 2 mm. wide, although they were probably slightly wider distally than proximally. At most places the sporangia had disintegrated, releasing the spores which for the most part still remain within the spaces between the bract discs. Spores can be seen almost anywhere in the sections, having made their way as extraneous particles into breaks in the tissues of the axis. Two of the cones (Pl. I, Fig. 1; Pl. II, Fig. 2) contain only microspores but the third (Pl. II, Fig. 1) contains both microspores and megaspores.

CONE AXIS

The cone axis is slightly more than 1 cm. in diameter in the largest cone (syntype No. 34557) and proportionately smaller in others. There is a large cavity in the center which is surrounded in sequence by a layer of persistent pith tissue, the vascular cylinder composed of a ring of bundles reinforced by an incomplete layer of secondary xylem, the cortex, and the epidermis. In some sections the inner edge of the persistent part of the pith is coarsely crenulated (Pl. II, Figs. 1 and 2; Pl. III, Fig. 1).

The cortex contains an elaborate aerating system. In the upper half of the internode which is partly covered by the decurrent portion of the bract bases, the cortex contains a prominent "space ring" which is connected through the lower half of the internode to the "space ring" below by a circle of separate air canals or cavities. There are 15 of these cavities in each of the syntype specimens (Pl. III, Fig. 1), and they measure 0.60 to 0.75 mm. in diameter. They are regularly spaced, and are separated from each other by rays of cortex which are about as wide as the cavities themselves (Pl. IV, Fig. 1). In sections across the upper part of an internode the "space ring" appears to separate the cortex from the vascular tissue which lies inwardly from it (Pl. I, Fig. 1; Pl. II, Figs. 1 and 2; Pl. X, Fig. 1). In places where the cortex outside the "space ring" has decayed the outer xylem surface is exposed. Although in the preparations the whole aerating system appears to consist mostly of space, it was without doubt partly filled with parenchymatous tissue during life. An individual "space ring" located in the upper half of the internode, extends from approximately the level of a sporangiophore whorl to the bract disc above it (Pl. I, Fig. 2; Pl. V, Fig. 3) and is in that part of the axis surrounded by the coalesced decurrent portions of the bract bases. Actually, in longitudinal sections of the axis that show cross sections of the "space rings," each "ring" has the appearance of a cavity in the lower expanded portion of the bract base (Pl. V, Fig. 3). Situated where they are, the "space rings" had the effect of weakening the bract bases, and many of them broke there when the cones were crushed.

Some of the preparations show remains of large-celled parenchyma in the "space rings" (Pl. VIII, Fig. 1). The bract traces can be seen passing through the "space rings" (Pl. IX, Fig. 2) which also contain the melismatic tissue. This tissue shows in most sections (Pl. V, Figs. 1 and 2; Pl. VI, Fig. 1) and is conspicuous because of the black contents of its cells.

The vascular system of the axis is a dictyostele of about 30 approximately equally spaced strands. At places the cylinder of bundles is partly surrounded by an incompletely formed layer of secondary xylem. Although the bundles are about equally spaced, they are definitely paired with the cortical air spaces, two bundles lying against the inner face of each cavity (Pl. IV, Figs. 1 and 2). At some places additional bundles can be seen lying slightly lateral to the others and nearer the pith. This is the result of bundle branching which presumably took place at each node. Even though a few extra bundles may show in a section, it is clear that there is a definite two-to-one relationship between the bundles making up the vascular network and the cortical spaces. Each of the three syntype specimens shows 15 cortical cavities with 30 vascular strands adjacent to them. The fourth specimen studied (topotype No. 34560) has fewer cortical cavities and correspondingly fewer bundles. In all four specimens each vascular strand shows a conspicuous carinal canal (Pl. IV, Fig. 2) which does not pass through the internode (Pl. VI, Fig. 2).

Only the xylem portion of a vascular strand is preserved. Because the xylem abuts directly onto a cortical air cavity, some of the volume that is now space was originally phloem tissue, which does not show because it has decayed. Secondary xylem where present lies between the primary xylem strands and the air cavities (Pl. IV, Fig. 2). This tissue is never extensively developed and seldom exceeds a dozen cells in radial extent. It first began to form opposite the primary xylem masses. In some parts of the cone it is still confined to these locations but elsewhere it constitutes a continuous tissue laterally for some distance, even cutting across the rays that separate the air cavities.

Because the bundles making up the primary vascular system are small, and are relatively numerous and close together, the structure of the nodal region of the axis is not completely known. The presence of a small amount of secondary xylem associated with the bundles introduces a special difficulty in interpretation because it tends to obscure the primary tissues in the longitudinal sections. It is impossible in most instances to tell where a given bundle enters or leaves the section. Most of the bundles appear to pass through the nodes without alternation but each bundle probably produces at least one bract trace at each node although the bracts and bundles exist in a ratio of about 3 to 2. Also undetermined is whether the bracts and sporangiophores in their successive whorls alternate or stand in superposition. The strongest evidence of alternation is the arrangement of the free bract tips (Pl. VI, Fig. 3), but such a sequence cannot be correlated with positive evidence of bundle alternation in the axis. However, a system of bundles that alternate at the nodes does not appear essential for alternating bracts. A slight deflection of the traces to the right at one node and to the left at the next would have the same effect. Anatomical studies of *Equisetum* cones have shown that although the sporangiophores are in a whorled alternate arrangement, the vascular system that supplies them is an irregular network of strands which bears no relation to the whorled sequence (Barratt, 1920; Browne, 1920). In our cones the air cavities are aligned directly above one another through successive internodes, and as these seem to have a definite relation to sporangiophore arrangement, superposition of the sporangiophores is believed to exist.

BRACTS AND SPORANGIOPHORES

Each bract consists of two parts: the basal portion which is fused with adjacent members, and the free terminal lamina. Although the fused part is thin throughout most of its extent, the bract base is conspicuously thickened and rather strongly decurrent. The "space ring" part of the aerating system is situated at the base. In longitudinal sections the "rings" appear in series where the section passes through the solid tissue in the lower part of the internode (Pl. I, Fig. 2), but they form parts of continuous passageways separating the cortex and the vascular system where they happen to appear in line with the cavities (Pl. III, Fig. 2).

In some of the longitudinal sections the bract traces can be seen departing at wide angles to the axis (Pl. III, Fig. 2; Pl. VI, Fig. 2; Pl. VIII, Fig. 1; Pl. IX, Fig. 2). They pass outward with a slight upward slope and traverse the upper part of the "space ring." They then extend horizontally through the issues on the lower sides of the thin bracts as slender strands which, in most instances, are out of the plane of section. Occasionally two or more traces are visible in a transverse section extending outward like spokes of a wheel (Pl. IX, Fig. 3). At the nodal level there are more bracts in a whorl than bundles in the axis.

The sporangiophores were fragile organs about 1 cm. long which extended perpendicular to the axis and approximately parallel to the bracts. The stalk portions were very slender and had disintegrated for the most part before fossilization occurred. Except for their slightly enlarged bases they do not show at all in any of the median longitudinal sections. In some of the tangentially cut sections they show between the more or less disorganized sporangia as four-sided axes about 0.5 mm. in diameter.

Although the sporangiophore stalks themselves can rarely be seen, the places of attachment to the cone axis show distinctly as slight enlargements or (depending on where the section was cut) as openings through which the traces traversed the outer part of the cortex (Pl. III, Fig. 1; Pl. IV, Fig. 2; Pl. V, Fig. 1). It is thus possible to demonstrate their mid-internodal position and also to determine accurately the number in a whorl. There are 30 stalks per whorl in each of the syntype specimens, which is also the approximate number of vascular strands in the axis. There are more than 30 bracts in a whorl, but the total number of bracts is not a simple multiple of 30. In his account of *Palaesostachya multifolia* Anderson (1954, p. 409) said that the number of radial rows of sporangia and of bracts is about equal, and that because there is, in cross section, one sporangiophore for every two sporangia, there should be half as many sporangiophores as bracts. This would be a satisfactory explanation if it were supported by the actual counts. They show, however, that there are about 60 sporangia in a whorl—considerably more than the number of bracts. However, Anderson's report is a little confusing on this particular point because in his specific diagnosis (p. 410) he said "bracts 40–60 . . . sporangiophores 30 at node." Therefore the number of bracts cannot everywhere be twice the number of sporangiophores if the latter is always 30. Moreover, in the material that Anderson studied, even more than in ours, the disorganized condition renders accurate counting of the sporangia in cross section impossible.

It has not been possible to follow the course of a sporangiophore trace from its place of origin into the sporangiophore. The trace strands are not readily distinguishable from the axial strands in the nodal regions. The sporangiophore traces apparently arise at the nodes but their relationship to the departing bract traces is not clear, for they are small strands which are more or less immersed in and obscured by the secondary xylem which is present at most places. In addition, at their lower extremities they appear to be deflected around the large cortical air spaces that lie directly in front of the axial strands from which they arise and this slight deflection is sufficient to prevent the whole trace from showing in any one longitudinal section. Because of imperfect preservation it has not been possible to locate the same strand in successive sections.

The lowest point at which the sporangiophore trace can be distinguished in longitudinal section is just above the node where it arises as a vertical strand that stands parallel to and against the vascular tissue in the axis. The trace extends halfway up the internode and then bends abruptly outward—so abruptly, in fact, that the small tracheids composing it are sharply bent. The trace extends obliquely downward for a distance of 0.50 mm. or less, then curves upward again and passes obliquely through the cortical ray and the outer cortex. It next enters the sporangiophore base at the level of or slightly above the highest point reached farther back (Pl. VII; Pl. IX, Fig. 1).

The vertical part of the sporangiophore trace contains a small carinal canal (protoxylem lacuna) which is similar to that of the axial strand. In transverse sections taken in the lower half of the internode, the traces can be distinctly seen crossing the outer part of the cortex, and each one lies external to and opposite an axial strand (Pl. IV, Fig. 2). I am not certain whether each sporangiophore stands directly above a bract of the whorl below, although I believe the two organs are aligned in this manner. Of course the resemblance of the sporangiophore trace to that which Hickling (1907) first demonstrated in *Palaeostachya vera* and which Baxter (1955) has more recently found in *P. andrewsii* is obvious. The difference is in the shorter downward extension which results from the location of the sporangiophore higher above the node. However, the situation in both genera is fundamentally the same.

MELISMATIC TISSUE

The melismatic tissue, composed of elongate, thin-walled, loosely arranged cells with black amorphous contents, shows prominently in the nodal regions of the axis and in the bracts (Pl. V, Fig. 1; Pl. VI, Fig. 1). In the axis it constitutes a well-defined band at least 0.20 mm. wide within each "space ring" (Pl. II, Fig. 2). It shows in almost any section regardless of the direction of cutting. Narrow strips of the melismatic tissue pass into each bract and extend along the lower side of the vascular strand. Although in the preparation they occupy what appears to be empty space, this space, during life, was mostly parenchyma-filled (Pl. V, Fig. 3; Pl. VIII, Fig. 1). The melismatic tissue is always loosely arranged, but it is conspicuous because of the black opaque contents of its cells (Pl. VIII, Fig. 2). It seems to have disintegrated in portions of the cones that have not been well preserved and is rather obscure but recognizable in the sections that Anderson used in his study.

Melismatic tissue was previously reported in *Calamostachys* cones by Hickling (1910) but has been more frequently observed in the inner cortex of calamitean stems and the bundle sheaths of the foliage (Hick and Cash, 1884; Hick, 1893, 1894; Thomas, 1912). In the stem, its cells, which are slightly larger than those of adjacent tissues, are grouped opposite the vascular strands. Reed (1938) did not mention this tissue in her account of *Calamites multifolia,* nor is it specifically referred to by any other authors who have described American material. It is probable however, that the "mucilage canals" that Baxter (1955) described in the bracts of *Palaeostachya andrewsii* are of this nature.

SPORES

In two of the cones only microspores have been observed (Pl. I, Fig. 1; Pl. II, Fig. 2), but both microspores and megaspores occur in the third one (Pl. II, Fig. 1). None shows megaspores only, as Anderson claimed for some of his cones. However, none of the specimens so far studied is complete, so the occurrence of only one kind of spore in a portion does not prove that the same condition prevailed throughout the whole organ.

The two spore types seem to have been somewhat segregated in different regions of the cones. In the cone that contains the megaspores some sections show only these spores, whereas other sections contain both kinds (Pl. X, Fig. 1). The sporangia are all alike in size and shape, but a few contain microspores in one end and megaspores in the other (Pl. X, Fig. 2). Although heterospory was definitely developed in this fructification, the phenomenon did not involve the sporangial differentiation shown in the heterosporous lycopods.

The diameter of the microspores of *Calamostachys americana* ranges from 85 to 114 microns and that of the megaspores from 150 to 260 microns. These measurements do not differ greatly from those of Anderson.

Anderson mentions that the megaspores are smaller in cones with both kinds of spores than they are in cones with megaspores alone. In our material the megaspores are largest in those portions of the cones that contain only megaspores. They are smallest where the two kinds are mixed and along the zone of contact of the two kinds. Some of these megaspores are as small as 150 microns in diameter, whereas the normal range where they exist alone is from 230 to 260 microns. Although the smallest megaspores approach the largest microspores in size, the two types are distinct and do not actually intergrade; it has always been possible to distinguish the two.

The spores are of the *Calamospora* type: thin-walled, smooth, spherical, and with relatively small tetrad scars (Pl. XI). One ray of a tetrad scar is sometimes slightly longer than the others. In the angles of the rays, on the areas representing the contact faces during the tetrad stage of development, the wall is thickened, dark-colored, and rough (Pl. XI, Figs. 3 and 4). The relatively small size of the scar shows that in both types some enlargement had taken place between tetrad formation and maturity.

In no instance has the so-called perispore been observed. However, some of the microspores are still grouped in fours as they were in the tetrad stage. One noticeable feature, for which I can offer no explanation, is their tendency to be arranged in short chains (Pl. XI, Figs. 1 and 2).

ADDITIONAL MATERIAL

A fourth cone from the Berryville locality (Pl. XII), which was mentioned in the introduction to this paper, is smaller than the others. The preserved portion is 5.00 cm. long. It is slightly flattened, and measures 1.70 by 2.00 cm. in diameter. Its cross dimensions are therefore only one-half those of the largest syntype specimen. It is not as well preserved. The axis is broken (Pl. XII, Fig. 1) and the parts have moved out of position. The cortex is disorganized and the extent of the aerating system is obscured. There are, however, 10 to 12 large cortical air spaces, and each space is matched by a pair of vascular strands. The bract discs contain an estimated 30 to 35 fused units. The sporangiophores have disintegrated, although attachment in the *Calamostachys* manner is evident from position of the sporangia and sporangiophore bases on the axis (Pl. XII, Fig. 2).

The sporangia are smaller than those of the syntypes but are otherwise similar. Only microspores are present. The melismatic tissue is not shown, but this may have been lost during preservation.

In size and in number of cortical cavities this cone shows a closer resemblance to Reed's *Calamites multifolia* than do any of the three larger cones. Reed mentioned 40 coherent bracts, a figure somewhat larger than the estimated number of bracts in our specimen.

In describing new taxa of fossil plants, questions always arise about the amount of variation that can be expected to occur naturally within the group, and whether forms that differ in certain respects from the type material are to be regarded as belonging to it or to other taxa. In this particular instance the problem concerns the extent to which a specimen may differ from the syntypes and still be referable to *Calamostachys americana*. The cone described in the three preceding paragraphs has about one-half the diameter of the syntype specimens. It also has fewer sporangiophores per whorl, fewer air cavities in the cortex, and fewer vascular bundles. Thus there seems to be some relation between size and the number of parts composing the cones. But since the differences seem to be relative and since the overall structure remains the same, I believe that the large and the small cones are merely normal variants within one species. Although it is possible that cones both larger and smaller than those described may have been produced, it seems probable that the four described in this paper represent the size range within which the majority of the cones of the species would fall. Consequently, the specific diagnosis which follows is given in terms which include these variations. It seems quite certain that the relatively large number of bracts and sporangiophores in their respective whorls, the correspondingly large number of vascular strands in the axis, and the distinctive cortical aerating system are the distinguishing features of *Calamostachys americana*. The exact numbers of parts are not important and vary in proportion to the size of a particular specimen.

SPECIFIC DIAGNOSIS

Calamostachys americana, sp. nov.
(Pls. I–XII)

Palaeostachya multifolia Anderson, 1954, pp. 408–12, Figs. 22–24, 26, 28, 29.

Description.—Cone up to 4 cm. in diameter and exceeding 12 cm. in length; axis bearing successively whorls of bracts and peltate sporangiophores, the former being united basally into horizontally expanded discs spaced about 4.0 mm. apart; bracts about 40 to 45 per whorl; sporangiophores of delicate construction, up to 30 per whorl depending on size of cone, borne midway on axis between bract discs; vascular system of axis composed of up to 30 vascular strands arranged in pairs and partly connected by incomplete zone of secondary xylem; cortex with aerating system of up to 15 separate air spaces in lower half of internode and continuous "space ring" in upper part; conspicuous melismatic tissue in "space rings" and bracts; heterosporous; microspores 85 to 114 microns, megaspores 150 to 260 microns in diameter; spores of the *Calamospora* type.

Locality.—SW. ¼ NE. ¼ NW. ¼ sec. 7, T. 2 N., R. 13 W., western edge of Lawrence County, Illinois.

Age and horizon.—Calhoun coal, McLeansboro group, Pennsylvanian system.

Types.—Syntypes Nos. 34557, 34558, 34559, Museum of Paleontology of the University of Michigan.

DISCUSSION

The distinctive features of *Calamostachys americana* exhibited by the syntype specimens are: (1) large size, (2) the relatively large number of bracts and sporangiophores in their respective whorls, (3) numerous small vascular strands in the axis, (4) the elaborate cortical aerating system, (5) conspicuous melismatic tissue, (6) the slender and delicately constructed sporangiophores, (7) the elongated sporangia, (8) the flexed sporangiophore traces, and (9) the large crop of two kinds of spores. This species is distinct from all others, and no previously described *Calamostachys* can be confused with it.

With respect to the size of calamitean cones in general, *Calamostachys binneyana,* which is probably the best known of all species, is a small form, the cones being less than one centimeter in diameter. *C. zeilleri* is similar to *C. binneyana,* but *C. grandeuryi* is slightly larger (Renault, 1896). *Palaeostachya* is a genus of small cones that seldom exceed 1.50 cm. in width, although Selling (1944) described specimens of *P. schimperiana* that are 3 cm. in diameter.

Compressed specimens of *Calamostachys americana* would probably be referred to *Macrostachya.* No size limits have been set for cones of *Macrostachya,* but Scott said (1920, p. 64) that they are an inch or more in diameter. Darrah's *M. thompsonii* (1936) is about 2.50 cm. wide and Selling's *M. multibracteata* from China is 3.80 cm. broad at its widest place. Of course such dimensions are of limited value unless the differences reported are considerable, and figures expressing length are useful only when they are measurements of complete specimens, which are seldom available. Nevertheless, the three syntype specimens described here do fall within the dimensions reported for *Macrostachya,* and they appear to be exceeded in size only by cones of *M. infundibuliformis* (Scott, 1920). They are therefore among the largest calamitean cones. They are certainly the largest known petrified ones, and in the whole sphenopsid group they are rivaled only by the enigmatic *Cheirostrobus,* the cones of which are about the same size.

Our knowledge of the nodal anatomy of the new *Calamostachys* is incomplete. Each axial strand is probably connected in some manner to one bract trace and to one sporangiophore trace, but this simple relation cannot be demonstrated. Similar problems have been encountered in *Palaeostachya* and in other species of *Calamostachys* with simpler vascular systems, although in most instances a definite correlation was found to exist between the course taken by the vascular strands through the nodes and the arrangement of the bracts and sporangiophores. In our species these relationships are obscured by the small size of the parts and their large number. Since the flexed sporangiophore trace is not peculiar to *Palaeostachya,* the distinguishing feature of that genus is the one which Weiss (1876) originally designated, the axillary position of the sporangiophores. However, in both genera the traces supplying the bracts and sporangiophores arise, as far as we know, at the nodes, so the sporangiophores of *Calamostachys* would also have to be regarded as axillary if interpreted in this way. The term "axillary" as commonly used refers to position of the organ on the axis and not to the vascular connection.

The ultimate validity of sporangiophore position as a generic character in *Calamostachys* will depend upon the discovery of intermediate forms in which the sporangiophores are definitely above the bract axils but well below the mid-portion of a node. A situation suggestive of this is shown by *Palaeostachya decacnema* (Delevoryas, 1955) where the sporangiophore is rather high in the axil.

Hickling (1907), and even Weiss before him, concluded from the sporangiophore trace in *Palacostachya* that this genus had been derived from *Calamostachys* by a "phyletic slide." From its mid-internodal position in *Calamostachys,* the sporangiophore through an evolutionary process lowered itself into the axil, and the cone developed the characteristics of *Palaeostachya.* The flexed sporangiophore trace was offered by Hickling as proof that such a change had taken place. If this interpretation is accepted, the occurrence of a flexed trace in *Calamostachys* would indicate that this form is also derived. The ancestral form would have to have been one in which the sporangiophore was still higher. There are indeed calamitean fructifications—*Cingularia,* for example—in which the sporangiophore whorls are at the top of the internode immediately below the bract whorls. Neither *Cingularia* nor any of the others, however, can be accepted as the ancestral form, because they are unknown in the petrified condition and the compressions indicate strobili quite unlike the other two genera under consideration. There is no point in speculating further on *Paleostachya* or *Cingularia* as ancestral types.

Another possible interpretation of the evolution of the calamitean cone is that the sporangiophores were originally in an axillary position with a direct trace as described in *Palaeostachya decacnema.* The sporangiophore moved upward to about the middle of the internode, then down again, the several species of *Calamostachys* representing the near ultimate stage, and *Palaeostachya vera* and *P. andrewsii* representing the ultimate stage. In this event *Palaeostachya* with its axillary sporangiophores would represent both the primitive and the derived forms, but it seems most unlikely that this interpretation is correct.

Obviously, we lack the necessary information to explain the evolution of the calamitean cone. One of the striking facts revealed by the fossil record is the complexity and great diversity in the inflorescence structure displayed by the Paleozoic Sphenopsida. No other group of plants produced such elaborate reproductive organs. It seems improbable that any of the known calamitean fructifications are merely intermediate stages in a phylogenetic sequence. They are more likely the end products of a very complex developmental scheme.

SUMMARY

Calamitean cones from the Berryville locality in southern Illinois are conspecific with Anderson's *Palaeostachya multifolia* but the position of the sporangiophores shows that they belong to *Calamostachys* instead. The inadequate preservation of the holotype of *Calamites multifolia* renders this trivial name unsuitable for the new cones, so the new name *Calamostachys americana* is proposed for them.

Cones belonging to the new species are heterosporous, and are 2 to 4 cm. in diameter with successive verticils of bract discs and sporangiophores. Each sporangiophore verticil contains 20 to 30 sporangiophores, depending on the size of the cone. The bract discs contain a slightly larger number of fused bracts each of which consists of a horizontal portion and a free upturned terminal lamina. The vascular system of the axis contains 20 to 30 strands and a small amount of secondary xylem. The cortex contains an elaborate aerating system of "space rings" located within the decurrent portion of the bract bases in the upper half of the internode, and 10 to 15 vertical air ducts in the lower half of the internode. The "space rings" and the bracts contain conspicuous melismatic tissue. The sporangiophore trace is flexed as in *Palaeostachya vera* and in some of the other species of *Calamostachys,* and consequently this feature cannot be maintained as a generic character of *Palaeostachya*. Compressed specimens of *Calamostachys americana* would probably be identified as *Macrostachya*.

LITERATURE CITED

ANDERSON, B. R. 1954. A Study of American Petrified Calamites. Ann. Missouri Bot. Gard., Vol. 41, pp. 395–418.

ANDREWS, H. N. 1951. American Coal-ball Floras. Bot. Rev., Vol. 17, No. 6, pp. 431–69.

BARRATT, K. 1920. A Contribution to our Knowledge of the Vascular System of the Genus Equisetum. Ann. Bot., Vol. 34, pp. 201–35.

BAXTER, R. W. 1955. *Palaeostachya andrewsii,* a New Species of Calamitean Cone from the American Carboniferous. Amer. Journ. Bot., Vol. 42, pp. 343–51.

BROWNE, I. M. P. 1920. A Third Contribution to our Knowledge of the Anatomy of the Cone and Fertile Stem of Equisetum. Ann Bot., Vol. 34, 237–63.

DARRAH, W. C. 1936. A New Macrostachya from the Carboniferous of Illinois. Harvard Univ., Bot. Mus. Leafl. Vol. 4, No. 4, pp. 52–63.

DELEVORYAS, T. 1955. A Palaeostachya from the Pennsylvanian of Kansas. Amer. Journ. Bot., Vol. 42, No. 6, pp. 481–88.

HICK, T. 1893. *Calamostachys binneyana* Schimp. Proc. Yorkshire Geol. and Polytech. Soc., Vol. 12, No. 4, pp. 279–93.

——— 1894. On the Primary Structure of the Stem in Calamites. Mem. and Proc. Manchester Lit. and Philos. Soc., Ser. 4, Vol. 8, pp. 158–70.

——— and W. Cash. 1884. Contributions to the Fossil Flora of Halifax. Pt. IV. Proc. Yorkshire Geol. and Polytech. Soc., Vol. 8, No. 3, 370–77.

Hickling, G. 1907. The Anatomy of *Palaeostachya vera*. Ann. Bot., Vol. 21, pp. 369–86.

——— 1910. The Anatomy of *Calamostachys binneyana*. Mem. and Proc. Manchester Lit. and Philos. Soc., Vol. 54, No. 17, pp. 1–16.

Reed, F. D. 1938. Notes on some Plant Remains from the Carboniferous of Illinois. Bot. Gaz., Vol. 100, No. 2, pp. 324–35.

Renault, B. 1896. Bassin houiller et permien d'Autun et d'Épinac. Études gîtes minér. France. Flore Fossile (Pt. II)., Fasc. IV, Texte 18, 1896. Atlas, 1893.

Scott, D. H. 1920. Studies in Fossil Botany. Vol. I. London: Black.

Selling, O. 1944. Studies in Calamitean Cone Compressions by means of Serial Sections. Svensk Bot. Tidskr., Vol. 38, No. 3, pp. 295–330.

Thomas, H. H. 1912. On the Leaves of Calamites (Calamocladus Section). Philos. Trans. Royal Soc. London, Ser. B, Vol. 202, pp. 51–92.

Weiss, C. E. 1876. Beiträge zur fossilen Flora, Teil I. Steinkohlen-Calamarien, mit besonderer Berücksichtigen ihrer Fructificationen. Abhand. geol. Specialkarte von Preussen und den Thüringischen Staaten, Bd. II, Heft 1, pp. 1–149.

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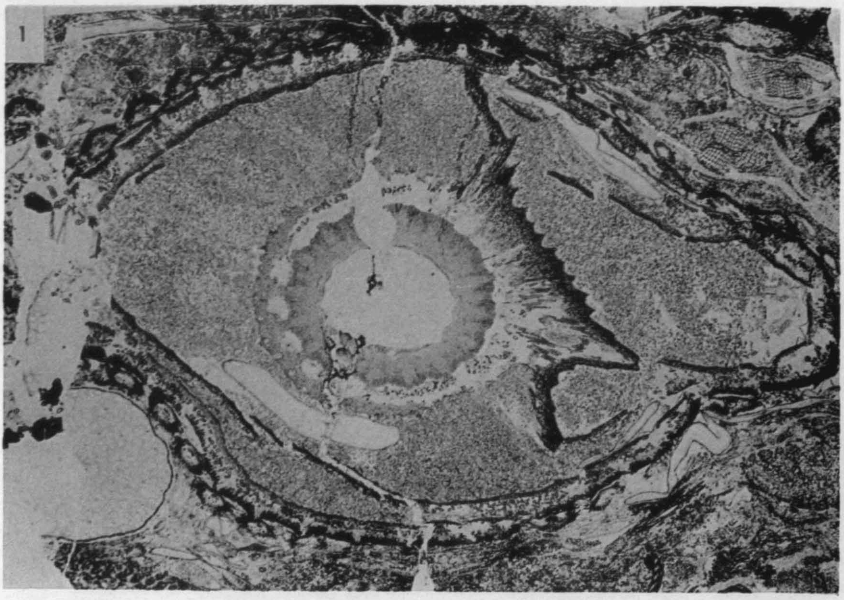
PLATES

EXPLANATION OF PLATE I

FIG. 1. Transverse section of the largest of the cones. The section, which is slightly oblique, shows a portion of a bract disc and a "space ring" on the right, and several cortical air cavities in the upper part of the internode immediately below on the left side of the axis. Syntype No. 34557. × 3.

FIG. 2. Radial longitudinal section of cone shown in Figure 1 of this plate. The "space rings" in the upper parts of the internodes show on opposite sides of the axis as two rows of spaces which are nearly empty except for the black melismatic tissue. The tissue separating the "space" rings is cortical ray tissue which laterally separates the cortical air cavities that do not show in this section. × 3.

PLATE I



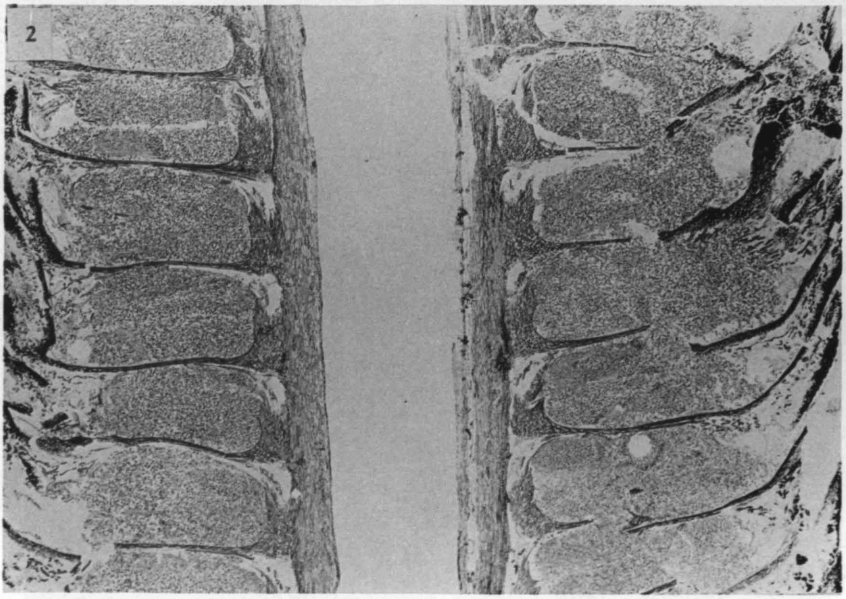
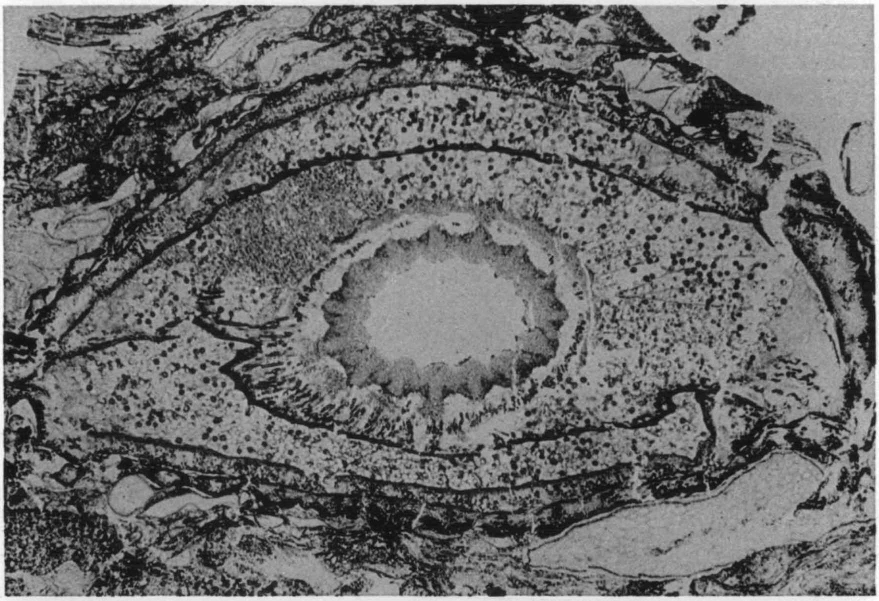
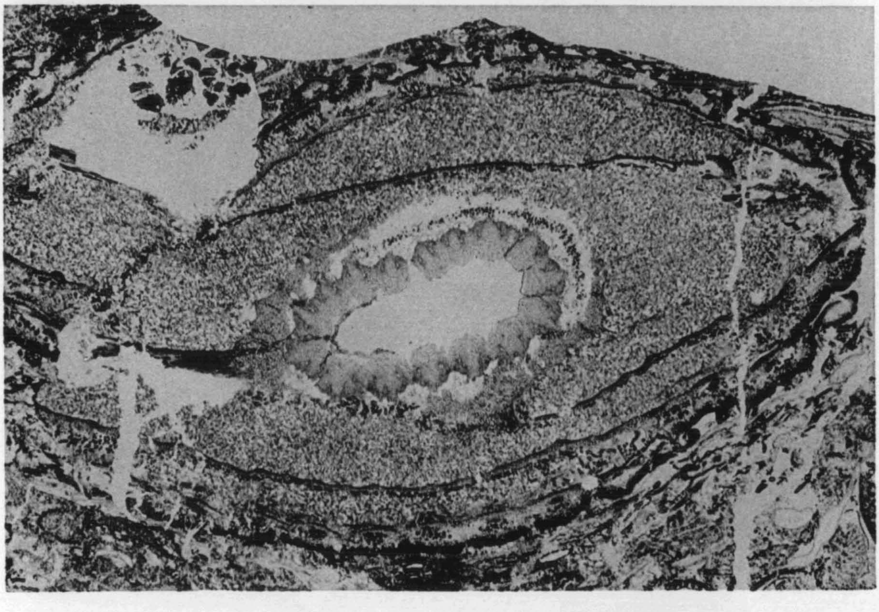


PLATE II





EXPLANATION OF PLATE II

FIG. 1. Cross section of cone containing microspores and megaspores. This section through the upper part of a node shows an almost complete "space ring" separating the outer cortex from the xylem layer. Syntype No. 34558. × 3⅓.

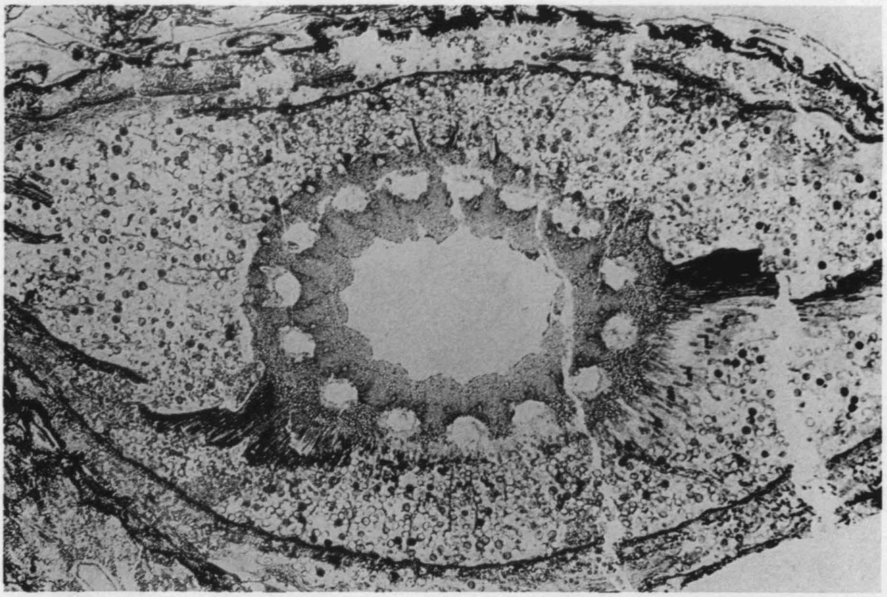
FIG. 2. Cross section of the smallest syntype specimen, which contains only microspores. Syntype No. 34559. × 3⅓.

EXPLANATION OF PLATE III

FIG. 1. Cross section of cone shown in Plate II, Figure 1, at slightly different level showing the 15 cortical air spaces, the position of the sporangiophores, and portions of a bract disc. Syntype No. 34558. × 4½.

FIG. 2. Longitudinal section of cone shown in Plate I, Figure 1, showing departing bract traces and "space rings" and cortical air spaces as continuous open passageways between the cortex and the interior of the axis. Syntype No. 34557. × 5.

PLATE III



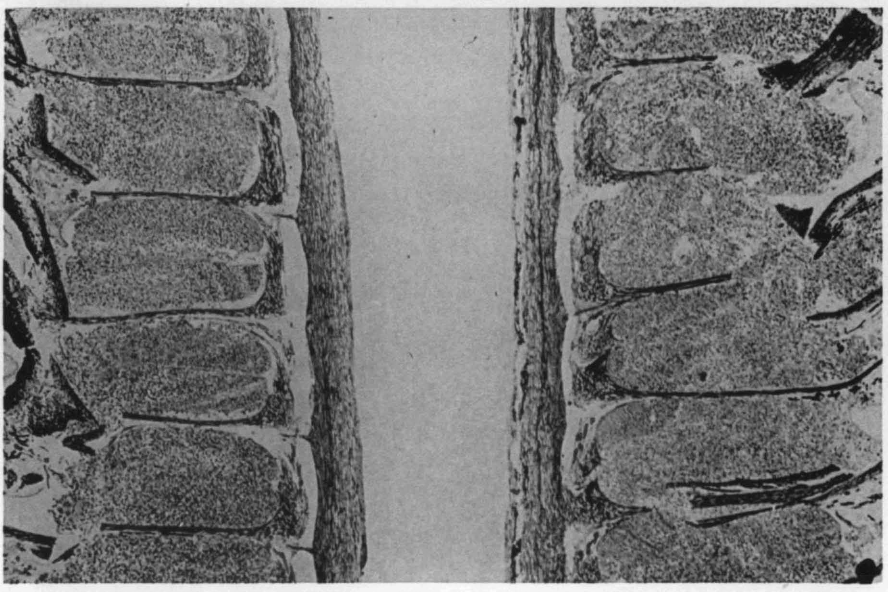
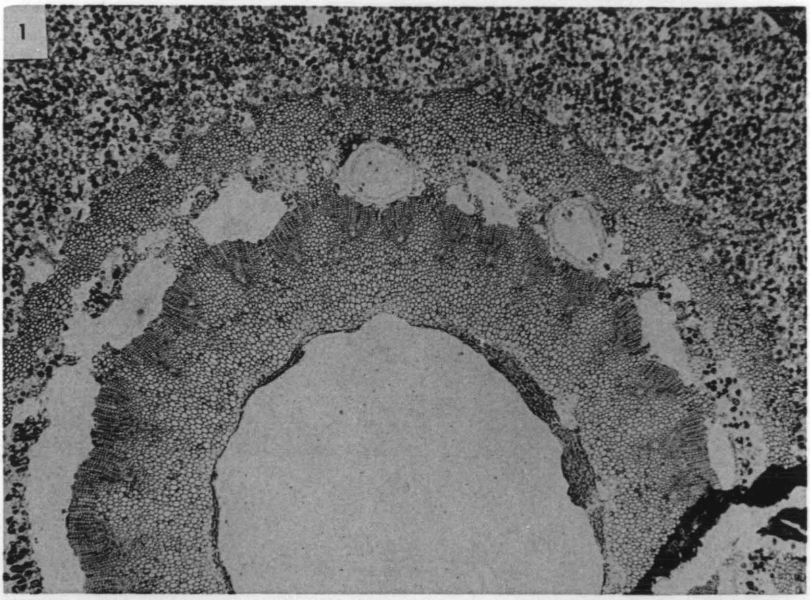
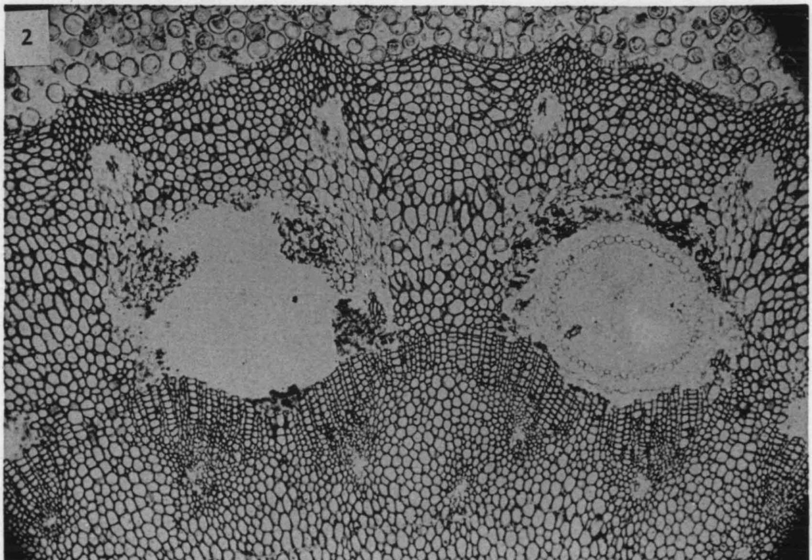


PLATE IV





EXPLANATION OF PLATE IV

FIG. 1. Portion of axis of specimen shown in Plate I, Figure 1, enlarged to show relation of the vascular strands to the cortical air cavities and the sporangiophores. The latter show at periphery of axis as small spaces through which the traces emerged. The section passes into a "space ring" which is at the left of the axis and which is slightly above the level of the sporangiophore whorl. Syntype No. 34557. × 10.

FIG. 2. Enlargement of portion of axis shown in Figure 1 of this plate, but sectioned at slightly differnt level to show detail of tissue structure. The two air cavities are separated by a cortical ray which is bridged by a narrow band of secondary xylem connecting the primary xylem strands which are paired with the air cavities. Emerging sporangiophore traces are shown between the air cavities and the epidermis. × 30.

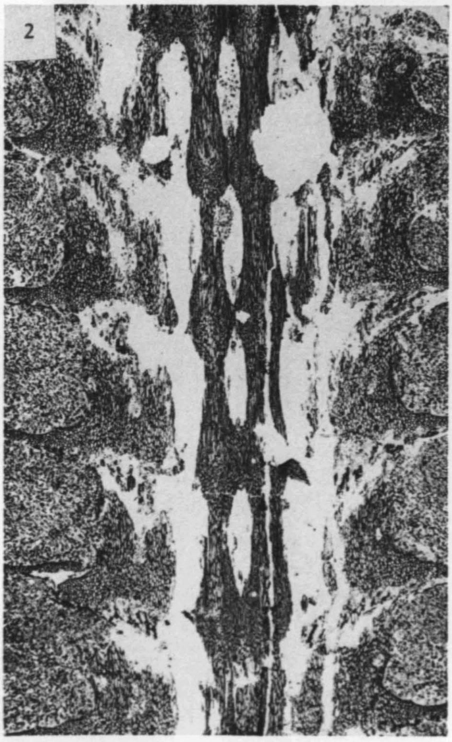
EXPLANATION OF PLATE V

FIG. 1. Tangential longitudinal section through cortical region of axis showing 4 nodes and "space rings" with melismatic tissue. The location of the sporangiophore whorls in the internodes is shown by the small openings through which the traces emerged. In the 2 lower nodes the "space rings" are connected by cortical air cavities. Syntype No. 34557. × 4.

FIG. 2. Tangential longitudinal section through cortical region showing vertically aligned air cavities in successive internodes. The cavities appear as separate closed openings because the plane of section is slightly beyond the innermost limit of the "space rings." Syntype No. 34557. × 5.

FIG. 3. Enlargement of lower left portion of section shown in Plate I, Figure 2, showing "space ring" in decurrent parts of bract bases and strands of melismatic tissue passing into the bracts. The place of attachment of the sporangiophores at the mid-point of the internode is shown. Syntype No. 34557. ×6.

PLATE V



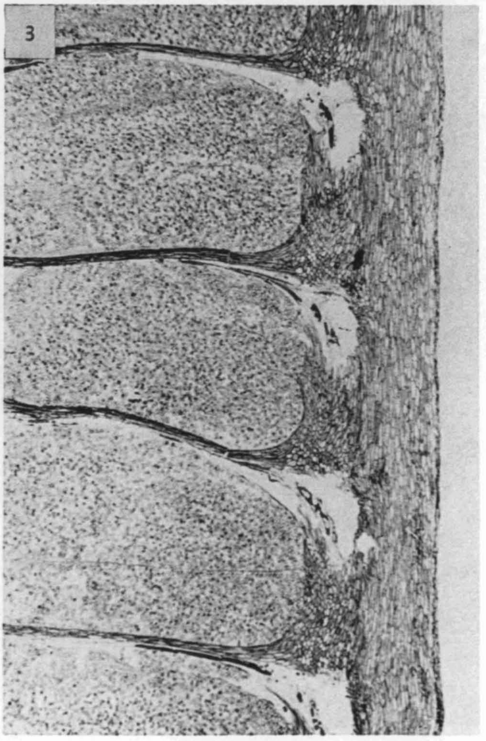
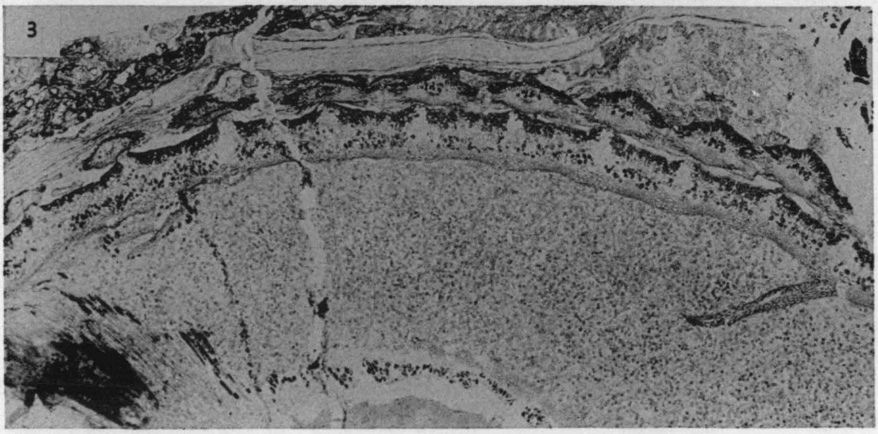


PLATE VI



EXPLANATION OF PLATE VI

FIG. 1. Tangential longitudinal section of specimen shown in Plate II, FIGURE 2, cut perpendicular to the bedding plane of the enclosing rock and showing displacement of bracts due to crushing. The bands of melismatic tissue within the "space rings" show in the mid-region. Syntype No. 34559. × 4.

FIG. 2. Radial longitudinal section of axis through a node showing an emerging bract trace and the carinal canal (protoxylem lacuna) of an axial strand which is closed at the node. Syntype No. 34557. × 25.

FIG. 3. Transverse section showing fused bracts in upturned portion of bract discs at periphery of cone and free tips of next bract whorl below in alternating positions. Syntype No. 34557. × 5.

EXPLANATION OF PLATE VII

Radial longitudinal section through portion of cone showing two nodes (*n, n*) with bracts (*b, b*), and the internode showing the flexed sporangiophore trace and place of attachment of the sporangiophore. Remains of parenchymatous tissue show in the "space ring" above the flexed trace. Syntype No. 34557. × 25.

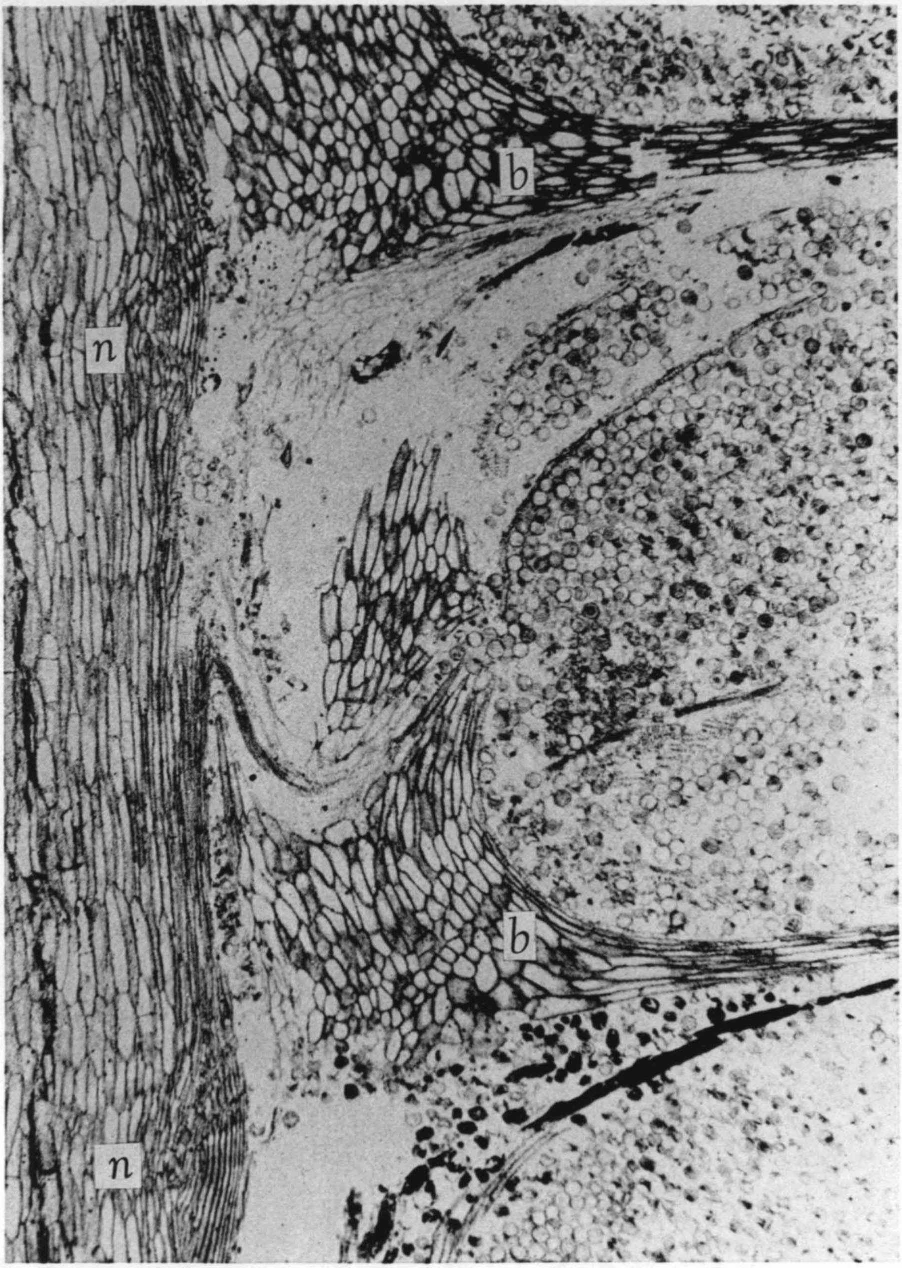
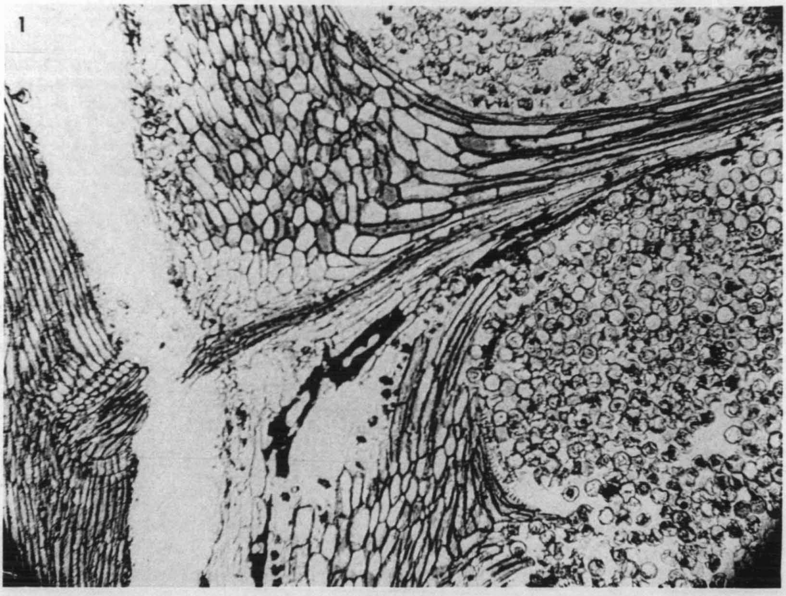

b
n
b
n

PLATE VIII



EXPLANATION OF PLATE VIII

FIG. 1. Longitudinal section through the nodal region of axis showing departing bract trace (accidentally broken) and melismatic tissue passing from "space ring" into lower side of bract. Syntype No. 34557. × 25.

FIG. 2. Detail of melismatic tissue in "space ring." Syntype No. 34557. × 40.

EXPLANATION OF PLATE IX

FIG. 1. Radial longitudinal section at mid-portion of internode showing flexed sporangiophore trace and its course into base of sporangiophore. Syntype No. 34557. × 30.

FIG. 2. Radial longitudinal section at node showing departing bract trace. Syntype No. 34557. × 30.

FIG. 3. Portion of transverse section of axis showing two outgoing bract traces. Syntype No. 34557. × 40.

FIG. 4. Portion of transverse section showing closely packed elongated sporangia containing microspores, and a continuous band of secondary xylem flanking "space ring." Syntype No. 34557. × 10.

PLATE IX

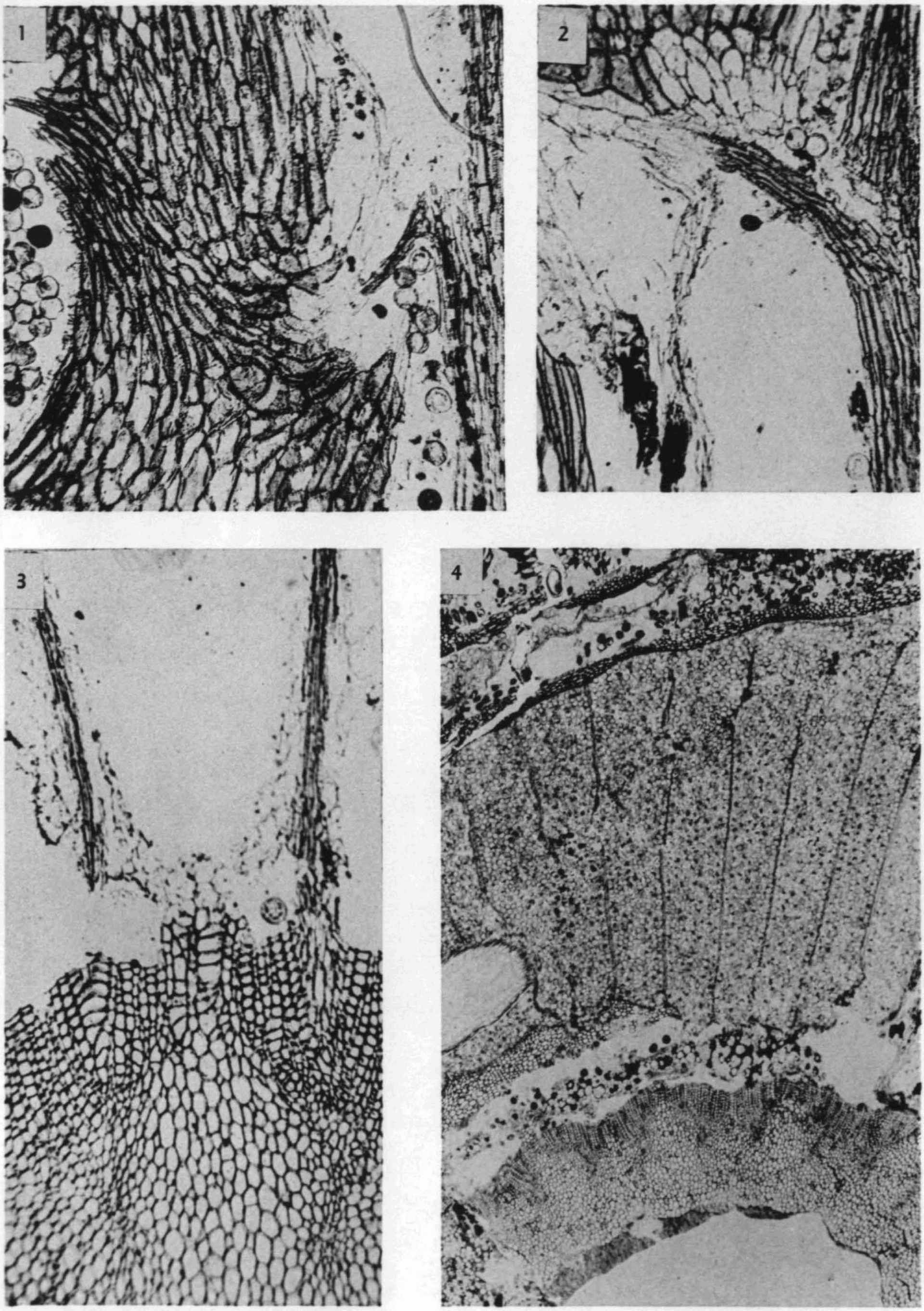
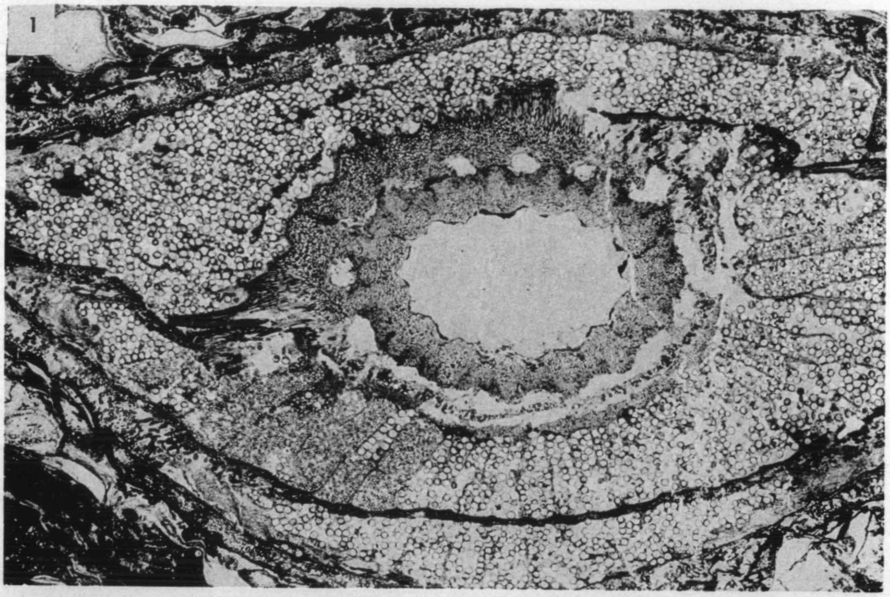
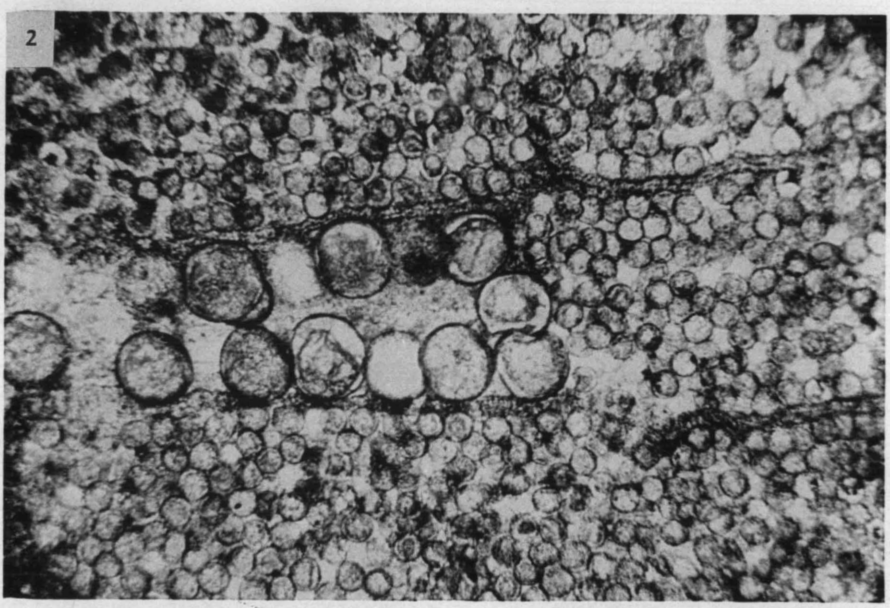


PLATE X





EXPLANATION OF PLATE X

FIG. 1. Transverse section of cone shown in Plate II, Figure 1, through portion containing microspores and megaspores. Section passes slightly obliquely through a node and shows (*above*) basal portion of bract disc encircling about one-third of axis and several air cavities whcih extend downward from internode above, and (*below*) portions of the "space ring" that lies immediately below the bract disc. Most of the sporangia contain only megaspores but at the lower left are several with microspores. Syntype No. 34558. × 5.

FIG. 2. Enlargement of lower left portion of section shown in Figure 1 of this plate. One sporangium contains both microspores and megaspores. × 45.

EXPLANATION OF PLATE XI

FIG. 1. Microspores, some showing tetrad scars and tendency toward catenulate arrangement. Syntype No. 34558. × 180.

FIGS. 2–4. Megaspores. Figure 3 and 4 show tetrad scars. Syntype No. 34558. × 180.

PLATE XI

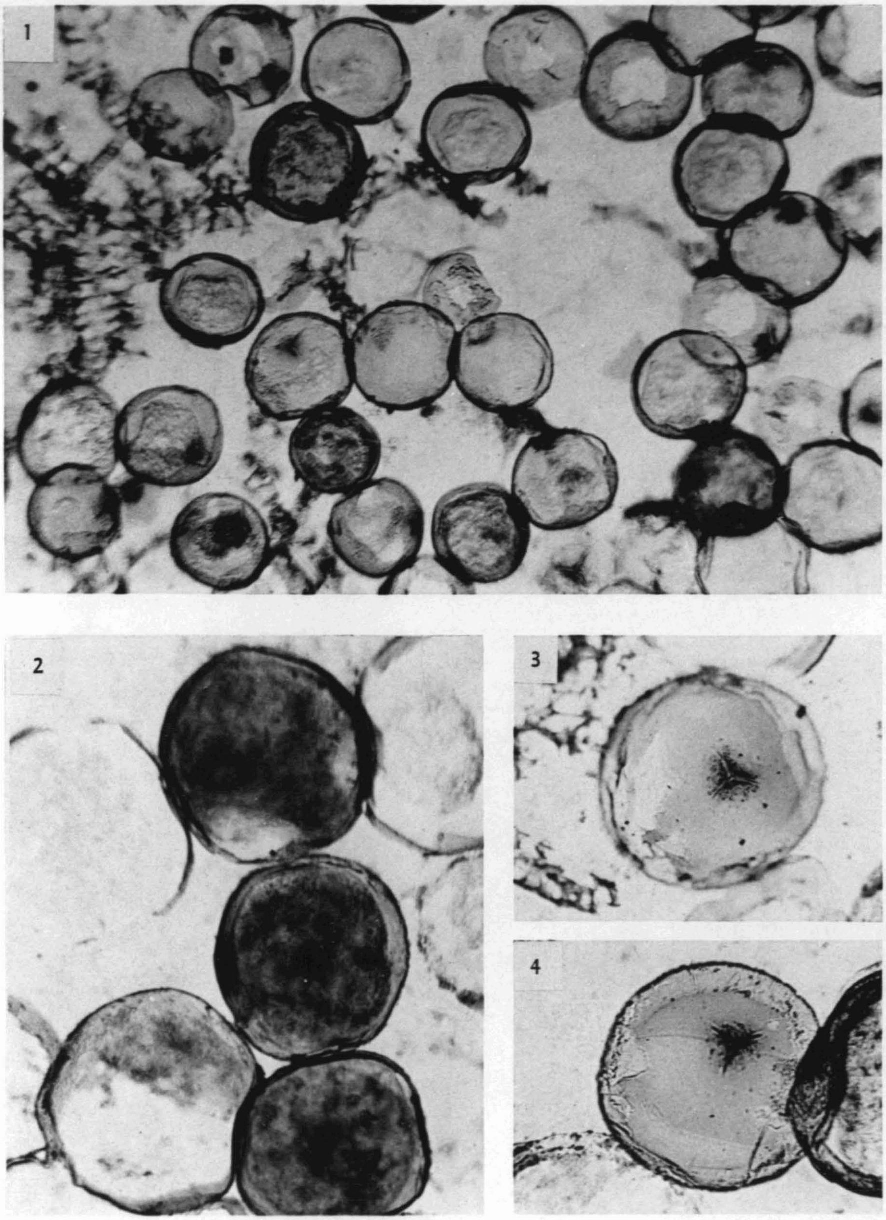
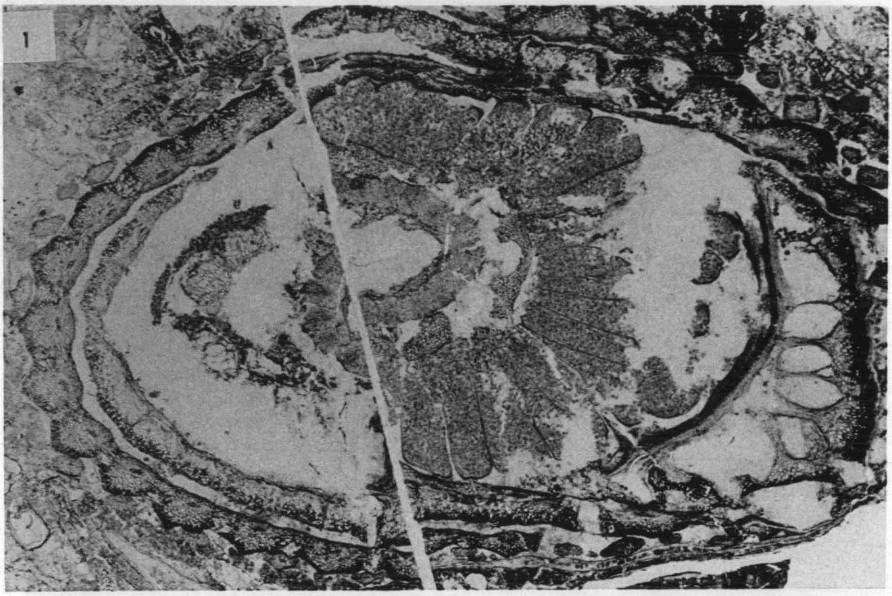
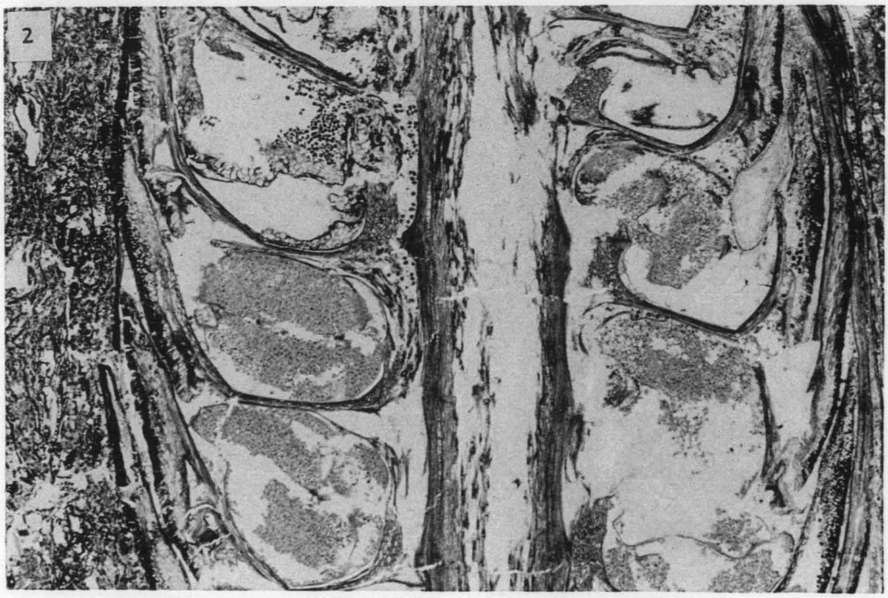


PLATE XII





EXPLANATION OF PLATE XII

FIG. 1. Transverse section of cone smaller than the syntype specimens showing the fused bracts at periphery of bract disc, the numerous elongate sporangia, and the somewhat disorganized axis. Topotype No. 34560. × 6.

FIG. 2. Radial longitudinal section of specimen shown in Figure 1 of this plate. × 6.