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CORYNEPTERIS INVOLUCRATA, SP. NOV., A NEW  
FERTILE FERN OF POSSIBLE ZYGOPTERID AFFINITIES  
FROM THE PENNSYLVANIAN OF KANSAS<sup>1</sup>

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ABSTRACT

*Corynepteris involucrata* is described as the first American species of the genus from Middle Pennsylvanian coal balls of southeastern Kansas. The new species is based on fertile, laminate pinnules bearing pairs of circular synangia flanking a central prominent midrib. Synangia consist of 5 to 6 sporangia with crowded sessile attachment to a short, central pedicel. Individual sporangia have a conspicuous annulus running down each side of the sporangium and over the abaxial side of the apex. Sporangial walls between the annuli bear numerous, small elliptical nests of sclereids indicating a possible relationship to *Biscalitheca musata* and *Zygopteris illinoiensis*. The most distinctive feature of the new species is a cup-shaped involucre surrounding each synangium.

INTRODUCTION

Generally, most paleobotanical investigations begin with the discovery and description of individual fragments of isolated plant parts such as roots, stems, and leaves, and it is the ultimate aim and responsibility of the paleobotanist to assemble these parts into the entire plant. Only in this way can any real, meaningful picture of the ancient floras and their evolutionary trends be obtained.

Whereas this is nearly always a difficult task requiring the cooperation of numerous investigators over a period of many years, it has nowhere proved more difficult than in the order Coenopteridales, which has served as a nebulously defined assemblage of Paleozoic ferns ranging from the Devonian through the Permian.

The special problems of the coenopterid ferns

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lie largely in their extreme diversity of habit, ranging from large shrub-like plants such as the Upper Devonian *Rhacophyton zygopteroides* (Leclercq, 1951) to forms such as the Middle and Upper Pennsylvanian *Zygopteris illinoensis* (Baxter, 1952), which seems to have had a horizontal rhizome anchored by numerous adventitious roots with possibly erect, large dimorphic fertile and sterile leaves. The problem is compounded by an apparent extreme diversity of fertile appendages in which the sporangia are sometimes borne in loose clusters at the tips of ultimate telomes, as in *Botryopteris*, to synangial aggregations of sessile sporangia on the abaxial surface of pinnately compound leaves such as in *Corynepteris* and *Chorionopteris*.

The family Zygopteridaceae of the Coenopteridales has presented particular difficulties in that the single genus, *Zygopteris*, seems to have possessed all of the variable characters mentioned above combined with an unusual stem anatomy with secondary xylem, unique among the Paleozoic ferns. Some newly discovered fertile pinnules from Middle Pennsylvanian coal balls of south-

eastern Kansas, which appear to have zygopterid affinities, are the subject of this paper. These specimens are described below as *Corynepteris involucrata* Baxter & Baxendale, *sp. nov.*, and constitute the first members of this presumably zygopterid leaf genus to be discovered in American coal balls.

#### ACKNOWLEDGMENTS

The fossils described are contained in coal balls collected at Mine #19 of the Pittsburg and Midway Coal Company. The cooperation of this company and their officials has been a large factor in the successful investigation of Kansas coal-ball plants over a period of more than 25 years. All photographs were taken by the senior author, but thanks are due Roger B. Williams of the University of Kansas Paleontological Institute who helped to assemble the plates, and to Mary Makepeace of Lawrence, Kansas, for her assistance in the reconstruction shown in Figure 1. We are also grateful to Dr. Russel A. Peppers of the Illinois Geological Survey for the loan of the type slides of *Notoschizea robusta* Graham.

#### SYSTEMATIC DESCRIPTION

##### Order COENOPTERIDALES Morgan & Delevoryas, 1954

##### Family ZYGOPTERIDACEAE Morgan & Delevoryas, 1954

##### Genus CORYNEPTERIS Baily, 1860

##### CORYNEPTERIS INVOLUCRATA Baxter & Baxendale, new species

Figure 1; Plates 1-7

*Diagnosis*.—Fertile pinnules averaging 2.2 mm in width with revolute margins; midrib oval in cross section, measuring  $0.8 \times 1.0$  mm, and traversed by a centrally placed single small midvein. Lamina abruptly thinner, measuring only 0.2 mm in thickness and consisting of rectangular cells traversed by slender lateral veins perpendicular to the midvein. Mesophyll tissue undifferentiated. Sporangia borne on abaxial surface of lamina in two circular, synangial clusters on opposite sides of the midrib. Sporangia elongate,

1.0-1.3 mm long  $\times$  0.5-0.6 mm wide with a conspicuous V-shaped annulus running down opposite sides of sporangium and over the abaxial side of the apex. Sporangium wall between annuli with oval nests of dark-brown sclerotic cells ranging from  $30 \times 60$  to  $40 \times 110 \mu$ . Sporangia sessile on a common base forming a circular synangium of 5 to 6 sporangia. A 2- to 3-layered involucre arising from the same common base, outside the sporangia, encloses each synangium. Spores spherical, averaging  $50 \mu$  in diameter, with a proximal trilite scar.

*Type material*.—Coal-ball and slide-peel preparations M-1476 in the paleobotanical collections of the University of Kansas, Lawrence, Kansas. Holotype is shown on Plate 1, figure 1.

*Occurrence*.—Fleming or Mineral Coals, Cabaniss Formation, Cherokee Group, Desmoinesian Stage, Middle Pennsylvanian; Pittsburg and Midway Coal Mine #19, five miles northwest of Hallowell, Kansas.

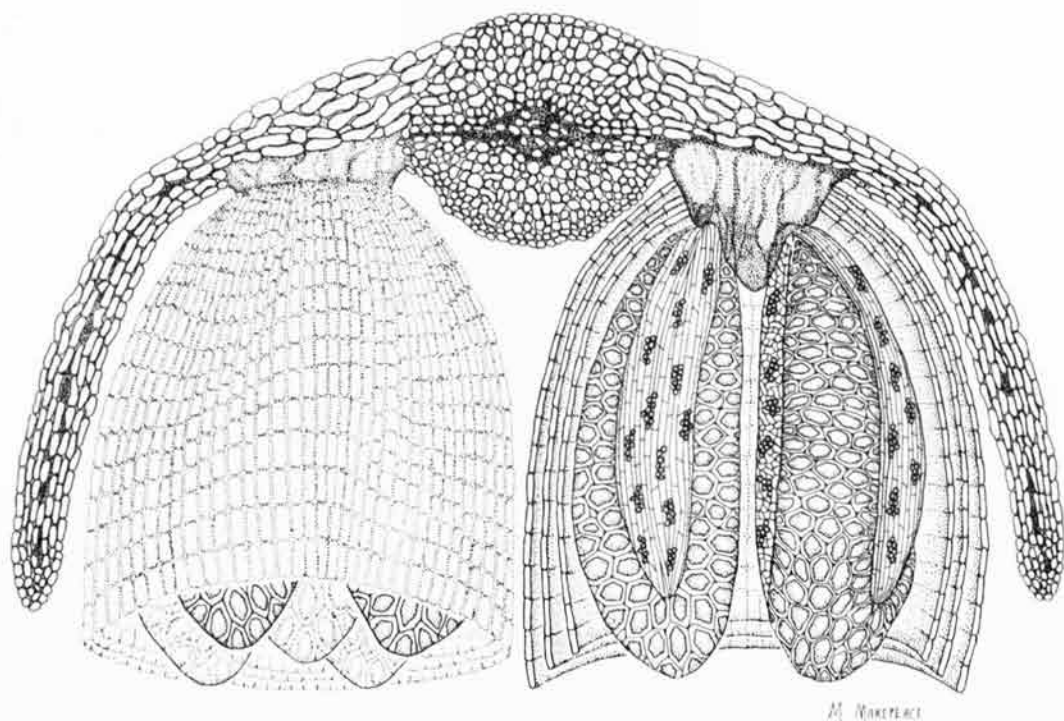


FIG. 1. *Corynepteris involucrata* Baxter & Baxendale, n. sp. Reconstruction of a fertile pinnule shown in transverse section,  $\times 32.5$ . Syngangium on right has proximal side of multiple involucre removed to show characteristic sporangia with their large, massive annuli running down each side of the sporangium and over the abaxial side of the apex. Syngangium on left is shown with just the tips of five sporangia extending below the base of the cup-shaped involucre. The sporangia are shown in cellular detail, but the representation of the involucre is purely diagrammatic.

## MORPHOLOGIC DESCRIPTION

*General remarks.*—The fertile pinnules were exposed in a preliminary cut of coal-ball M-1476 as a single linear row of up to 11 pinnules or more in number. Because the width of the individual pinnules from one revolute margin to the other is 2.2 mm and the average distance between the pinnules measures 1.1 mm, this means that the length of the pinna bearing these pinnules was at least 3.6 cm, and probably greater, as poorly preserved fragments of sporangia and pinnules extended at least another 1.5 cm on each side of the 11 well-preserved pinnules.

The evidence of other species of *Corynepteris* and of the reconstruction of the seemingly related *Biscalitheca musata* indicates that the sporangial clusters were borne in two rows parallel to the elongated lateral pinnae, or pinnules; accordingly,

the above configuration could be obtained by a cut parallel to the main pinna and at right angles to the lateral pinnules.

Unfortunately, the saw kerf must have destroyed the central area of the pinna, as sections at right angles to the original cut failed to expose any sections of the pinna itself, whereas repeated peel sections of the row of pinnules ended with them disappearing into the coal-ball matrix. Several *Etapteris scotti* petioles are associated with the fertile pinnules as well as scattered fragments of *Etapteris* secondary pinnae.

*Pinnules.*—The individual pinnule lobes (as seen in cross sections) measure 2.2 mm in width from one revolute margin to the other (Pl. 1, fig. 1; Pl. 2, fig. 1). As each margin incurls toward the abaxial side of the pinnule approximately 1.0

mm, the pinnule would measure about 4.0 mm in width if completely flattened out. The central axis of each pinnule consists of a prominent elliptical midrib measuring 0.8 mm in thickness by 1.0 mm wide. Except for a small, centrally placed vein, the midrib consists solely of uniform lamellar collenchyma cells with an average diameter of  $60 \times 40 \mu$ . The size of the cells diminishes gradually toward the abaxial side but remains the same on the upper (adaxial) side (Pl. 4, fig. 1). The lamina is much thinner than the midrib, measuring a uniform 1.8-2.0 mm in thickness from its attachment to the midrib to its margin. It is of very simple structure, consisting of uniform rectangular cells 20 to  $30 \mu$  wide and  $200 \mu$  or more in length, the greater length being perpendicular to the midrib. There is no differentiated mesophyll and no obvious epidermis. Very small lateral veins pass at right angles from the midrib to the pinnule margin with abaxial branches into the base of the circular syngangia. The simplicity of the pinnule is such that it almost resembles a flattened cladophyll more than a leaf.

*Sporangia.*—The sporangia are elongate, measuring 1.0 mm in length by 0.5 mm in width, with a convex abaxial wall and a straight to only slightly concave adaxial wall. They are sessile and attached directly to a common central pedicel projecting downward from the abaxial surface of the lamina closely adjacent to each side of the midrib (Pl. 1, fig. 1; Pl. 4, fig. 1). The pedicel measures  $270 \mu$  in length by  $180 \mu$  in width, with the 5 to 6 sporangia being attached to the lateral margins, forming a circular to nearly globular syngangial cluster due to the convex, curved outer walls (Pl. 1, fig. 1).

A conspicuous annulus runs down each side of the sporangium (Pl. 7, fig. 1) from the sessile base over the abaxial side of the apex. The annulus cells have evenly thickened walls and are roughly diamond-shaped as seen in face view with average measurements of  $30 \times 180 \mu$  (Pl. 2, fig. 1). At the base and middle of the annulus they are oriented at right angles to the length of the sporangium but become larger and nearly parallel to the sporangial length at its apex, forming a rounded to slightly projecting tip (Pl. 2, fig. 1). In side view they are rectangular with a periclinal average measurement of  $30 \mu$  and an

anticlinal average length of  $180 \mu$  (Pl. 3, fig. 2).

The sporangial walls between the annuli consist of a single layer of thin-walled cells with elliptical nests of small sclereids scattered among them. The groups of sclereids are dark brown to black and present a striking contrast to the light, thin-walled cells (Pl. 6, figs. 1,2). The nests of sclereids range from 2 to 4 cells in width and 5 to 7 cells in length with average measurements of  $30 \times 60$  to  $40 \times 110 \mu$ . Like the comparable tissue in *Biscalitheca musata* (Mamay, 1957), the shape of the wall cells and orientation of the nests of sclereids varies between the adaxial and abaxial surface of the sporangium. The wall cells are rectangular with parallel orientation of the elliptical sclereid nests on the abaxial side of the sporangia (with reference to their syngangial grouping) and are irregular in shape with somewhat irregular orientation of the sclereids on the adaxial side.

Whereas many of the sporangia are partly or completely devoid of spores, the general lack of any detailed structure in those spores present indicate that the sporangia were possibly immature at the time of preservation. Another feature suggesting possible immaturity is the lack of any clearly recognizable line of dehiscence in any of the numerous sporangia, particularly as seen in cross section (Pl. 5, figs. 1,2; Pl. 7, fig. 1). The dehiscence was undoubtedly longitudinal and possibly occurred on both the adaxial and abaxial surfaces due to contraction of the double annulus.

*Involucre.*—A unique feature of these fertile pinnules is the presence of a 2- to 3-layered involucre forming a multiple-layered cup-shaped enclosure around each sporangial cluster. This compound involucre, which can be clearly seen in longitudinal section in Plate 1, figure 1, and Plate 3, figure 1, as well as in cross section in Plate 5, figures 1,2, consists of thin-walled rectangular cells,  $180 \times 40 \mu$  as seen in side view and just a single cell in tangential thickness. The involucre membranes are attached directly to the common syngangial pedicel directly outside of the sporangia and appear to be constant multiples of 2 to 3 separate layers. They are equal in length to the sporangia so that they form an open cup, the margin of which is even with the tips of the sporangia.

*Spores.*—As stated above, many of the sporangia appear to have reached a stage of dehiscence as indicated by the general paucity of spores, and the poor preservation of the spores still present in the sporangia seems to indicate a possible state of immaturity. The spores are

spherical, averaging  $50\ \mu$  in diameter, with a trilete scar on the proximal surface (Pl. 7, fig. 2). The spore walls appear smooth, but the spores are so generally collapsed and distorted that it would be presumptuous to attempt palynological identification.

## DISCUSSION

The specimens described here are placed in the genus *Corynepteris* (Baily, 1860) on the basis of their double annulus, running down opposite sides of the sporangium and over the abaxial surface of the tip, and their grouping into sessile, circular synangia on the abaxial surface of elongate, slightly laminate pinnules. The genus was originally established for compressions of fertile pinnae with almost completely fused sporangia, but the generic concept has recently been expanded to include forms with sporangia having only a very slight degree of basal fusion or possibly just sessile on a common base (Remy & Remy, 1955).

Although the degree of fusion of the sporangia in *Corynepteris involucrata* consists of little more than their sessile attachment to a common base, it is still as great as in the extant *Angiopteris* and the fossil *Scolecopteris*, both placed in the synangiate Marrattiaceae.

*Corynepteris involucrata* can be most closely compared to *Notoschizea robusta* (Graham, 1934), *Musatea globota* (Galtier, 1968), and to *Corynepteris silesiaca* (Remy & Remy, 1955). All are described as having circular clusters of sporangia with sessile attachment to a common, blunt pedicel on the abaxial surface of laminate pinnules.

The sporangia and spores of *Notoschizea robusta* Graham are nearly identical in size and shape to our specimens, but are described as having abaxial dehiscence and paired annuli covering nearly all of the sporangium except for a narrow dorsal region of dehiscence. Graham's illustrations are all drawings except for one photograph (shown in his figure 26) of a poorly preserved transverse section of a cluster of five sporangia, two of which seem to show an adaxial dehiscence in contrast to his description. Through the kindness of Dr. Russel H. Peppers of the Illinois Geological Survey we were able to secure and study

all of Graham's original slides of *Notoschizea* (Nos. 549 to 553). The five slides, each of which bear one peel except for number 552 that has three peels, make a total of eight small peels on which the genus was based. In all of the peels, the sporangia are in generally fragmentary, oblique cross sections. There are no longitudinal sections of any sporangia and a very careful study of slides 552 and 553 (which Graham references for his drawings, figs. 1 and 2) failed to disclose any material remotely resembling the drawings. As these drawn figures are the only basis for the description of the sessile attachment of the sporangia to a laminate pinnule, some doubt must be attached to this character as well as the anatomical structure of the pinnule shown in his figure 1.

A close study of all of the sporangia seen in cross section seems to show as many or more stages with apparent adaxial dehiscence than abaxial. Because Graham stated in his closing discussion of the genus that except for its different mode of dehiscence and broader annulus it was identical to *Corynepteris*, its eventual assignment to that genus may be suspected. The concept of the apparent extensive annulus may be partly explained by the oblique angle of the cross sections, but it seems possible that the annuli do cover much of the adaxial surface of the sporangia, and in this, Graham's specimens may be compared to *Musatea globota*.

*Musatea globota* (Galtier, 1968) is based on thin sections from Lower Carboniferous silicified petrifications. Four to six banana-shaped sporangia are shown in a sessile attachment to a common pedicel on the lower surface of a laminate pinnule that has a clearly differentiated epidermis and mesophyll. The single annulus covers the entire sporangium except for a narrow, adaxial dehiscence zone. Galtier considered the fructifications as probably belonging to the abundantly

associated rachis fragments of the typically Lower Carboniferous genus, *Diplolabis*. The spores are subcircular, trilete, and measure 30 to 35  $\mu$  in diameter.

Although superficially similar to our specimens, *Musatea* differs in many major features including its geologic horizon, annulus, spore size, anatomy of lamina, and lack of an involucre.

*Corynepteris silesiaca* (Remy & Remy, 1955) is founded on compression specimens of fertile pinnules bearing circular abaxial clusters of 5 to 6 sporangia, sessile on a common pedicel or only slightly fused at their base. The sporangia are comparable to *Corynepteris involucreta* in size but differ in having a U-shaped annulus running over the sporangial apex (rather than V-shaped), larger spore size (70-80  $\mu$ ) and in the lack of an involucre.

Other genera that have been described with similar annulus characters are *Biscalitheca musata* (Mamay, 1957; Phillips & Andrews, 1968), *Biscalitheca kansana* (Cridland, 1966), and *Etapteris lacatei* (Renault) Bertrand (1911), all of which, however, differ from *Musatea* and *Corynepteris* in having pediculate sporangia on nonlaminar pinnules.

*Biscalitheca* was first described by Mamay (1957) from Upper Pennsylvanian coal-ball material. The description was subsequently amplified and modified with a reconstruction of the fertile frond by Phillips and Andrews (1968). In the interim, Cridland described *B. kansana* from an Upper Pennsylvanian compression, also giving a reconstruction of the fertile frond. Although based on the very different form of preservation of coal balls versus compressions, the two reconstructions agreed remarkably well on the aspect of the pinnate to bipinnate frond, which has long, slender, lateral pinnule-bearing paired clusters (pinnules?) of elongate banana-shaped sporangia on slender pendent pedicels. The distinctive feature of the genus (in which it agrees closely with *Etapteris lacatei*) is the large size of the curved sporangia (up to 4.0 mm in length) and the prominent, double annulus running down opposite sides of the sporangium.

Whereas Mamay considered *Biscalitheca musata* generically distinct from *Etapteris lacatei* on cellular details of the annulus and sporangium wall, he and Phillips and Andrews emphasized

that a close relationship probably exists between the genera. Cridland also stressed these relationships as well as suggesting a similar close relationship to *Corynepteris*. *Corynepteris involucreta* adds additional evidence as to this relationship in the distinctive nests of sclereid cells that occur in the sporangium wall of *Biscalitheca musata* and *Corynepteris involucreta* as well as in the epidermis of *Zygopteris illinoensis* stems and petioles. This is discussed more fully below.

If these relationships are valid, we have the interesting problem of two apparent lines of development, one with sessile, synangial clusters of sporangia on the abaxial surface of laminar pinnules and the other with pendent, pedicellate clusters of sporangia borne on nonlaminar pinnules. As Mamay (1957) pointed out, these two lines probably diverged as early as the Late Devonian from a common ancestral group. Whereas forms with sessile sporangia on laminar pinnules, such as *Musatea globata* and *Corynepteris involucreta*, are from the Mississippian and Middle Pennsylvanian, respectively, as compared to the pedicellate Upper Pennsylvanian *Biscalitheca musata*, it seems extremely unlikely that the sessile laminar form gave rise to the nonlaminar, pedicellate form, but rather that both represent divergent lines of an ancestral group probably having its origin in the Upper Devonian.

One of the most difficult problems of attempting to compare *Corynepteris involucreta* to other species of the genus is in their different forms of preservation, i.e., "petrification" versus compression. The single dominant midrib of *C. involucreta* with only few perpendicular lateral veins to the paired sporangial clusters does not agree well with the branching, oblique, marginal veins and dentate pinnules of *Alloiopteris*, which is generally accepted as the sterile front of *Corynepteris*.

However, in reviewing descriptions of compression species of *Corynepteris* we note that there is considerable evidence that the fronds were dimorphic with a much simpler structure and form characterizing the fertile pinnules than the sterile. Zeiller (1883) in his description of *Corynepteris coralloides* showed a striking difference between the fertile and sterile fronds, with the former having elongate lateral pinnules with a strong mid-vein and evenly spaced pinnatifid margins, whereas the sterile frond resembles

*Sphenopteris* or *Alliopteris*. Remy & Remy (1955) included as an integral part of their specific diagnosis of *Corynepteris silesiaca* the statement, "Die fertilen Wedel sind vollig metamorph." Although their illustrations are not detailed, they also seem to show rather simple linear pinnules. It seems possible, therefore, that the plane of the section exposed by the primary cut of the coal ball containing *Corynepteris involucrata* was at right angles to similar lateral pinnules, exposing the synangial clusters on each side of the mid-rib of individual pinnule cross sections.

The most distinctive feature of *Corynepteris involucrata* is the involucre itself. In all of our specimens it is open, forming a shallow cup around the sporangia, but the possibility must be considered that it may have originally been globose like the indusium in the extant *Cyathea arborea*, in which with maturity the upper half of the sphere is ultimately shed, leaving a shallow cup. However, because the spores of *Corynepteris involucrata* appear to be undeveloped and few of the sporangia have dehisced it seems more reasonable to assume that the specimens were relatively immature and that the involucre was probably originally cup shaped.

The fact that none of the previous compression specimens of *Corynepteris* are known to have an involucre is recognized as a possible argument against the assignment of our specimens to the genus. However, we believe that the similarities are more important than the differences. The involucre, which could easily be missed in the compression form of preservation, is less sig-

nificant than the essentially identical synangiate sporangia, and apparent relationship to the vegetative organ genus, *Zygopteris*.

With respect to the above comparison of the involucre to the indusium of *Cyathea* the question arises as to whether the term "indusium" might be preferable to "involucre." Our feeling is that involucre is a more general term than indusium and does not necessarily imply a direct comparison to the indusium of living ferns. The indusium in extant ferns is defined by Jackson (1928) as "an epidermal outgrowth covering the sori in ferns." In *Corynepteris involucrata* the double- to triple-layered tissues of the cup arise directly from the sporangial pedicel and appear to have no direct connection to the pinnule epidermis.

*Corynepteris involucrata* is closely associated with numerous fragments of *Etapteris scotti* rachis and pinnae, suggesting a possible attachment. This theoretical association is supported by the observations of Dennis (1974) that *Zygopteris illinoensis* and its attached *Etapteris* petioles show the same small elliptical nests of sclereids in their epidermis as are found in the sporangium epidermis of *Biscalitheca musata* and *Corynepteris involucrata*.

In fact, these elliptical nests of sclereids are so similar in both size and shape, as can be seen in a comparison of Dennis' (1974) figure 41 and our Plate 6, figure 1, that it seems quite possible that *Corynepteris involucrata* may be ultimately proven to be the fertile frond of *Zygopteris illinoensis*.

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## EXPLANATION OF PLATES

### PLATE 1

*Corynepteris involucrata*.

#### FIGURE

1. Transverse section of a single pinnule showing large midrib flanked by sessile sporangia on abaxial surface of thin lamina,  $\times 55$ . (Arrow indicates involucre.)

### PLATE 2

*Corynepteris involucrata*.

#### FIGURE

1. Transverse section of a single pinnule. Syngangium to left of midrib shows two sporangia with side and face views of the prominent double annulus,  $\times 55$ . (Arrows indicate involucre.)

### PLATE 3

*Corynepteris involucrata*.

#### FIGURE

1. A portion of a single syngangium in longitudinal section. Sporangium on right is exposed in an oblique section showing the paired annuli,  $\times 55$ . (Arrow indicates the multiple involucre.)
2. Syngangium in longitudinal section showing three of six sessile sporangia on common pedicel. Sporangium in center shows side view of annulus,  $\times 55$ . All sporangia in oblique section.

### PLATE 4

*Corynepteris involucrata*.

#### FIGURE

1. Transverse section of pinnule with two syngangia.

Lamina normal on right, missing on left; syngangium on left shows different aspects of annuli,  $\times 40$ .

2. Portion of a pinnule with median longitudinal section of syngangium to left of pinnule midrib showing annulus curving over tip of sporangium and multiple involucre,  $\times 40$ .

### PLATE 5

*Corynepteris involucrata*.

#### FIGURE

1. Transverse section of a single circular syngangium of six sporangia,  $\times 70$ . (Involucre indicated by arrow.)
2. Enlargement of a portion of specimen in figure 1 showing opposite paired annuli on sporangium in lower left corner,  $\times 107$ .

### PLATE 6

*Corynepteris involucrata*.

#### FIGURE

- 1,2. Longitudinal sections of sporangia showing prominent annulus and thin sporangium wall with nests of sclereids,  $\times 118$ .

### PLATE 7

*Corynepteris involucrata*.

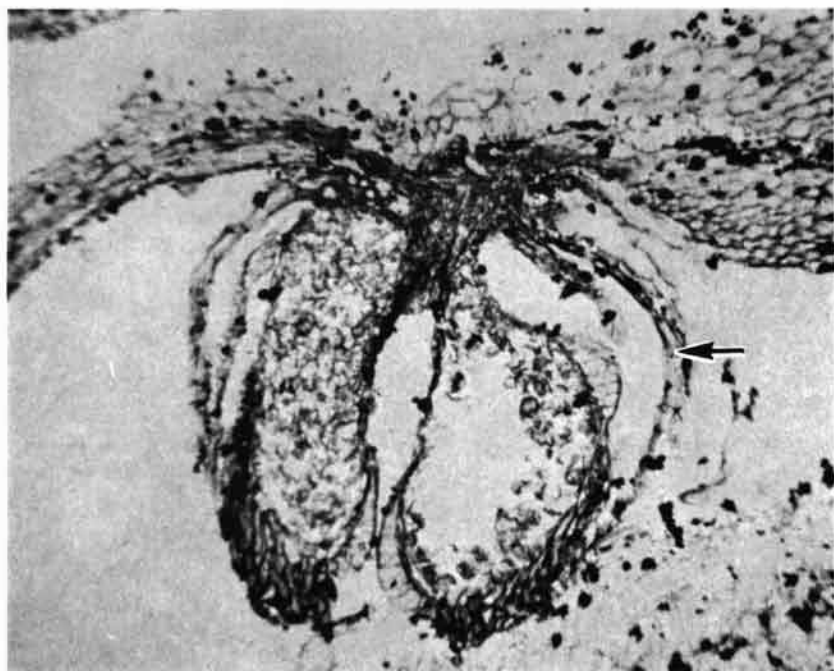
#### FIGURE

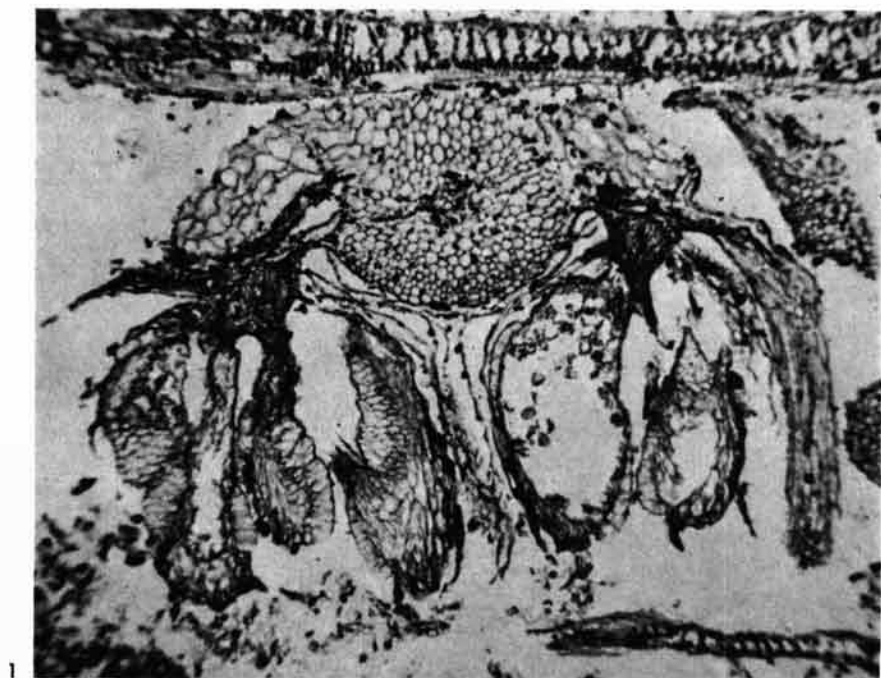
1. Transverse section of a single sporangium showing prominent double annulus,  $\times 185$ .
2. Spherical spores; one in center shows trilete scar,  $\times 720$ .

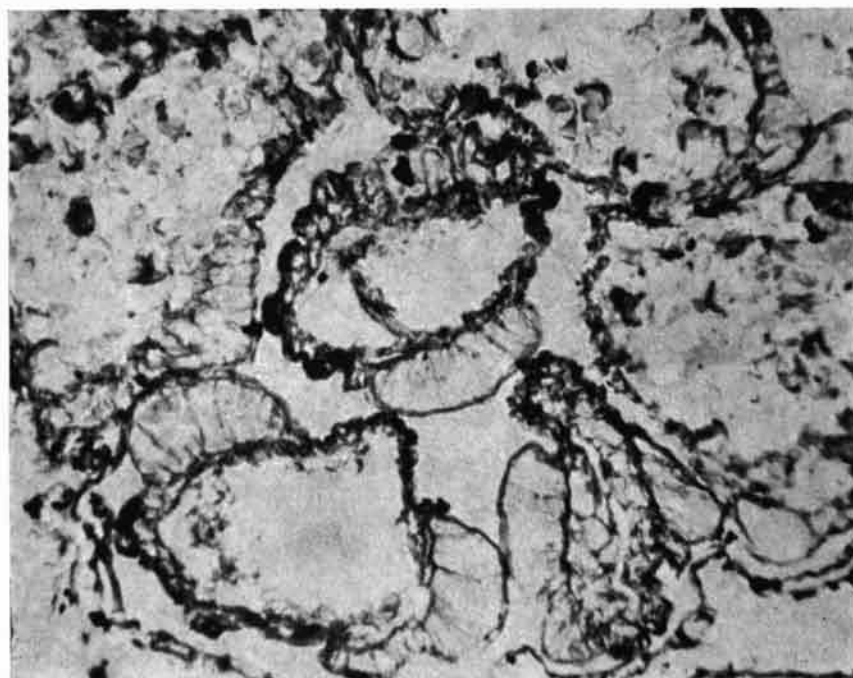
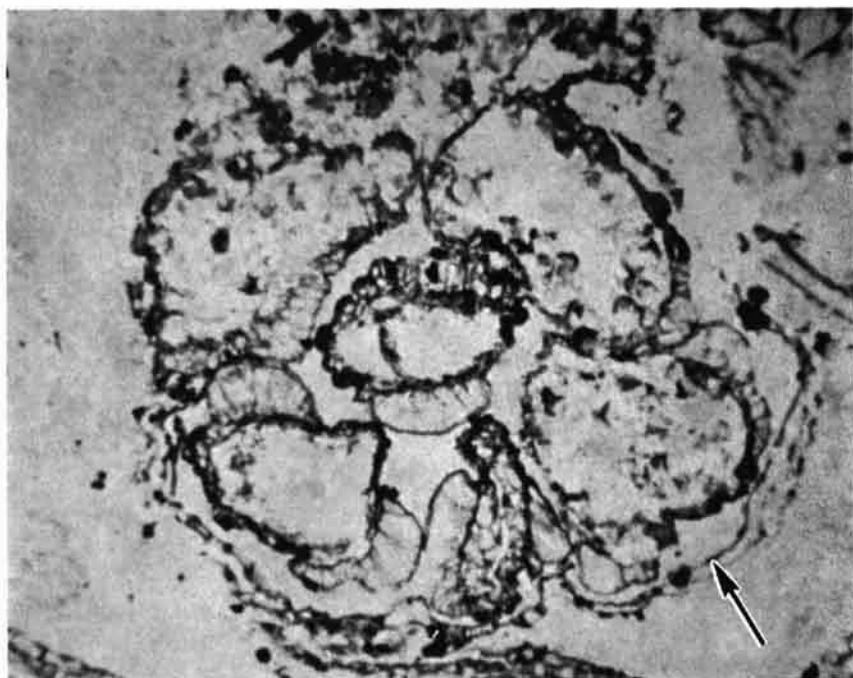


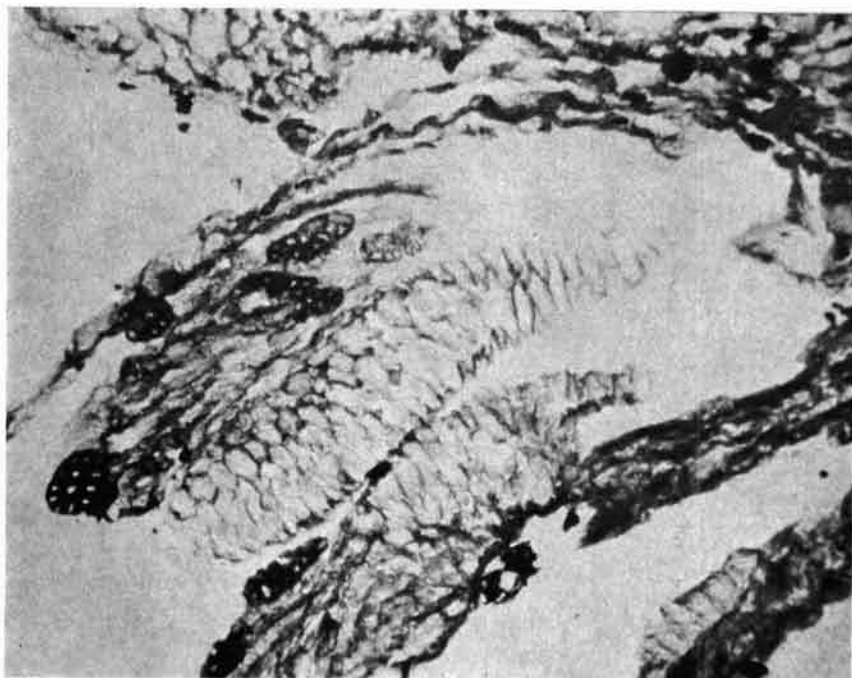




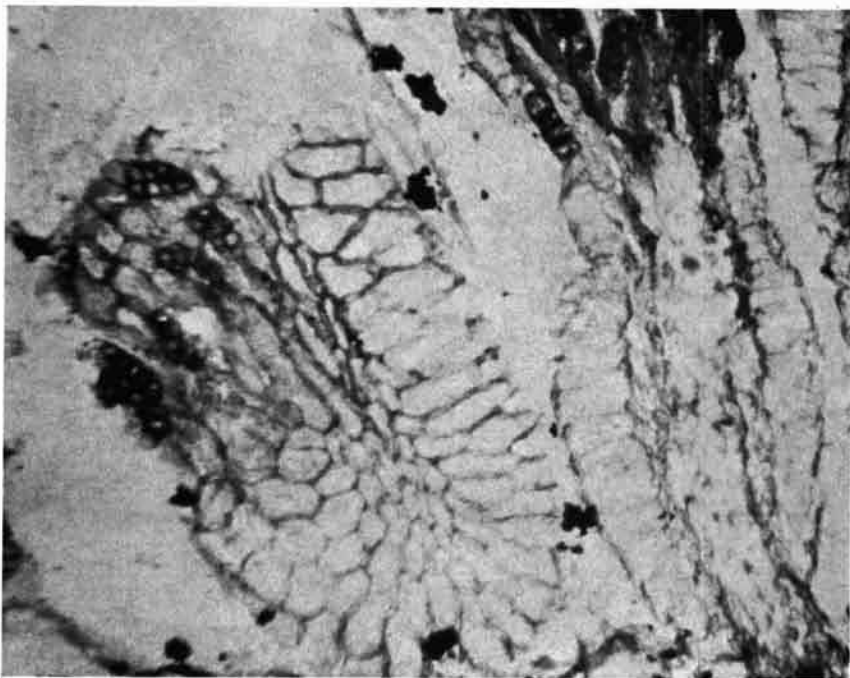




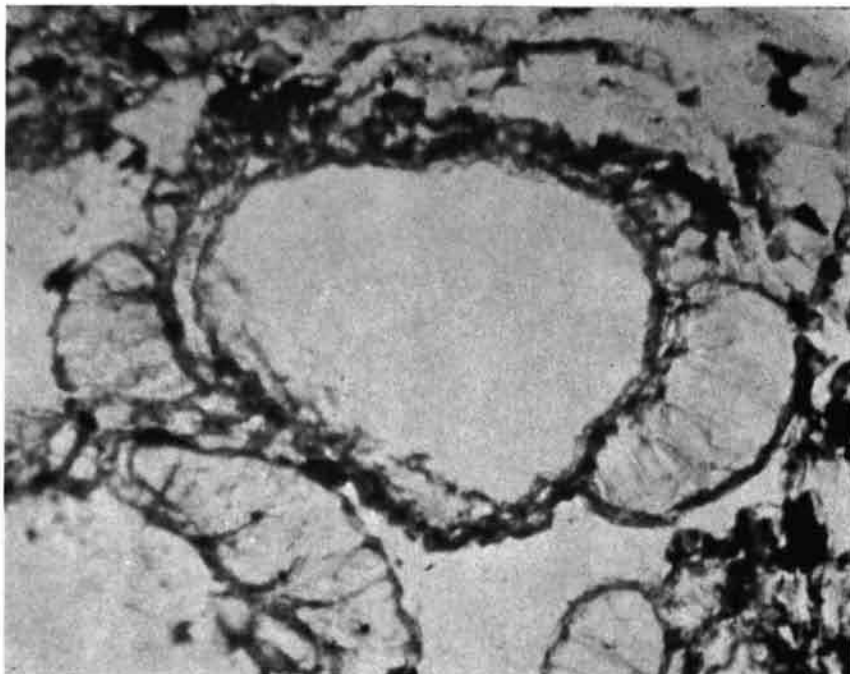




1



2



1



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