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THE FOSSIL FLORA OF IOWA COAL BALLS

II. THE FRUCTIFICATION OF BOTRYOPTERIS

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BOTRYOPTERIS is a genus of primitive ferns belonging to the extinct class or order known as the *Coenopteridales* (5,6). Nearly a dozen species have been described but all except the genotype (15) are very imperfectly known. The described species are restricted to the Carboniferous rocks of France (4), England, Scotland (18), Germany (8), Belgium (13), Holland (12) and Illinois (9,11).

Among the most abundant plants present in the coal balls from Dallas County, Iowa, are many petioles referable to three species of *Botryopteris*, one of which bears a large globose mass of sporangia. Seven specimens of this fructification have been collected in the Shuler Mine, and an additional specimen in the Urbandale Mine (7).

Botryopteris forensis Renault (15), the type of the genus, is the only species known from the fructification, the petiole, and presumably the leaf. All other members of the genus are known only from petrified petioles. The shape of the xylem of the stele, as viewed in transverse section, is the chief generic character (2,4). The petioles, which are circular in section, have a broad cortex, and the xylem has a *w* or *ω* shape. The three points of the stele point towards the axis. The leaves are believed to

have been highly compound and to have had fleshy lobed pinnules, probably of the *Sphenopteris* type.

The original specimen described by Renault, which he described as "le fragment, qui contenait seulement une portion de ces fructifications", had the following dimensions:

length (height)	4 to 5 cm.
diameter (width)	3 to 4 cm.
diameter (thickness)	2 to 3 cm.

This last measurement was taken at right angles to the width ("largeur").

The pyriform sporangia had a maximum diameter of 0.7 to 1.0 mm., and a length of 1.5 to 2.0 mm. The sporangia were attached in groups of five or six, sometimes more, and their total aggregation must have amounted to thousands.

The Iowa material is, on the whole, very similar to *Botryopteris forensis* but in many details differs so that it is here regarded to be specifically distinct.

Material at hand

Specimens in the Collections of the Botanical Museum of Harvard University:

Shuler Mine, Dallas County, Iowa:

42159 Cotype, nearly complete
42635 Cotype, nearly complete
42160 large mass, showing extensive surface
42161 branched axis, impression view, not sawn
42162 large mass of sporangia
42163 large mass of sporangia
42618 small portion of a fructification

Urbandale Mine, Dallas County, Iowa:

42679 fairly large mass of sporangia

DIMENSIONS OF THE FRUCTIFICATIONS

	Specimen 42159	*Specimen 42635*
maximum diameter	58 mm.	56 mm.
minimum diameter	49 mm.	27 mm.
height	47 mm.	not determined
xylem of petiole, breadth	2.2 mm.	1.8 mm.
"length" of petiole	8 mm.	6.5 mm.
"width" of petiole	4.5 mm.	4.2 mm.

The sporangia vary in length from 1.5 to 1.7 mm., and in diameter from 1 to 1.2 mm. Many smaller "diameters" have been measured and recorded, but they are invariably from planes which are not median.

The spores measure 0.05 to 0.065 in diameter and are nearly spherical in shape. The tetrad scar is prominent though not large. Some spores, especially those viewed from the apex or scar end, appear to be slightly triangular in outline, but this may be due either to preservation or immaturity.

The sporangium is constructed of two layers of cells, an outer layer composed of more or less cubical, thick-walled cells, enlarged over one side to form an annulus, and an inner layer of thin-walled cells, smaller in size than those of the outer layer. This inner layer is only occasionally preserved, and since its ontogeny is unknown, it is not possible to term it tapetal. The sporangia are grouped in numbers varying from three to ten (sometimes even more) attached to short pedicels, which are the termini of a much-branched axis. The pedicels are provided with a vascular strand composed of several cells of scalariform tracheids. The "petioles" which bear the pedicels have the characteristic Botryopterid ω-shaped stele.

COMPARISON WITH BOTRYOPTERIS FORENSIS

It is obvious that the spores of the Iowa species are

smaller than those found in *Botryopteris forensis* from St. Etienne, France. I have before me, two ground sections of detached sporangia collected in 1935 from Comberigolle (Grand 'Croix) near St. Etienne, prepared by one of my students, Mr. William S. Benninghoff. The spores in these sporangia have a maximum diameter of 0.07 mm. and agree in size with the recordings of Renault. The sporangia in the Iowa specimens are much less elongate, more nearly spherical. In other details such as the annulus, sporangial wall, attachment and spore number, the two forms are very similar.

Comparison with other Botryopterid sporangia

In 1902, Oliver (14) described a remarkable vascular sporangium from Grand'Croix which he was inclined to refer to *Botryopteris*, perhaps even *Botryopteris forensis*, assuming that the preservation of his specimen could have been better than that of Renault's types. However, the spores in this sporangium have a diameter of only 0.02 mm., instead of 0.06 to 0.07 mm. as in *Botryopteris forensis*. The unusual tracheidal nature of the cells of the outer wall, at once distinguishes this specimen from the Iowa form.

Renault (15) also described sporangia under the name of *Botryopteris dubius*, which are characterized by an elaborate sporangial wall, at least two layers in thickness, of which the outer is three or four cells deep. The spores have a diameter of 0.08 mm. The Iowa specimens have a much more simple wall and much smaller spores. Renault subsequently (17) referred this form to *Zygopteris*.

Description of the specimens

On the first plate, the figure at the top shows the broken surface of a mass of sporangia in a vertical plane beyond, i.e. outside of, the axis. In other words it pre-

sents a longitudinal view of a sporangial mass. The very numerous pyriform sporangia are grouped around the ultimate divisions of a much-branched axis. The arrangement of sporangia can be seen in the upper right quadrant of the illustration.

The lower figure on the first plate shows a cut surface, sawn within a few degrees of a right angle to the axis. Here again we can observe the prodigious number of sporangia and the enormous size of the fructification.

On the second plate there is illustrated a small portion of a section taken diagonally through the axis. It is nearly transverse and shows the petiole giving off a branch. The stele of the petiole has the characteristic trident-shape which is known to be a generic character. The sporangia here seem to have walls which are only one cell in thickness, but this is due to incomplete preservation. There is an annulus which is evident on several of the sporangia near the top right.

The figure on the third plate shows a longitudinal view through a mass of sporangia and through the petiole or axis. At the lower left, a group of five (six?) sporangia are clustered around a pedicel. A similar cluster is shown at the top right.

The figure on plate four shows portions of seven sporangia—three of them nearly complete.

The number of spores in each sporangium is large—several hundred being a minimum estimate.

The sporangia on plate five show clearly the crowded condition of the sporangial mass and the relative size of the spores. Near the top left corner the sporangium adjacent to the limb of the petiole shows the annulus. A number of the sporangia show the rather decomposed, at least poorly preserved, inner cell layer. The sporangium at the bottom center, and several near the true center of the illustration, reveal this moderately well.

The illustration on plate six gives an excellent idea of the complicated branch system. The main petiole or "stem" which bears this fructification has branched several times, so that at the plane of this preparation, four "secondary" petioles carry the actual fruiting portion of the plant. These are branched many times, as is most evident.

DIAGNOSIS OF THE SPECIES

Botryopteris *Renault* 1875 Ann. Sci. Nat. (Bot.) (6e Ser.) T.1, p.223.

Botryopteris globosa *Darrah sp. nov.* 6 plates.

Fern fructification, naked, pedicellate, composed of a great globose aggregation of sporangia measuring approximately 5 cm. $\times$5 cm. $\times$6 cm., borne terminally upon a petiole provided with the typical Botryopterid stele. Sporangia moderately large, approximately 1.5$\times$1.0 mm. in diameter, more or less angular in shape but slightly pyriform, borne in clusters of from three to ten, or more, upon short pedicels, which are the ultimate branches of the petioles. Spores moderately large, nearly spherical, varying in diameter from 0.05 to 0.065 mm.

Foliage unknown.

IOWA: Dallas County, Waukee, Shuler Coal Mine, and Urbandale Coal Mine. F.O.Thompson Collection 42159, 42635 COTYPES, also 42160, 42161, 42162, 42163, 42618 all Shuler Mine. 42679 Urbandale Mine.

CARBONIFEROUS: Pennsylvanian: Des Moines Series: Coal number 7.

Specimens in the Paleobotanical Collections of the Botanical Museum of Harvard University.

Scott (18) suggested that the large mass of crowded sporangia represented "no doubt, the collective output of a compound fertile frond". He interpreted the fructi-

fication as a branched rachis. Scott figured (loc.cit. figure 153) the oft-copied original of Renault which shows four sporangia attached to a short pedicel on a portion of a branch of the axis. This drawing gives a most inadequate conception of the plant.

Seward (19) reproduced another of Renault's original drawings which gives a somewhat better idea of the robust size of the fructification, but here again, the illustration represents a mere fragment of the whole.

Renault, in 1896, figured what he considered to be two leaflets of *Botryopteris*. These fleshy pinnules appear to have been provided with unusually thick cross veins, giving a very unlife-like aspect. It is curious to observe, however, that the branch system which bears the sporangial aggregation of *Botryopteris* is strikingly similar. Hirmer's (10) reproduction of Renault's figure is probably more generally available than the original. It is figure 653 on page 535. A rather crude drawing of the specimen can be consulted also in Seward (19), vol. 2, p.445, fig. 309 B.

Renault has interpreted *Botryopteris forensis* as being heterosporous. He described spores with a triradiate scar as being megaspores and similar spores but with multicellular construction as microspores.

Zeiller (1900, p. 74, fig. 73) refigured two of Renault's drawings but questioned their heterospory.

Most investigators since Zeiller have doubted that Renault really observed endosporal development and regard the conclusion that *Botryopteris forensis* was heterosporous as unfounded.

Two workers, however, have made interesting use of the possibility (Thomson (21), Benson (1)). The evidence derived from *Botryopteris globosa*, of course, cannot be used to challenge any conclusion based entirely upon observations on *Botryopteris forensis*, but it is significant

that all of the spores studied in the Iowa species are of a single type and size, bearing a normal tetrad scar which certainly indicates a homosporous eusporangiate fern, and we have not observed the slightest evidence of endosporal development. The degree of preservation is not as good as desirable—no fossil ever is—but such contents as are preserved in some of the spores appear to have been non-cellular.

There are several important questions relating to the Coenopterids which at this time suggest themselves. As yet we are not in possession of facts sufficient for satisfactory answers.

Is this massive fructification a strobilus? The ferns are non-strobilar, but here is a much-branched axis constructed, not on a pinnatifid, but upon a radial plan. The pyriform sporangia are pedicellate. It is true that *Stauropteris*, a still more "primitive" Coenopterid fern is radially symmetrical and bush-like but the sporangia are believed to have been borne terminally in small lax clusters (3).

If the fructification is strobilar, or "pseudo-strobilar", what is its possible relationship to the pteridosperms? One of the fundamental gaps or "missing-links" in our knowledge of the earliest gymnosperms is their degree of kinship with the filicinean pteropsids.

In any case, this unique structure among the ferns, now partially understood, will reshape our conception of the *Coenopteridales*. That they were a very diversified group is well-known. How diversified is still a matter for speculation, but with certainty more than any of us have supposed.

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EXPLANATION OF THE ILLUSTRATIONS

PLATE I. BOTRYOPTERIS GLOBOSA *Darrah*. The figure at the top shows the broken surface of a mass of sporangia in longitudinal view. The plane is not median, but beyond the main axis. The branching which appears in this view is that of a secondary petiole. Near the left of the upper right quadrant of the sporangial mass is a cluster of sporangia grouped around a short pedicel. Natural size. Heliotype reproduction of a photograph of specimen number 42159 (COTYPE), Paleobotanical Collection of the Botanical Museum.

The figure at the bottom shows a transverse view of a fructification, sawn at a right angle to the main axis. The axis ("petiole") is located slightly below the center of the illustration. In this specimen it is surrounded by crystalline calcite which appears as a white region in the figure.

Specimen number 42159. Natural size.

PLATE II. BOTRYOPTERIS GLOBOSA *Darrah*. Heliotype reproduction of a photograph of a cellulose nitrate peel prepared from the surface of the specimen illustrated at the bottom of Plate I. The stele of the petiole shows the departure of a branch. The ω shape of the xylem of the stele is evident at the bottom of the illustration. Magnified twenty times natural size.

PLATE III. BOTRYOPTERIS GLOBOSA *Darrah*. Vertical (longitudinal) section through the main axis bearing the sporangial mass. The plane of the section is tangential to the axis, i.e. all of the tissue shown in the petiole is cortical. At the top left a secondary branch shows several pedicels, which are surrounded by sporangia. A similar cluster is shown at the bottom right. Twenty times natural size.

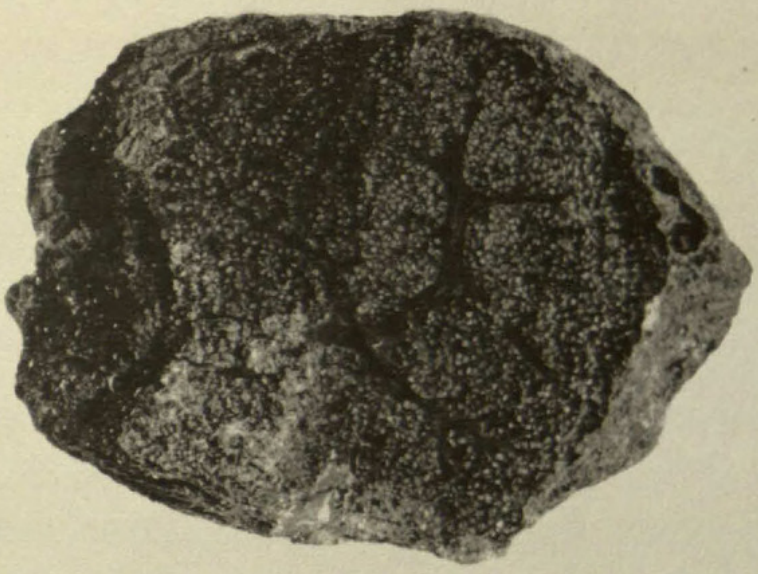
Reproduced from a photograph of a cellulose nitrate peel from specimen number 42159.

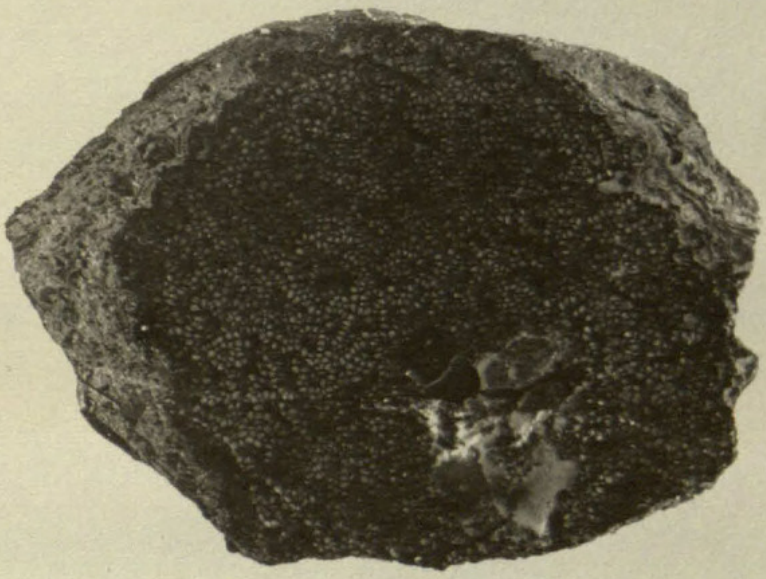
PLATE IV. BOTRYOPTERIS GLOBOSA *Darrah*. Several sporangia, filled with spores. Reproduced from a photograph of a cellulose peel taken from specimen number 42159. Fifty times natural size.

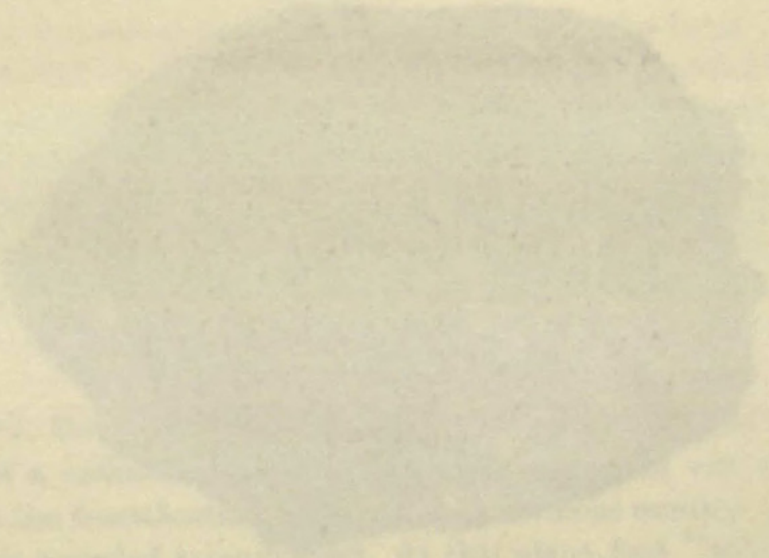
PLATE V. BOTRYOPTERIS GLOBOSA *Darrah*. Reproduction of a photograph of a cellulose nitrate peel showing a number of sporangia which have the sporangial walls fairly well preserved. The sporangium adjacent to the limb of the petiole near the upper left corner shows a few cells of the annulus. Several of the sporangia near the center show remnants of the inner cell layer. This layer is usually indicated as a shrunken tissue that has pulled away from the outer layer. This is best demonstrated by the sporangium at the bottom center and the contiguous sporangium above it. Reproduced from a photograph of a cellulose nitrate peel from specimen number 42635 (COTYPE) in the Paleobotanical Collection of the Botanical Museum. Twenty times natural size.

PLATE VI. BOTRYOPTERIS GLOBOSA *Darrah*. Reproduction of a photograph of a cellulose nitrate peel from a specimen cut transversely through the fructification, showing the enormous number of sporangia and their crowded arrangement. At this plane, four "secondary petioles" are visible. These have resulted from repeated branching of the main axis ("primary petiole") and carry the sporangial mass. The two petioles near the center indicate the nature of the subsequent branching. The small ultimate branches are scattered throughout the mass. Peel taken from specimen number 42635. Five times natural size.

Plate I







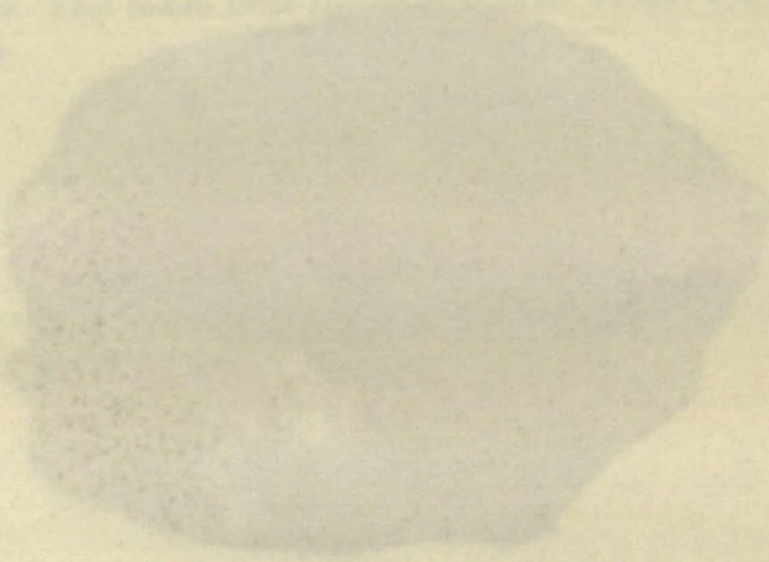


Plate II

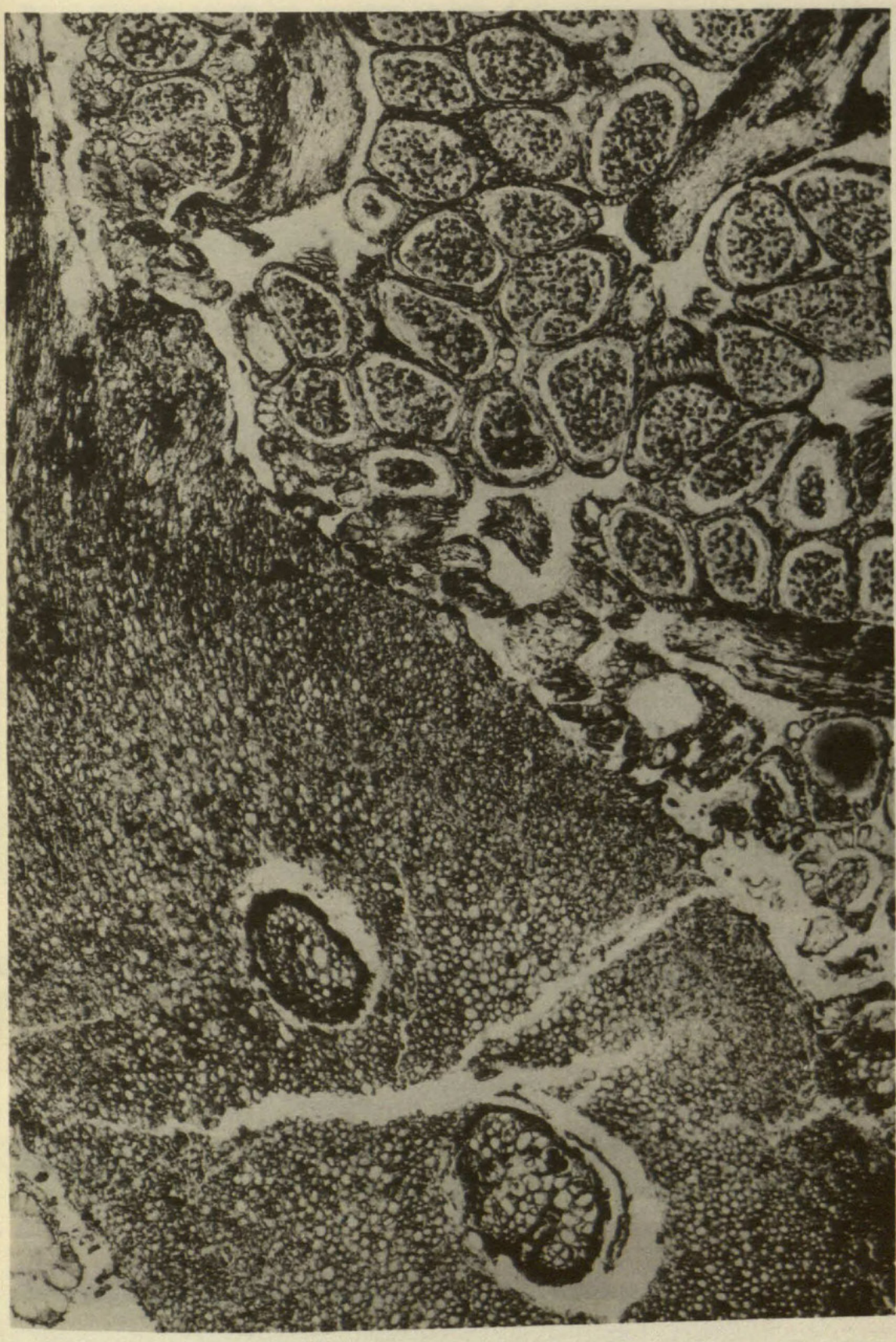


Plate III

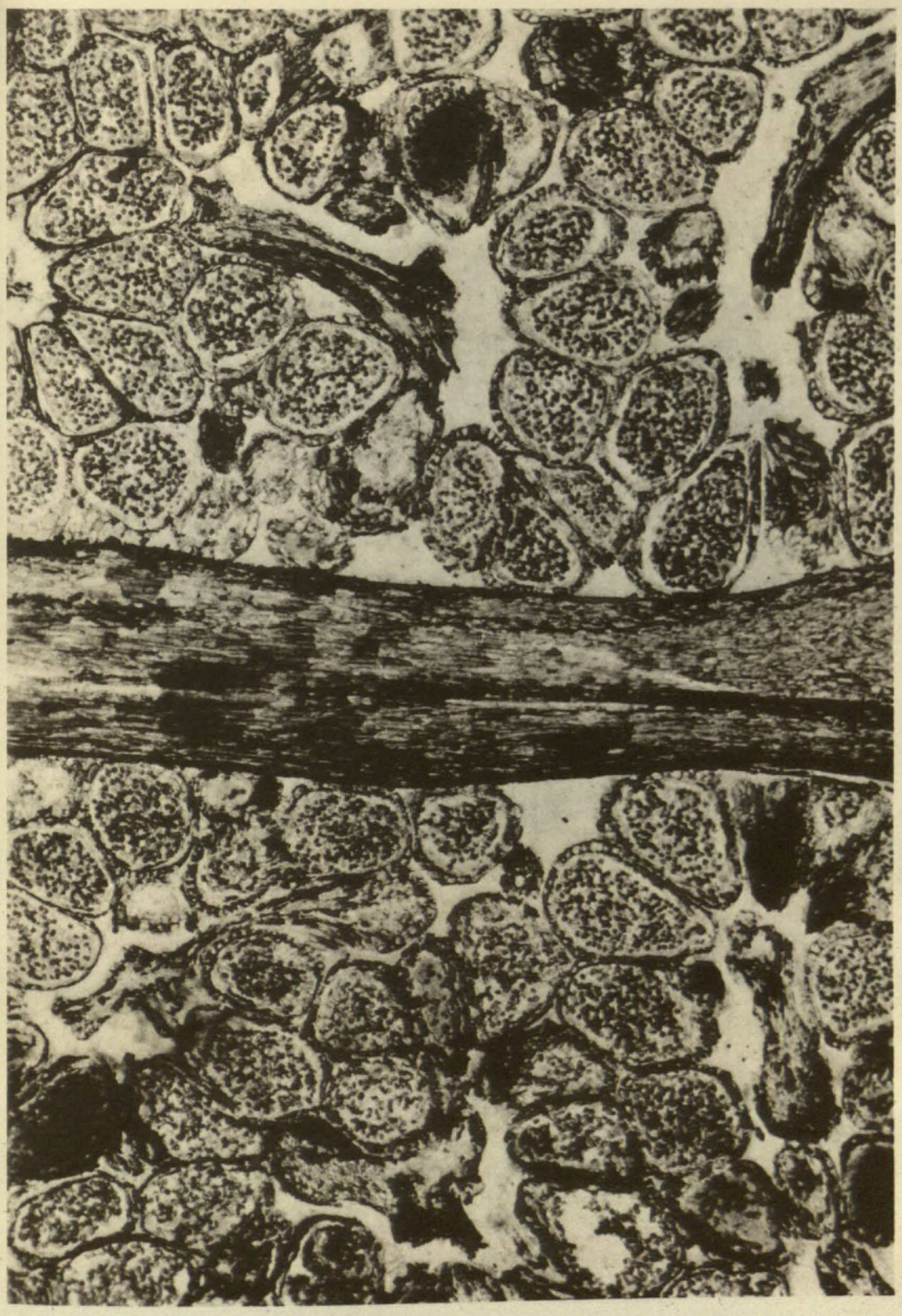


Plate IV

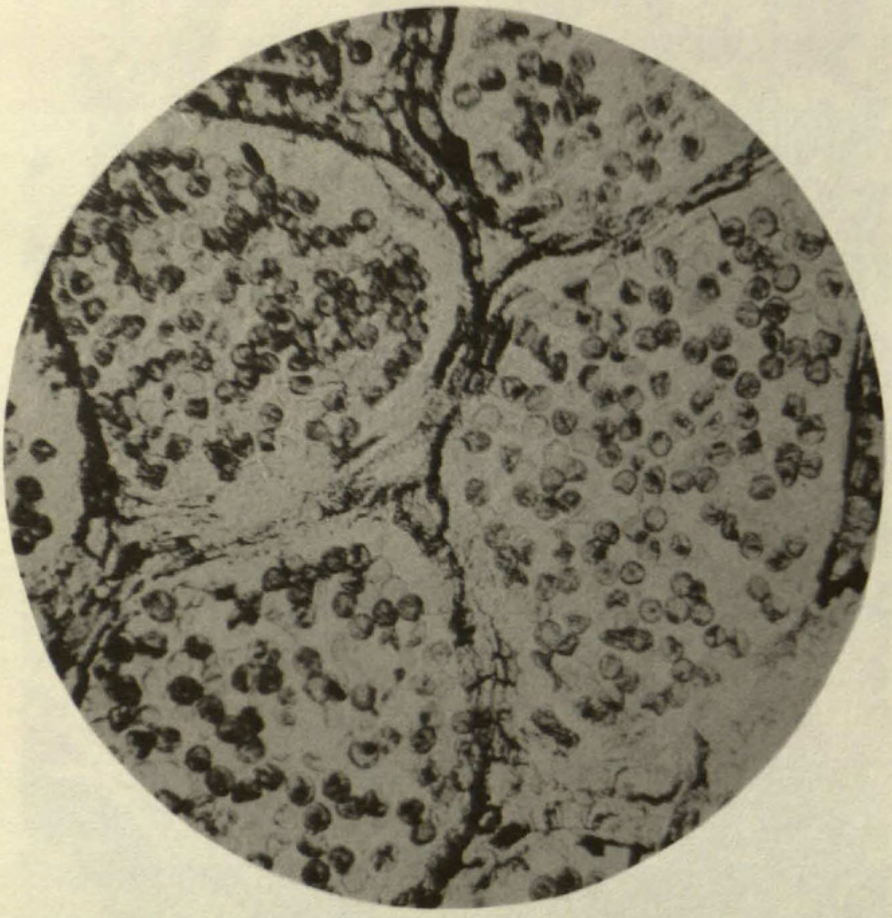


Plate V

Plate VI