THE MORPHOLOGY OF *STAUROPTERIS BURNTISLANDICA* P. BERTRAND AND ITS MEGASPORANGIUM *BENSONITES FUSIFORMIS* R. SCOTT

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CONTENTS

The Lower Carboniferous *Stauropteris burntislandica* is described here in detail. The frond of the plant consists of a repeatedly dichotomizing branch system which is traced up to the ultimate tips. The structure of the node and degree of branching in various orders of branches is described. A reconstruction of a part of the frond is made which suggests that the frond may have been supported on an underground stem. *Bensonites* has now been shown to be the megasporangium of *Stauropteris burntislandica* which normally carries two well-developed megaspores, a condition which is unknown elsewhere in the plant kingdom. The sporangium containing small spores which was already known now becomes the microsporangium of the plant.

It is suggested that heterospory may be found in other species of *Stauropteris* also. A comparison is then made with the Zygopterideae and the Psilophytales. Finally, the systematic position of *Stauropteris* is discussed in the light of new evidence.

I. Introduction

The genus *Stauropteris* is one of those problematical plants which gave rise to much controversy in the past. This, indeed, was to a great extent due to our incomplete knowledge about the genus. This paper is a contribution towards the elucidation of its earlier species and gives new information which has some bearing on the morphology and systematic position of the genus.

The genus consists of two species*, *S. oldhamia* Binney from the Upper Carboniferous and *S. burntislandica* P. Bertrand from the Lower Carboniferous. Of the two species *S. oldhamia* is the best known. The stem is still unknown in both the species.

* One additional species, *Stauropteris americana* Darrah, has been reported from N. America, but has not been fully described (Darrah 1941, p. 239).

In 1872 Binney established the genus, and two years later Williamson (1874) described the main features of the fossil under the name *Rachiopteris oldhamia*. He showed that the branches are given off in pairs and noted the absence of leaves. It was Bertrand (1907, 1909, pp. 15–70) who described in great detail the anatomy and branching of the axes up to the IVth order, but he, too, did not trace the branching up to the minute tips of the frond. In 1905 Scott described the sporangium and showed its connexion with *Stauropteris oldhamia*. A year later (1906) he discovered some germinating spores in the sporangium. In 1927 Hirmer (p. 491) gave a reconstruction of a part of the frond of *S. oldhamia*, but since the branching in the ultimate segments was not known his reconstruction is doubtful.

The other species *S. burntislandica* is very little known. Although Bertrand (1909, p. 40) established the species he described only briefly its differentiating characters from *S. oldhamia*. Mrs R. Scott (1908) discovered its sporangia and also some peculiar spindle-shaped bodies, which she named *Bensonites fusiformis*, in association with the branches of *Stauropteris burntislandica*. These bodies she considered were the glands borne on the fronds of the plant. This view was later supported by Chodat (1912).

A good deal of theoretical controversy was also centred round *Stauropteris*. Lignier (1912) and later on Bower (1935, p. 316) doubted whether the plant possessed a stem sharply delimited from the frond, a contention with which Scott (1920, p. 415) did not agree. Bertrand in 1909 maintained that *Stauropteris* was a specialized member of the Zygopterideae; but Lignier regarded it as more primitive and therefore that it could not be included in the same family. Scott (1920, p. 335) placed *Stauropteris* provisionally under Zygopterideae and regarded it as representing a line of descent which separated far back from that of the other Zygopterideae. In 1933 Bertrand raised *Stauropteris* to a family equal in status with the Zygopterideae. But later (1941) he thought that in spite of some similarities *Stauropteris* shows with the primitive ferns, it has more clear affinities with Sphenophyllales and Equisetales. He, therefore, created a new group of Stauropteridales, Sphenophyllales, Equisetales and Psilotales under an order Psilopsidales which he placed intermediate between Filicales and Lycopodiales.

II. Material and methods

The material was obtained by Mr W. Hemingway from the calciferous sandstone series (Culm), Pettycur, Fife, Scotland. It was purchased by the Botany School, Cambridge, and kindly handed over to me by Dr H. H. Thomas for further investigation.

A series of sections was prepared from a number of blocks by the well-known peel method. A block was ground smooth and etched in 5 % HCl for 30 to 45 s. The etched surface was then washed and allowed to dry. Before pouring the cellulose solution, it was found useful to wet the etched surface with acetone. It facilitated the spreading of cellulose and avoided the formation of air bubbles. The sections peeled off easily after drying for about 12 h. The sections were then treated with dilute HCl and pressed in blotting paper. Since immediate sections were not necessary for tracing the branches of the frond, the blocks were ground slightly after each section. Hundreds of peel sections were made from different blocks for this study.

For detailed observations on megasporangia (=*Bensonites fusiformis*) Mr B. D. Harrison prepared fifty serial peel sections without intermediate grinding, and these were very kindly sent to me by Professor T. M. Harris. Each section represents the plant tissue in a thin layer of rock. Earlier sections are 10μ thick and later ones are 50μ. Thick sections were better for observation.

III. Description

(1) *External morphology*

The stem of the fossil is still unknown. I believe a frond as shown in figure 5 must have been supported by an underground axis, which may have been something like that of *Diplolabis* or *Metaclepsydropsis*. In the latter we know how a simple rhizome gives out a complicated H- or X-shaped leaf trace. The same thing might have happened in *Stauropteris*.

The frond of *S. burntislandica* represents a highly divided branch system on which dichotomy is strongly stamped (figures 1 and 5). It must have been held erect. The main

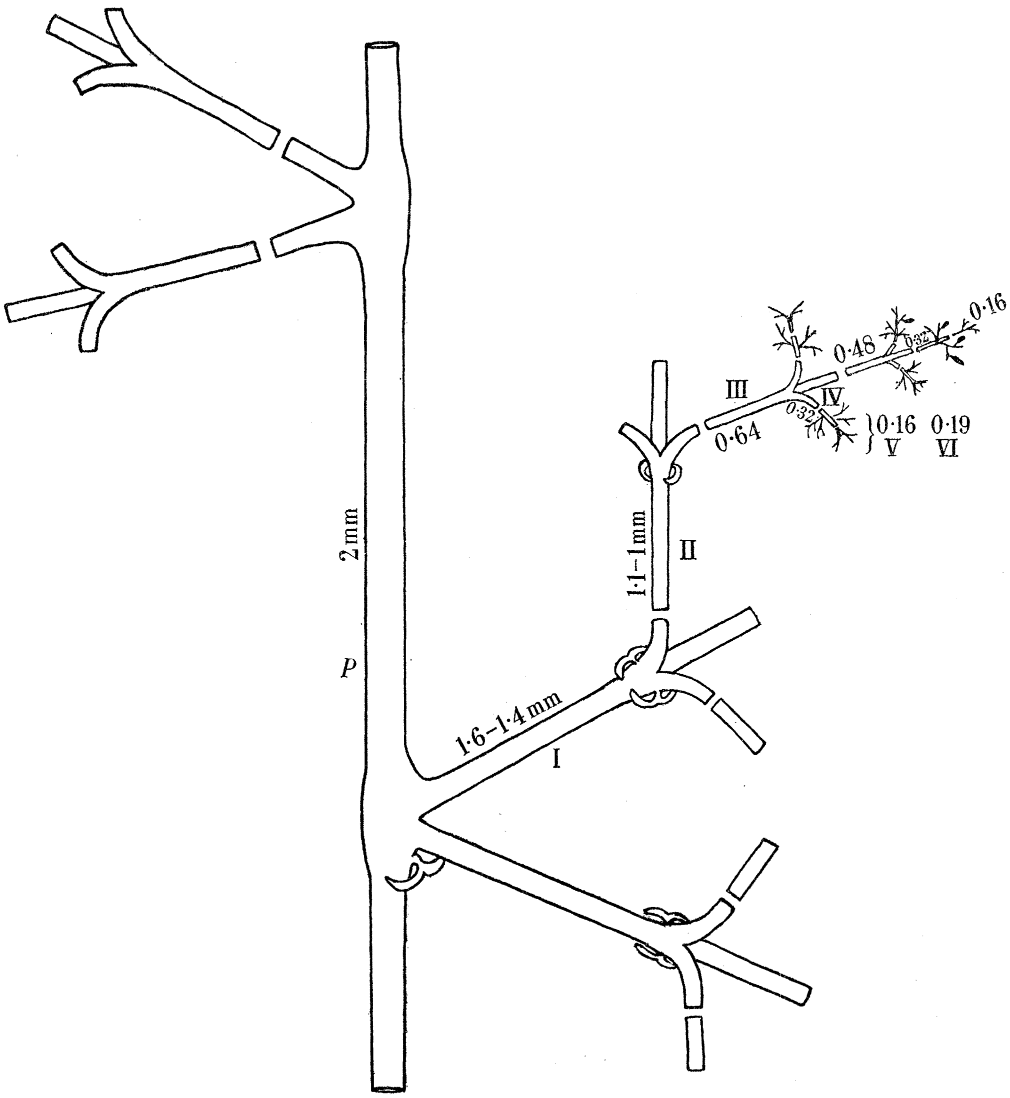

Figure 1. A diagrammatic reconstruction of branches from Ist to VIth orders borne on a petiole (*P*). Breaks are shown where branches have not been observed in actual connexion. The branching of 0·48, 0·32 and 0·16 mm branches as described in the text is drawn here diagrammatically. The sizes and orders of branches are indicated in the figure. (Magn. × 2·5.)

petiole of the frond carries four rows of alternate branches, each pair being formed by an equal dichotomy of the daughter stele. The nodes of the branches are somewhat swollen, and this helped to support the complex branch system. The main petiole diminished by about 0·2 to 0·4 mm in diameter after branching twice, which suggests that the entire frond must have been quite long, possibly from 10 to 15 cm or even more.

(2) *Anatomy*

A. *Frond*

(i) *Petiole.* A petiole measures 2 to 2·5 mm in diameter (figure 8, plate 1) and increases up to 4 mm in the region of branching. The epidermal cells are somewhat characteristic; they are comparatively large, four-sided and thin-walled. Such epidermal cells are present even in the smallest branches of the frond and help in the identification of the detached branches. The epidermis is followed by the cortical region which is divisible into outer and inner parts. The outer cortical cells are small and compactly arranged, and the inner ones are round and loosely arranged. No endodermis or pericycle could be recognized.

The stele is situated in the centre (figures 10, 11, plate 1). In cross section it shows four lobes of xylem joined together in the form of H or X (about $1{\cdot}1 \times 0{\cdot}8$ mm in size) and four alternating phloem groups. The four lobes of xylem do not separate from one another as in *S. oldhamia*. Each xylem lobe carries one protoxylem group at the outer end which is always surrounded by a few metaxylem tracheids. The metaxylem tracheids are scalariform and the protoxylem tracheids have spiral thickenings. The elongation of the stele in the antero-posterior plane is often well marked as in *S. oldhamia* (Bertrand 1909). The branches are given off at right angles to this plane of symmetry. The four groups of phloem fill in the bays between four lobes of the xylem. Some thin-walled cells also surround the xylem. As in *S. oldhamia* the two phloem groups situated in the antero-posterior plane always show three big sieve tubes (figure 8, plate 1).

Branching. At commencement of branching, the anterior and posterior lobes* of the xylem broaden out on the side which is to produce a branch. The protoxylem in each lobe then divides into two (figure 2*A*), one of which migrates towards the outer side. The inner protoxylem divides again, but this time the division is parallel to the antero-posterior plane, that is, if three protoxylems are joined by a line they form roughly a right angle (figure 9, plate 1; figure 2*B*, *C*). The newly formed protoxylem, together with a few metaxylem tracheids, moves away to form an aphlebia trace.

After this stage, only two protoxylems remain in each lobe. Within a distance of half a millimetre a joint-trace-bar is developed. A few thin-walled cells appear between the joint-trace-bar and the two xylem lobes and later extend right up to the inner protoxylem group in each lobe (figures 10, 12, 14, plates 1 and 2). As a result the joint-trace-bar looks somewhat constricted in the middle. Then the outer protoxylems of the joint-trace-bar divide into two. Finally, the inner protoxylems in the anterior and posterior lobes also bifurcate and the joint-trace-bar separates from the parent stele (figure 11, plate 1). One protoxylem remains behind in the stele of the petiole, which is thus restored to its original state, while the other protoxylem continues in the inner end of the joint-trace-bar and

* These terms are used in the same sense as Bertrand did in *S. oldhamia* (1909).

divides immediately into two. Thus at the time of separation the joint-trace-bar carries eight protoxylems, four protoxylems situated at each end. Of these four protoxylems two are situated at the outer and two at the inner side of the bar.

The joint-trace-bar itself then divides into two by equal dichotomy. This division is effected at right angles to the antero-posterior plane as shown by the arrow in figure 11 plate 1. As a result, two daughter steles, exactly similar in structure and appearance, are formed.

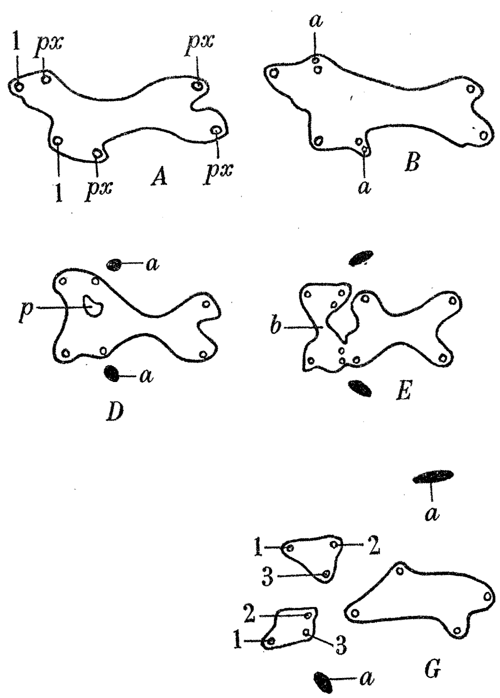

FIGURE 2. Figures *A* to *G* illustrate the stages in the branching of the stele of a secondary branch. In *A* the two main protoxylems on the left side (*px*) have given out one protoxylem each (1). *B*. The two main protoxylems divide again and supply the aphlebiae (*a*). In *D* a patch of parenchyma (*p*) develops and a joint-trace-bar (*b*) is formed, which separates from one end in *E*, and divides into two daughter steles (*d*) by dichotomy in *F*. At this stage the two daughter steles have three protoxylems (1, 2, 3) each as seen in *G*. (Magn. × 23.)

Within the distance of 1 mm from this stage the aphlebia traces of the two daughter steles move outwards through the cortex of the petiole. The angle of divergence between the daughter stele and its aphlebia trace is always more than 90°. The aphlebia trace often bifurcates immediately after coming out of the petiole (figure 15, plate 2).

The two daughter steles diverge from one another as they move outwards and gradually assume their characteristic X-shape. They also possess three big sieve tubes in the two phloem groups situated in the antero-posterior plane, and this plane of the two daughter steles is roughly parallel to that of the petiolar stele. Eventually each daughter stele passes out into a branch of the Ist order, which is often wider at the base but soon diminishes upwards. A petiole about 2 mm in diameter gives out a pair of branches of the Ist order measuring 1·6 to 1·28 mm in diameter.

In one case a petiole 2 mm in diameter was observed to branch twice, thus producing two alternate pairs of branches. The distance between the two pairs was 4·5 cm.

(ii) *Branches of the Ist order*. The branches of the Ist order measure from 1·6 to 1·28 mm in diameter. The epidermis is similar to that of the petiole, but the cells in the outer cortex are somewhat smaller and increase gradually in size inwards (figures 9, 12, 14, 15, plates 1 and 2). The difference in size is, however, not so well marked.

The xylem is more often X-shaped, 0·62 to 0·48 × 0·54 to 0·4 mm in size and flattened laterally. The four lobes carrying four protoxylem groups are less developed than those of the petiolar stele. The phloem, again, possesses three big sieve tubes in the two phloem groups situated in the antero-posterior plane and branching occurs at right angles to this plane of symmetry.

Branching. Figure 2 illustrates the branching in the branches of the Ist order. The stages up to the formation of the joint-trace-bar are similar to those described in the petiole, except for the fact that in the former the outer ends of the joint-trace-bar carry only one protoxylem instead of two (figure 2*F*, *G*; cf. figures 10, 11, plate 1), so that when the joint-trace-bar divides by equal dichotomy into two daughter steles each daughter stele possesses three protoxylems instead of four (cf. petiole) and the daughter steles become tetrarch only just before they enter into branches of the IInd order. This is accomplished by the bifurcation of the protoxylem at the outer end of each daughter stele, so that a protoxylem occupies each corner of the quadrangular xylem mass. The orientation of the two daughter steles, remains parallel to that of the parent stele.

Sometimes the two branches of the IInd order remain fused at the base, but they soon separate and diverge from each other. The branches of the IInd order thus given out possess a tetrarch stele, but the arms of the xylem lobes are feebly developed.

It is mentioned above that a petiole 2 mm in size was observed to give out two pairs of branches of the Ist order. These branches of the Ist order were again observed to give out a pair of branches of the IInd order at a distance of about 2 cm from the petiole. If the petiole of *Stauropteris* is supposed to be upright then the branches of the Ist and IInd order were arranged in a horizontal plane (figure 5).

(iii) *Branches of the IInd order*. These branches are smaller in size, 1·1 to 0·8 mm in diameter, and are structurally almost similar to those of the petiole and the branches of the Ist order. Here the cortex is more or less uniform and the stele is somewhat rectangular or square (0·32 to 0·24 mm × 0·3 to 0·2 mm) with slightly drawn-out corners where protoxylems are situated. Three big sieve tubes could be recognized again in the two phloem groups situated in the antero-posterior plane.

Branching. The manner of branching is similar to that of the petiole and the branches of the Ist order, except for a few differences mentioned below.

When a branch 0·8 mm in diameter divides, the aphlebia traces are not formed until the joint-trace-bar separates from the parent stele. Consequently the joint-trace-bar supplies the protoxylem to the aphlebia traces, a condition which is invariably found in the branches of still smaller sizes. Similarly, the aphlebia traces do not bifurcate immediately after coming out of the parent branch but may, however, bifurcate within the distance of 1 mm.

The joint-trace-bar divides equally from the middle into two daughter steles which supply a pair of branches of the IIIrd order. Each daughter stele is triangular and carries only three protoxylem groups, one situated in each corner of the stele (cf. figure 2*G*).

There is no bifurcation in any protoxylem at any stage so that the stele of the branch of the IIIrd order remains triarch.

(iv) *Branches of the IIIrd order*. The branches of this order measure 0·64 to 0·48 mm in diameter and are simpler in structure (figure 16, plate 2). The epidermal cells as usual are big and the cortical cells are more or less uniform and thin-walled. The stele is triarch and triangular. Three phloem groups are situated on three sides of the triangle.

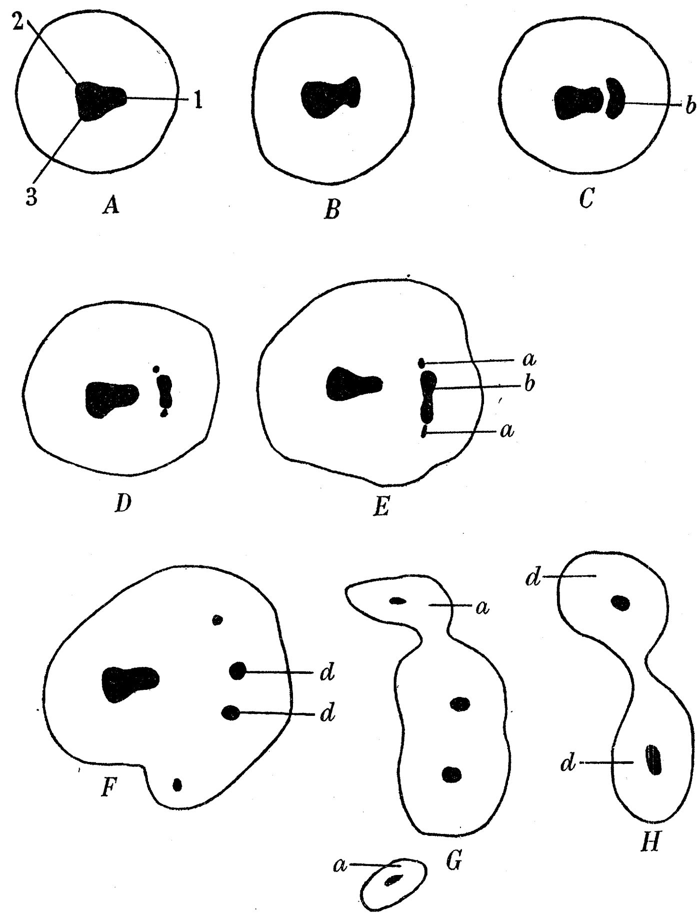

FIGURE 3. Figures *A* to *H* illustrate the stages in the branching of a triangular stele with three protoxylems (1, 2, 3) as seen in *A*. The stele gives out a joint-trace-bar (*b*) in *C*, which in its turn gives out aphlebia traces (*a*) in *D*, *E* and divides into two branches (*d*) by equal dichotomy (*F*). The daughter branches separate from the parent branch when still enclosed in common tissue (*G*, *H*). Subsequently they separate from each other. (Magn. × 32·5.)

Branching. Figure 3 illustrates the stages in branching of the triangular stele. One corner of the stele flattens out (figure 3*A*, *B*) and one protoxylem situated there divides into two. The newly formed protoxylem then immediately bifurcates into two, each protoxylem occupying one end of the joint-trace-bar which is formed simultaneously (figure 3*C*, *D*, *E*).

The joint-trace-bar looks like a narrow elongated plate. On its way outwards it gives out aphlebia traces, one from each end and divides from the middle into two daughter steles which supply the branches of the IVth order (figure 3*D*, *E*, *F*, *G*). Each daughter stele carries one mesarch protoxylem.

The two branches of the IVth order are usually fused at the base (figure 3 *G*, *H*), but they soon separate and diverge from each other. Each daughter branch measures from 0·32 to 0·24 mm in diameter.

Some branches of the IIIrd order, 0·64 mm in size, were traced farther upwards after they had given out a pair of daughter branches of the IVth order. The triangular stele of the branch of IIIrd order disintegrated into three monarch steles. Two steles gave off daughter branches (figure 20, plate 3). The third monarch stele remained in the parent branch which at this level diminished to 0·32 mm in diameter. This shows how a branch with triarch stele is reduced to a monarch condition after giving out two pairs of daughter branches which are also monarch.

The branches 0·48 mm in diameter behaved in a similar way, and the stages in its branching are illustrated in figure 4. Here two protoxylem groups (instead of one as mentioned above) of a triarch stele are involved in producing a pair of daughter branches. Each protoxylem divides into two, and the newly formed protoxylems enter into the two

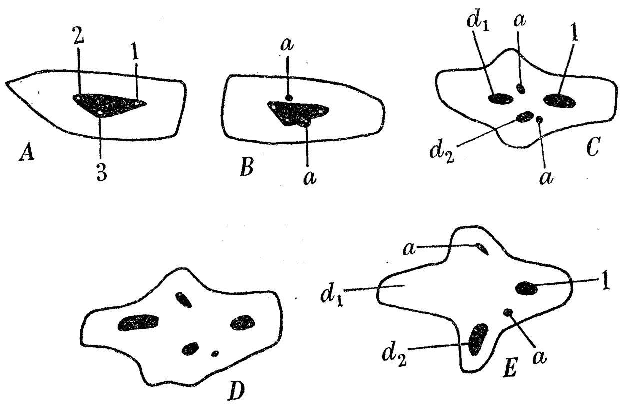

FIGURE 4. Figures *A* to *E* show how a triangular and triarch (1, 2, 3) stele is reduced to a monarch stage by disintegrating into three monarch steles (1, d_1, d_2 in *C*, *D*, *E*) two of which (d_1, d_2) enter into a pair of branches and produce aphlebiae (*a*). (Magn. ×26·5.)

aphlebia traces. The stele then disintegrates into three monarch steles. The two steles, protoxylems of which gave off aphlebia traces previously, enter into a pair of daughter branches (figure 4 *C*, *D*, *E*), which measure 0·32 mm in diameter. The main branch is thus left with a monarch stele and is itself diminished to about 0·4 mm in diameter. As a result all branches, including the parent branch, are reduced to a monarch condition which is observed in all branches 0·4 mm and below in diameter.

Thus, with the progressive diminution in size of the branches, as we pass towards the distal region of the frond, the stele is progressively reduced from tetrarch to triarch and finally to monarch condition.

(v) *Branches of the IVth order*. These branches measure 0·4 to 0·24 mm in size and can be recognized by their size (figures 17, 18, plate 2). The epidermal cells are comparatively big and possess stomata. A stoma measures $55{\cdot}2 \times 36{\cdot}8\,\mu$ and possesses two guard cells $22\,\mu$ long and two subsidiary cells. The cortical cells are round and thin-walled. The stele consists of a few scalariform tracheids with only one protoxylem and surrounded by the phloem.

Branching. A branch of this order was observed to produce daughter branches at two places. The stele first gave off a few tracheids on one side, which immediately bifurcated into two groups, and finally entered into two equal daughter branches (figures 17, 18) which measure 0·16 mm in diameter. About a millimetre upwards the stele of the parent branch again gave off a few tracheids, this time opposite to the first. This is seen in figure 18, in which the previous pair of daughter branches are also seen. The tracheid mass again bifurcated and supplied a pair of daughter branches 0·16 mm in diameter. These 0·16 mm branches were further traced through 3 mm, and their branching is described below under the branches of Vth and VIth orders. The monarch branch of the IVth order thus appears to give off alternate pairs of daughter branches as the petiole.

The branch of the IVth order after giving out two pairs of daughter branches diminished to 0·24 mm in size, the branching of which could not be traced further. However, other detached branches of the same size are observed to fork into two branches of 0·16 mm in size.

(vi) *Branches of the Vth and VIth orders.* A branch of the Vth order measures 0·16 mm in diameter and appears to be the penultimate branch of the frond.

It is 2 to 3 mm long and circular in cross-section (figure 22, plate 3). The epidermal cells are comparatively big and possess stomata. One such stoma is shown in figure 19, plate 2. It is somewhat oval in surface view and measures $36{\cdot}8 \times 29{\cdot}4\,\mu$. The two guard cells are sunken, $14{\cdot}7\,\mu$ in length and surrounded by two comparatively big subsidiary cells. The cortex is only a few cells in thickness. The cells are round and thin-walled. The cells situated just under the epidermis are not elongated. The stele consists of a few delicate-looking scalariform tracheids surrounded by a thin-walled tissue.

Branching. The branches of the Vth order divide by simple forking (figure 21, plate 3). The forks measure from 0·09 to 0·1 mm in diameter and are the branches of the VIth order. The smallest branches observed in the Pettycur material measure 0·08 mm. Perhaps all the ultimate branches tapered to this size. No branching has been observed in branches (VIth order) 0·09 to 0·08 mm in diameter.

(vii) *The reconstruction of the frond.* From the above description it is obvious that *S. burntislandica* possesses a highly divided 'frond'. From the material at my disposal it was not possible to trace completely such a highly divided branch system. Figure 1 shows diagrammatically the parts of the frond I have observed in actual connexions, the breaks indicating those which were not observed in connexion.

For the reconstruction shown in figure 5 I depended chiefly on the observations made on the detached branches of various sizes and their interrelationship as shown in table 1.

In this table the branches are arranged under different size groups, and each group has been assigned a definite order. These branches of each order are easily recognized by the structure and size of the steles. The branches show a fine graduation in size, a fact which suggests that the frond of *Stauropteris* tapered gradually, both upwards as well as laterally.

Also the branches of the frond show a definite relationship with one another. A petiole gives out a pair of branches 1·6 to 1·28 mm in diameter, the latter produces branches 1 mm in diameter, which give out branches 0·64 mm in diameter and so on. This provides a complete sequence of lateral branching in the frond as shown in figure 1. This is the basic plan on which the frond shown in figure 5 is reconstructed.

In the reconstruction of this frond some assumptions are made. The biggest branch is supposed to be the petiole of the frond. A 2 mm branch is supposed to be the main rachis which was held erect and gave off alternate pairs of lateral branches, the first pair being 1·6 mm in diameter. It is presumed that a 1·6 mm branch diminished gradually higher up through the following sizes: 1·28, 1, 0·8, 0·64, 0·48, 0·32 and 0·16 mm. The branching in detached branches of all these sizes have been observed (see table 1). It is therefore

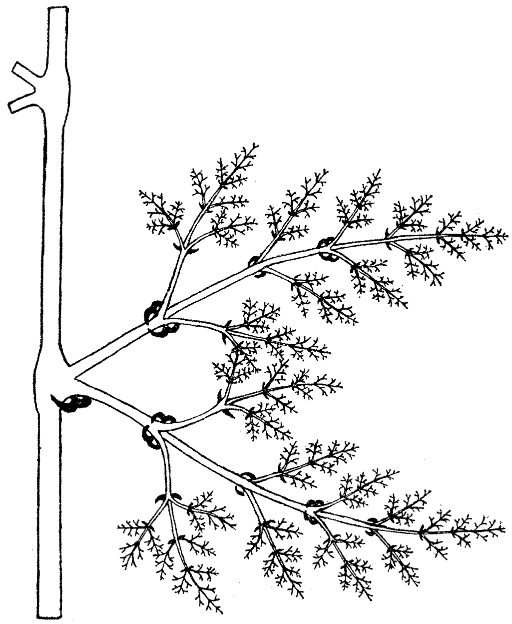

FIGURE 5. A diagrammatic reconstruction of a part of the frond of *Stauropteris burntislandica* based on the plan shown in figure 1. The aphlebiae are drawn in solid black. The microsporangia and megasporangia are not shown.

TABLE 1

Petiole 2 mm in diam. gives off a pair of branches 1·6 to 1·28 mm diam.
Branch of Ist order 1·4 mm in diam. gives off a pair of branches 1 to 1·1 mm diam.
Branch of Ist order 1·28 mm in diam. gives off a pair of branches 0·9 to 0·8 mm diam.
Branch of IInd order 1 mm in diam. gives off a pair of branches 0·64 mm diam.
Branch of IInd order 0·8 mm in diam. gives off a pair of branches 0·48 mm diam.
Branch of IIIrd order 0·64 mm in diam. gives off a pair of branches 0·32 mm diam.
Branch of IIIrd order 0·48 mm in diam. gives off a pair of branches 0·24 mm diam.
Branch of IVth order 0·32 mm in diam. gives off a branch 0·24 mm diam.
Branch of IVth order 0·24 mm in diam. gives off a branch 0·16 mm diam.
Branch of Vth order 0·16 mm in diam. gives off a branch 0·1 to 0·09 mm diam.
Branch of VIth order 0·1 mm. Does not branch further.

presumed that a 1·6 mm branch (Ist order) gave off opposite pairs of daughter branches when it diminished to 1·28, 1, 0·8 mm, etc. It is known that a 1·6 mm branch gave off the first pair of daughter branches at a distance of 2 cm from the main rachis. The distances between the successive pairs of daughter branches would then presumably be less than 2 cm, for when the branches become smaller in size they give out daughter branches at shorter distances. The daughter branches of a 1·6 mm branch measure about 1 mm in diameter. These branches are also supposed to taper through 0·8, 0·64, 0·48 mm, etc., to about 0·16 mm diameter at the apex and branch at the above-mentioned levels. Similar behaviour is presumed for all other branches of different sizes.

Thus, when complete branching of the branches of every size is drawn it produces a frond as shown in figure 5. This, in essential, is a repetition of the basic plan shown in figure 1.

B. *Megasporangium* (= Bensonites fusiformis *R. Scott*)

Mrs R. Scott (1908) described under the name *Bensonites fusiformis* some peculiar spindle-shaped bodies which she suggested might have been borne on the frond of *Stauropteris burntislandica* as glands, although she did not observe a clear attachment between the two. In 1911 Dr R. Chodat showed attachment of *Bensonites* with a branchlet of the 'order *n*' of *Stauropteris burntislandica* and upheld the same view.

In my serial sections there are several instances of attachment of these bodies with the ultimate branchlets (0·1 to 0·09 mm in diameter) of *S. burntislandica*. The branches bearing *Bensonites* show the same typical characters, such as big epidermal cells, big thin-walled cortical cells and the structure and the appearance of the stomata, as numerous branchlets of *Stauropteris burntislandica*. There is thus no possibility of mistaking the branchlets bearing *Bensonites* as belonging to any other plant present in the sections. I have also traced several 0·1 mm branches upwards through successive transverse sections and have found that they terminated in *Bensonites*. Moreover, indirect evidence is provided by the fact that the stalk of *Bensonites* and an ultimate branchlet of *Stauropteris burntislandica* frond are identical in size and structure. Figure 26, plate 4, shows a megasporangium attached by a short stalk to a branchlet 0·16 mm in diameter which shows a stoma (*s*) identical with that shown in figure 19, plate 2. Figure 27, plate 4, provides another example where a branch of the Vth order has given out a branch of the VIth order which in its turn bears a megasporangium (*sp*). Figure 28, plate 4, shows two megasporangia borne on a single stalk (*sk*).

Thus there is no doubt left now that *Bensonites* are borne on the ultimate branchlets of the frond of *Stauropteris burntislandica*. Since they contain megaspores they are referred to here as megasporangia of the plant. It is further suggested that the name *Bensonites* should now be dropped.

General structure

The megasporangium is spindle-shaped, about 1·3 mm in length and 0·48 mm in diameter in the broadest part (figure 24, plate 3; figure 28, plate 4). Its lower two-thirds consists of a solid cellular body with the vascular supply in the centre, while the upper one-third contains the sporangial cavity. In the solid body the epidermal cells are big, thin-walled and four-sided in transverse section and many times longer than broad in longitudinal section. More often the epidermal cells are collapsed. The inner cells are round, more or less uniform and are loosely packed, but in longitudinal section those which surround the vascular bundle are longer than broad while the others are round. In the centre runs a delicate-looking vascular strand composed of a few scalariform tracheids and surrounded by thin-walled cells. The vascular bundle enters from the stalk into the solid body and runs in the middle right up to the base of the sporangial cavity.

The cells lining the sporangial cavity are also more often collapsed, but sometimes they are seen with inner and tangential walls somewhat thickened (figure 25, plate 3). In the sporangial cavity is often seen an hour-glass-shaped structure (figure 28, plate 4) which was also observed by Mrs Scott (1908). It is the membranous 'spore bag' which encloses the spores (figure 7). Normally the megasporangium carries two well-developed megaspores (figures 29, 30, plate 4), a condition unknown elsewhere in the plant kingdom. The spore wall comes out in bits in many sections. Sometimes a 'spore print' is clearly seen. It is a translucent mark which indicates the spore outline. Occasionally a complete spore may also come out (figure 24, plate 3). The megaspore wall is smooth, about 0·11 to 0·16 mm in diameter and shows a clear triradiate mark.

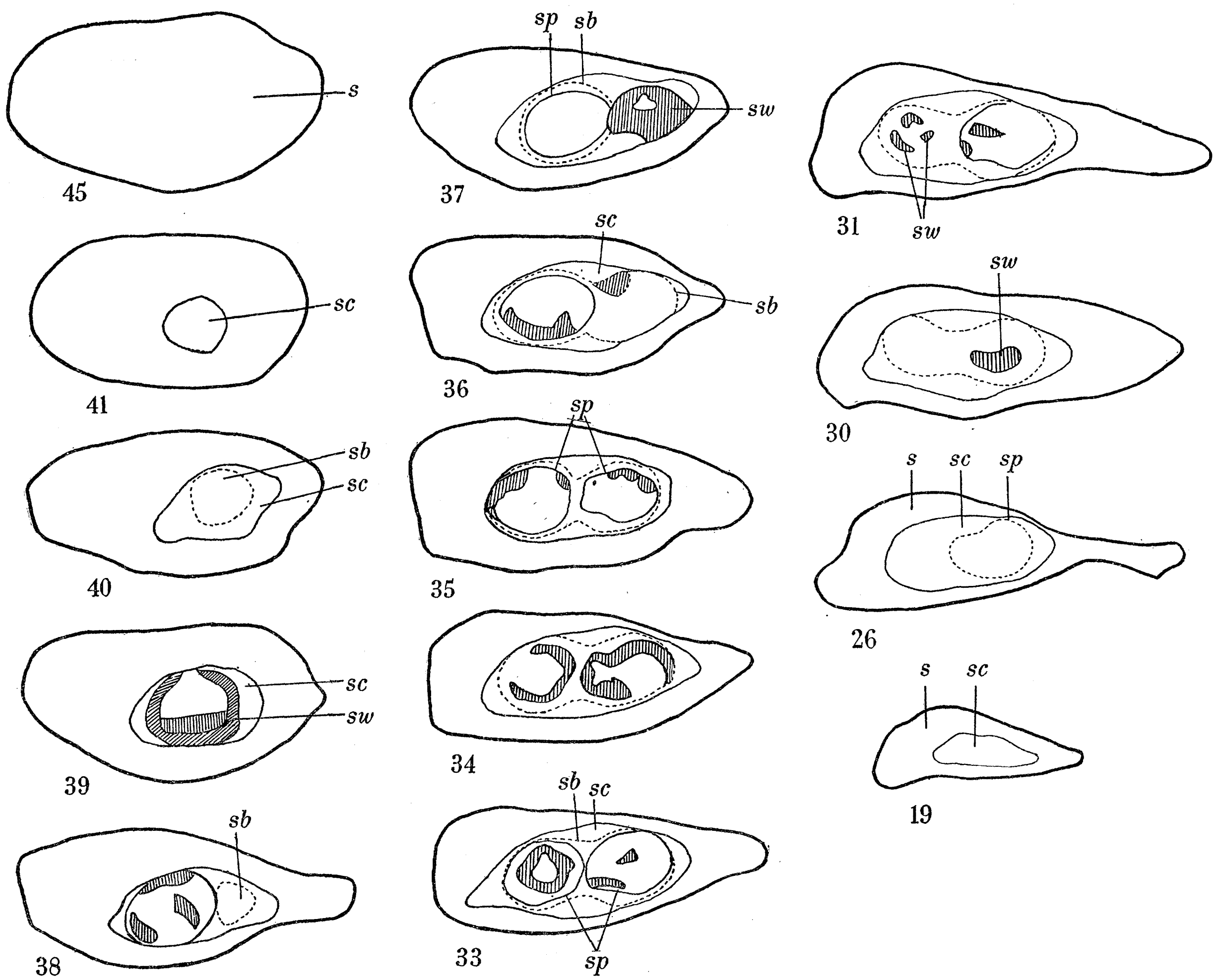

FIGURE 6. Selected camera lucida drawings through one megasporangium (*s*). 45 to 19 are the numbers of the peel sections. *sc*, sporangial cavity; *sb*, spore bag; *sp*, spore print; *sw*, spore wall.

In order to confirm the unmber of megaspores, a number of megasporangia were followed through successive peel sections, kindly sent to me by Professor T. M. Harris which were prepared by Mr B. D. Harrison. They confirm that there are two well-developed megaspores in a megasporangium.

Figure 6 shows some selected sketches of camera lucida drawings from one megasporangium. In section 45, only the cellular body of the megasporangium (*s*) is seen. In 41 and 40 the sporangial cavity (*sc*) appears and a little of the membranous spore bag (*sb*) is seen. In 39 the spore wall of the first spore (*sw*) appears and in 38 the spore bag of the second spore appears. From 37 to 33 portions of spore wall are seen in both the spores. Section 31 shows the last of the spore wall of the first spore and section 30 that of the second spore. In subsequent sections spore bag and sporangial cavity disappear, and finally there is no trace left of the megasporangium.

Figure 7 shows a reconstruction of the megasporangium, and the numbers there indicate the approximate plane of sections from which figure 6 is drawn.

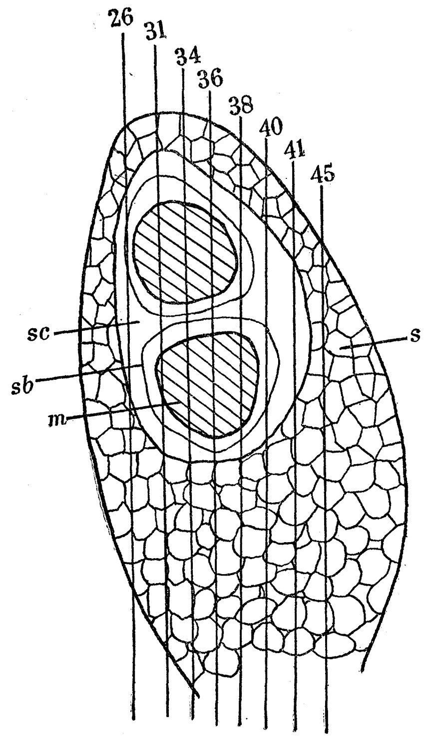

FIGURE 7. Reconstruction of the same megasporangium showing two well-developed megaspores (*m*). Other letters similar to figure 6.

Mr B. D. Harrison has provided another very interesting observation. In one megasporangium there was, in addition to the two large megaspores, a small one which showed triradiate marks. The spore shown in figure 24, plate 3, may have been a similar spore. This implies that there were four young megaspores of which two developed and two degenerated. Perhaps rarely one of the degenerating megaspores became cutinized. There may have been, therefore, meiosis in the formation of the tetrad of megaspores.

There is no indication how the megasporangium dehisced. Perhaps the U-shaped thickened sporangial wall cells may have helped in the liberation of the spores. Or more probably the sporangium did not dehisce, but the spores were liberated by rotting away of the cellular body, which may have helped dispersal, e.g. by flotation.

C. *Microsporangium*

Mrs R. Scott (1908) in her paper on *Bensonites* assigned some detached sporangia to *Stauropteris burntislandica*. In some cases a sporangium was seen borne terminally on a small branchlet, but in all such cases the preservation of the branchlets was so poor that they could not be identified with certainty. However, the similarity between this sporangium and that of *S. oldhamia*, where a connexion was definitely established by Scott (1905), is striking, and therefore it is very likely that the sporangium described by Mrs Scott (1908) belonged to *S. burntislandica*. Since *Bensonites* has now been shown to be a megasporangium, this sporangium with small spores must be the microsporangium of *Stauropteris burntislandica*.

The microsporangium is oval to oblong in section and $0{\cdot}6 \times 0{\cdot}4$ mm in size. The sporangium wall is composed of a single layer of uniformly thickened cells with a well-marked stomium (figure 23, plate 3). The microspores are small, about 0·03 mm in diameter. Each spore has a smooth wall and possesses triradiate marks.

The microsporangia and megasporangia are often preserved near one another, but it is difficult to say whether they were borne on the same or different fronds.

IV. Comparisons and discussion

(1) *Comparison with* Stauropteris oldhamia

The stem still remains to be discovered in both the species of *Stauropteris*. Although Lignier (1912) and Bower (1935) doubted its existence, I agree with Scott (1920) that *Stauropteris* must have possessed some underground axis which supported the aerial frond. Bertrand (1941) even postulated that *S. oldhamia* must have possessed an irregularly branched, underground rhizome with lobed exarch xylem, like its aerial branches and similar to that in Psilotales. I, however, think that the stem of *Stauropteris* might be somewhat like that of *Metaclepsydropsis* or *Diplolabis*. After all, the branch system of *Stauropteris*, except for its repeated branching in pairs, is very similar to these genera, which possessed an underground rhizome supporting erect fronds.

The petiole in *S. burntislandica* is somewhat small in size, possesses no lax cortical tissue under the epidermis, and its stele is always H- or X-shaped. In *S. oldhamia* the rachis is bigger in size, possesses a lax cortical tissue, and its stele has four xylem lobes arranged like a cross and separated by phloem in the centre. It appears that the X-shaped xylem of the older species had just split up into four lobes in the younger species. The branches of the Ist and IInd orders also have X-shaped steles and are strikingly similar in appearance in both the species. This similarity increases with the diminution of sizes in the branchlets of the frond. In both species the stele is tetrarch, but in *S. burntislandica* a single row of tracheids lies outside the protoxylem whereas in *S. oldhamia* there are two rows of tracheids outside the protoxylem.

The branching in the petiole and the branches of the first two orders differ in detail in the two species. In *S. burntislandica* the aphlebia receives its protoxylem directly from the parent stele, and the second outer protoxylem of the daughter stele is formed simply by the bifurcation of the first and therefore is not derived directly from the parent stele. In *S. oldhamia*, on the other hand, the protoxylem of the aphlebia is supplied by the daughter stele, and its second outer protoxylem is derived directly from the parent stele. Again, in *S. oldhamia* the two daughter steles become tetrarch immediately after they are detached from the parent stele, whereas in *S. burntislandica* the petiole resembles *S. oldhamia*, but the daughter branches attain tetrarch condition only just before leaving the petiole.

As regards the branches of the IIIrd order, I have not observed in *S. burntislandica* the six-protoxylem stage as shown in *S. oldhamia* by Bertrand, but in both the species the resultant daughter branches have triangular steles. Branching in the branches of further orders is not known in *S. oldhamia*.

The ultimate branchlets in the two species also differ to some extent. In *S. oldhamia* the outer cortical cells are elongated and form a kind of palisade tissue, whereas in *S. burntislandica* the cortical cells are practically round.

The microsporangium of *S. burntislandica* and the sporangium of *S. oldhamia* are also similar except for the fact that in the former the sporangial wall is only one cell in thickness, whereas in the latter it is multiseriate.

From the above comparison one cannot but be impressed by the fact that, except for some minor differences, the two species are very closely related. Now that heterospory is shown in *S. burntislandica* it is suggested that megasporangia should also be found in the other species. It is likely that the Upper Carboniferous, and therefore more recent, species may be more advanced, e.g. its megasporangia may show further reduction to one megaspore per megasporangium at maturity. Also mega- and microsporangia may have grown on different plants (this may be so in both the species also).

(2) *Comparison with the Zygopterideae*

Among the genera of the Zygopterideae, the quadriseriate types look more like *S. burntislandica* than the biseriate types in the rachis, stele, and the branching in pairs. However, as pointed out by other authors, *Stauropteris* differs in maintaining a persistent quadriseriate type of branching and the same form of stele up to the branches of the IInd order. Now a third differentiating character can be added, and that is the heterosporous nature of *S. burntislandica*. So far no Zygopterid plant is known to be heterosporous. But since heterospory has not been seen in other *Stauropteris* species, might not this be also true for other so-called 'primitive ferns'?

The rachis bundles of *Diplolabis*, *Metaclepsydropsis*, *Etapteris*, *Zygopteris* and *Stauropteris* may be regarded as modifications of X- or H-shaped xylem, that is to say, in Bertrand's terminology, the median band, antennae and receptive pieces of the bundle were developed to different degrees, giving the bundle a definite appearance peculiar to each genus. Such a type of bundle has consequently two planes of symmetry. In structural details *S. burntislandica* shows some difference in possessing mesarch protoxylems, while the above-mentioned Zygopterids have exarch protoxylems situated in small depressions.

As regards the branching of the petiole, the branching in *S. burntislandica* remains the same in principle as that in *Diplolabis* and *Metaclepsydropsis* (Gordon 1911 *a*, *b*), but since the 'pinna' in *Stauropteris burntislandica* has a stele like that of the petiole, the branching differs in details. In *Diplolabis* and *Metaclepsydropsis* the pinna stele is C-shaped.

Exannulate sporangia are common to *Diplolabis* and *Stauropteris burntislandica*. However, the sporangium in the latter has now been shown to be a microsporangium.

S. burntislandica thus may show some similarity to *Diplolabis* in the appearance and branching of the rachis stele and in the exannulate sporangia, but it differs widely from the other quadriseriate types of the Zygopterideae. Now with the discovery of megasporangium in *Stauropteris burntislandica* I believe it will be better to exclude it from the Zygopterideae.

(3) *Comparison with the Psilophytales*

Kidston & Lang (1917–21, part III) compared *Asteroxylon* with *Stauropteris*. The resemblance between the two as regards the branches and sporangia is indeed striking. On the general hypothesis of Lignier and others, a general comparison is possible between the branch system of *Stauropteris* and *Hostimella* twigs of *Asteroxylon*. According to this hypothesis the leaves of the vascular cryptogams were evolved by cladodification of the lateral branches of the thallus. *Stauropteris* may be considered to form a stage in this process, where apparent radial symmetry still prevails throughout most of the frond. *Psilophyton* and *Asteroxylon* are the earlier links in the chain, for here the radial symmetry is complete throughout. As for the aphlebiae I agree with Scott (1920, pp. 413–414) and Bower (1935, p. 628) that they are comparable to *Thursophyton* leaves of *Asteroxylon*.

The somewhat primitive structure of the megasporangium of *Stauropteris burntislandica* can be interpreted as a modified end of the branchlet containing spores as in *Rhynia* and *Hornea*. It is tempting to compare the two megasporangia on a single stalk as shown in figure 28, plate 4, with the bifurcated sporangia described in *Hornea*.

Sporogonites, a member of the Psilophytales (Halle 1936), may show a similarity in organization to the megasporangium of *Stauropteris burntislandica*. *Sporogonites*, like the megasporangium, consists of a stalk carrying a long terminal capsule, the basal part of which is sterile while the upper part is hollow and contains spores. No special device for the disposal of spores is seen in either of them. However, the megasporangium of *Stauropteris burntislandica* perhaps shows an advance over *Sporogonites* in the presence of megaspores.

(4) *Systematic position of* Stauropteris

There are mainly two views about the systematic position of *Stauropteris*, one is that of Lignier (1912) and the other of Bertrand (1909, 1933, 1941).

According to Lignier, *Stauropteris* is more primitive than any of the Zygopterideae, and though on the same line of descent it cannot be included in the same family. Bertrand first (1909) regarded *Stauropteris* as a highly developed member of the Zygopterideae, but later on (1933) raised it to a family of its own, 'Stauroptéridées', on the same level as 'Zygoptéridées. More recently Bertrand (1941) removed *Stauropteris* altogether from the class of ancient ferns and placed it under a separate class named Psilopsidales, including the orders Stauropteridales, Psilotales, Sphenophyllales and Equisetales. This class was supposed to be intermediate in position between primitive ferns and Lycopodiales. He compared the sporangia of *Stauropteris* with those of *Sphenophyllum* and secondly he postulated that the underground rhizome of *Stauropteris* would be like its aerial branches, except that the protoxylem would be exarch. He therefore concluded that in spite of some analogies *Stauropteris* shows with the primitive ferns, it really has close affinities with the Sphenophyllales and Psilotales.

It should be pointed out here that Bertrand's grouping of *Stauropteris* with the Sphenophyllales and Psilotales is not convincing. First because the speculation regarding the structure of *Stauropteris* rhizome is based on an assumption for which there is no evidence, and the weight that should be attached to it is very doubtful. Secondly, the comparison between the sporangia of *Stauropteris*, and those of Psilotales and Sphenophyllales, is not convincing. In fact, the terminal position of the sporangium was not peculiar only to

Stauropteris, it was a common feature in the Devonian and early Carboniferous plants. Similarly, I see no resemblance between a synangium of *Psilotum* or a strobilus of *Sphenophyllum* and a simple terminal sporangium of *Stauropteris*, which, indeed, is more like that of *Asteroxylon*. The discovery of the heterosporous nature of *Stauropteris* has further complicated the matter.

Stauropteris is, in fact, remarkable in showing a strange combination of characters of different groups, a fact which perhaps explains the difficulty in assigning to it a correct position in the plant world. In some respects it resembles the Psilophytales, from which it has most probably evolved. At the same time it also shares some important characters with the Zygopterideae. Further, since advanced heterospory is demonstrated in *Stauropteris* it can no longer be included among the primitive ferns. Nothing else is known similar to this type of megasporangia. The megasporangium of *S. burntislandica* with two megaspores shows a more advanced stage than that of *Archaeopteris*, where the number of spores is eight to sixteen (Arnold 1947). Perhaps *Stauropteris* may be regarded as a member of a series advancing in heterospory, possibly towards the evolution of seed habit from the terminal sporangium of the Psilophytales. It may also be a side line of development with no more recent representation.

Thus, morphologically, *Stauropteris* stands between the Psilophytales and the Zygopterideae on the one hand, and together with *Archaeopteris* between the Psilophytales and probably the Pteridospermae on the other. I therefore believe that *Stauropteris* deserves to be placed in a separate order of its own, which together with the Zygopterideae perhaps sprang up from the common ancestor the Psilophytales, but separated early from the Zygopterideae in the direction of the Pteridospermae. Has one of the much sought for intermediate groups in a phylogenetic system been stumbled on?

I am grateful to Dr H. H. Thomas, F.R.S., for the help he has given me in this work. Also my thanks are due to Professor T. M. Harris, F.R.S., for his suggestions and for allowing me use of the sections, drawings and notes on the megasporangia kindly prepared by Mr B. D. Harrison of Reading University.

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Description of plates 1 to 4

(Photographs by the author)

Plate 1

Figure 8. Transverse section of a petiole. The cortex is distinguishable into outer and inner parts. The xylem is H-shaped with two anterior (*al*) and two posterior lobes (*pl*). *Sl. no.* 483. (Magn. ×31.)

Figure 9. Shows the second phase in the branching of a branch of the Ist order. The two lobes of xylem on the right side have fused to form a broad plate which carries the first outer protoxylem of the daughter stele. The main protoxylem has given out an aphlebia trace (*a*). *Sl. No.* 484. (Magn. ×72.)

Figure 10. A joint-trace-bar (*b*) has formed in a petiolar stele. The outer protoxylems on the bar have already bifurcated. *Sl. no.* 491. (Magn. ×59.)

Figure 11. The same joint-trace-bar seen at a higher level. It has separated from the petiolar stele and has itself divided by equal dichotomy (see arrow) into two daughter steles with four protoxylems (*px*) each. The petiolar stele has again become tetrarch. *Sl. no.* 490. (Magn. ×59.)

Figure 12. A joint-trace-bar (*b*) formed by a branch of the Ist order in the process of detachment. Inner side of the bar carries two and outer side only one protoxylem at each end. *a*, aphlebia trace. *Sl. no.* 456. (Magn. ×66.)

Figure 13. A microspore showing triradiate mark, from a microsporangium assigned to *S. burntislandica*. *Sl. no.* 507. (Magn. ×396.)

Plate 2

Figure 14. A joint-trace-bar (*b*) in a branch of the Ist order. The bar carries only one protoxylem at each end on the outer side. *a*, aphlebiae traces. *Sl. no.* 433. (Magn. ×33.)

Figure 15. A branch of the IInd order which has produced two daughter steles still enclosed in its cortex. One aphlebia (*a*) showing bifurcation. *Sl. no.* 486. (Magn. ×49.)

Figure 16. A branch with a triarch (*px*) and triangular stele. *Sl. no.* 484. (Magn. ×79.)

Figure 17. Shows immediate bifurcation in a lateral branch (Vth order) produced by an axis 0·32 mm in diameter (IVth order). *Sl. no.* 141. (Magn. × 123.)

Figure 18. A branch of the IVth order (0·32 mm) giving out opposite pairs of daughter branches (Vth order). On the top right-hand side forking of the daughter branches is commencing. *Sl. no.* 463. (Magn. ×79.)

Figure 19. A stoma from a minute branch seen in surface view. (Magn. ×814.)

PLATE 3

FIGURE 20. A branch of the IIIrd order (0·5 mm) giving out two branches of IVth order and a pair of aphlebia traces (*a*). The triarch stele of the main branch has disintegrated into three monarch steles, two of which pass out into daughter branches (IV). *Sl. no.* 471. (Magn. × 70.)

FIGURE 21. Bifurcation (VI) in a branch of 0·16 mm size (Vth order). Sections of other branches of different orders are also seen in the photograph. *Sl. no.* 484. (Magn. × 94.)

FIGURE 22. Transverse section through one of the penultimate branches (Vth order) of the frond showing big epidermal and cortical cells and a delicate vascular strand in the centre. *Sl. no.* 459. (Magn. × 374.)

FIGURE 23. Transverse section through a microsporangium assigned to *S. burntislandica*. The wall of the sporangium has large uniformly thickened cells and a stomium (*st*). *Sl. no.* 506. (Magn. × 95.)

FIGURE 24. One megasporangium (= *Bensonites fusiformis*) in longitudinal section, showing the cellular body (*sp*) at the lower end, and sporangial cavity (*spc*) with one intact megaspore (*m*) at the upper end. The megaspore shows a triradiate mark. *Sl. no.* 500. (Magn. × 78.)

FIGURE 25. A transverse section through the sporangial cavity showing U-shaped thickened cell walls. *Sl. no.* 505. (Magn. × 106.)

PLATE 4

FIGURE 26. 0·16 mm penultimate branch bearing a megasporangium (*sp*) on one of its very short lateral branches. The former shows a stoma (*s*) which is identical with the stoma shown in figure 19. *Sl. no.* 499. (Magn. × 55.)

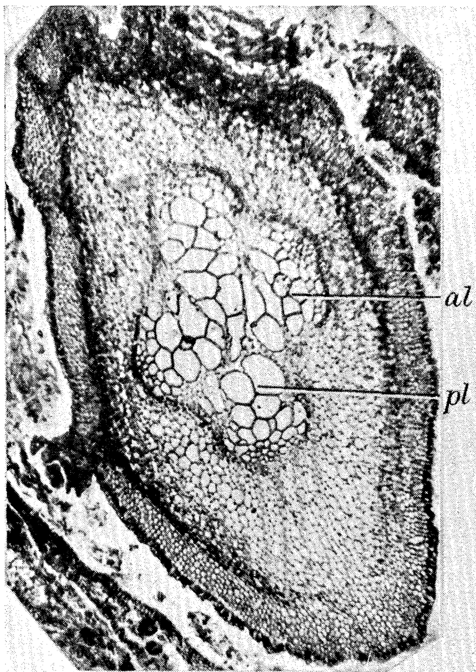
FIGURE 27. A 0·16 mm branch (V) of *S. burntislandica* seen in connexion with the megasporangium (*sp*) through its lateral branch (VI) which shows a tracheid (*tr*). *Sl. no.* 503. (Magn. × 97.)

FIGURE 28. Two megasporangia (*sp*) borne on a single stalk (*sk*); *spb*, spore bag. (Magn. × 100.)

FIGURE 29. Oblique longitudinal section through a megasporangium showing the cellular body (*sp*), sporangial cavity (*spc*), spore bag (*spb*) and two megaspores. In one megaspore (*m*) almost the entire cuticle is seen while the other shows a spore print (*p*) with a few bits of cuticle attached. (Magn. × 149.)

FIGURE 30. The megasporangium which is drawn in serial sections in figure 6. Two megaspores (*m*) show bits of cuticle of the wall. (Magn. × 142.)

FIGURE 31. Spiral and scalariform thickenings in the tracheids of a petiole. *Sl. no.* 488. (Magn. × 140.)



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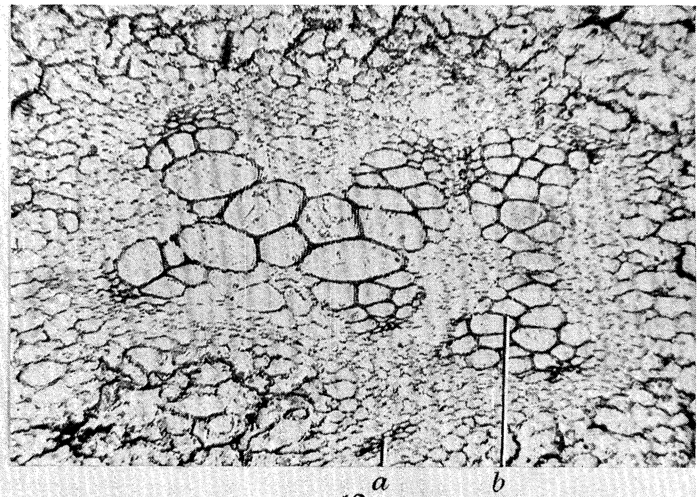

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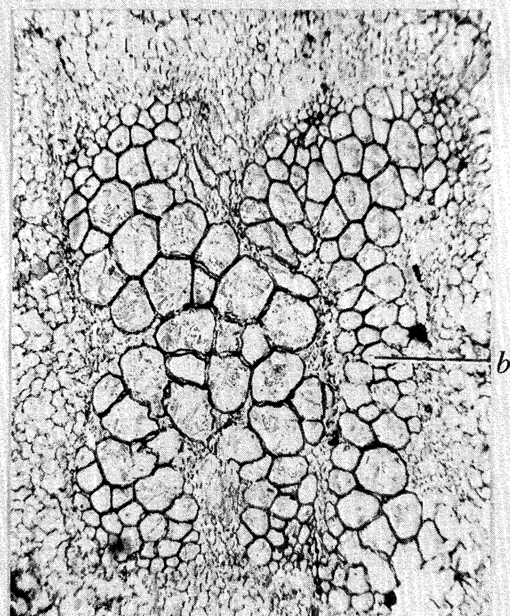

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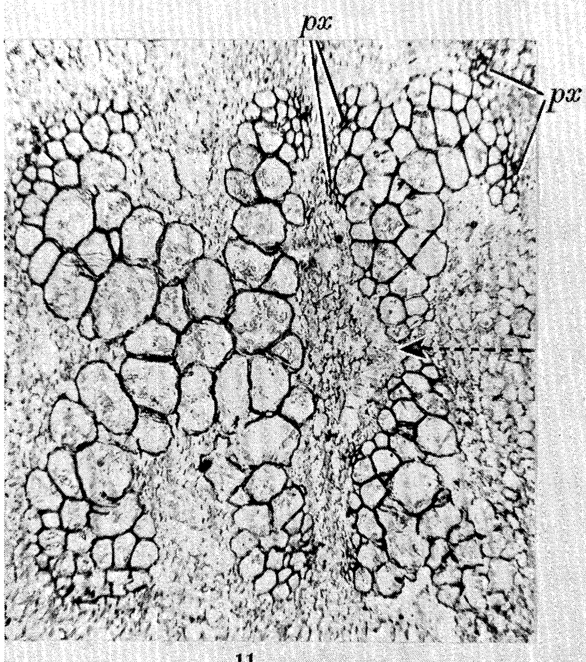

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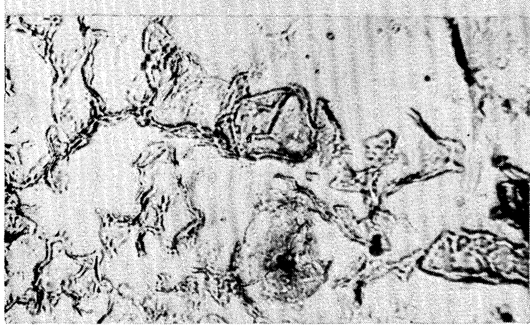

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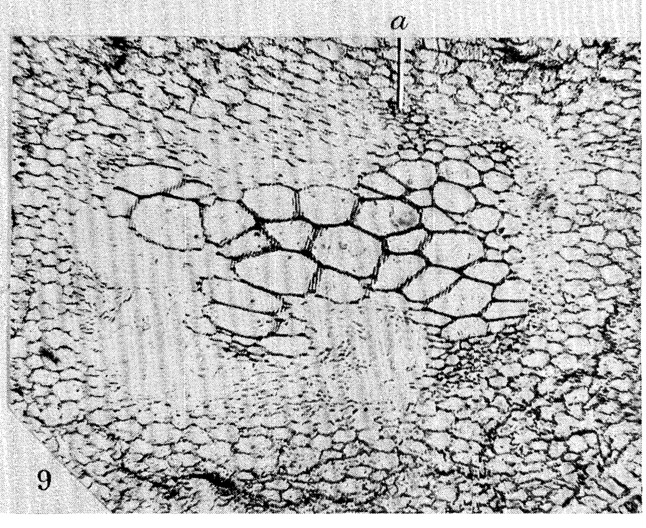

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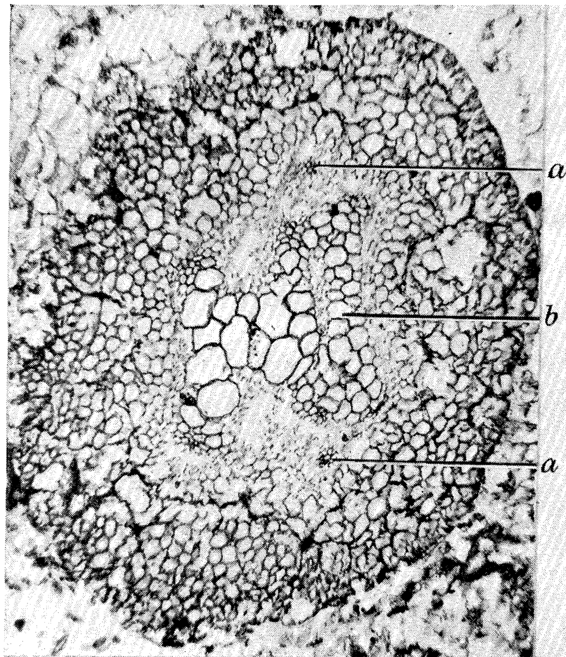

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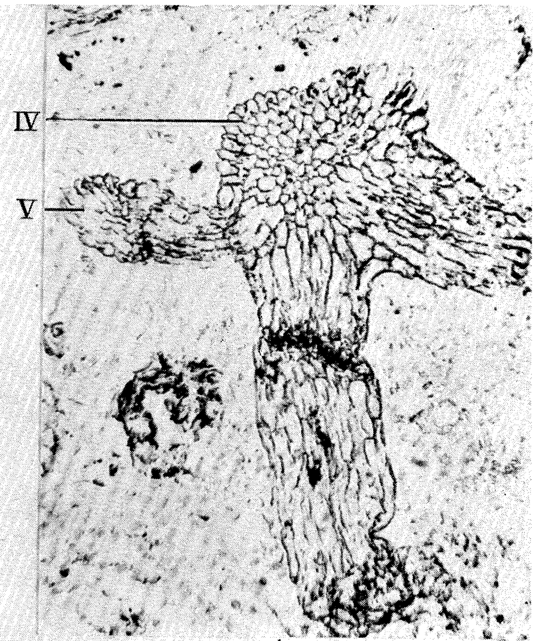

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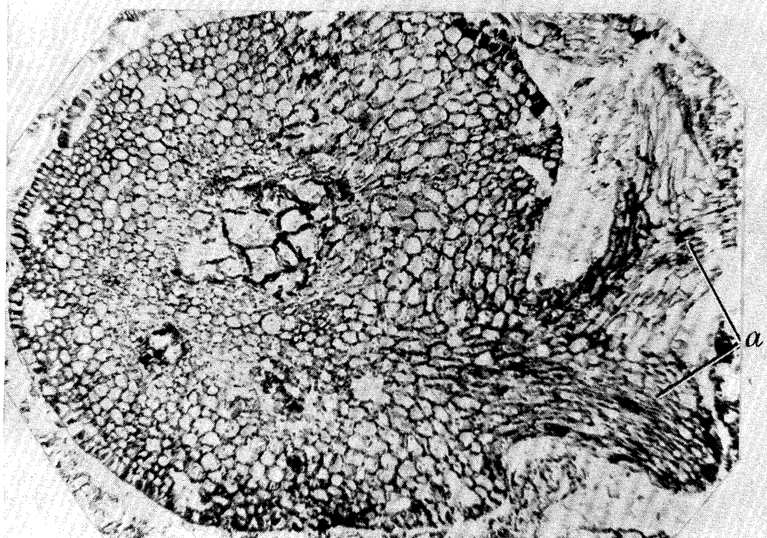

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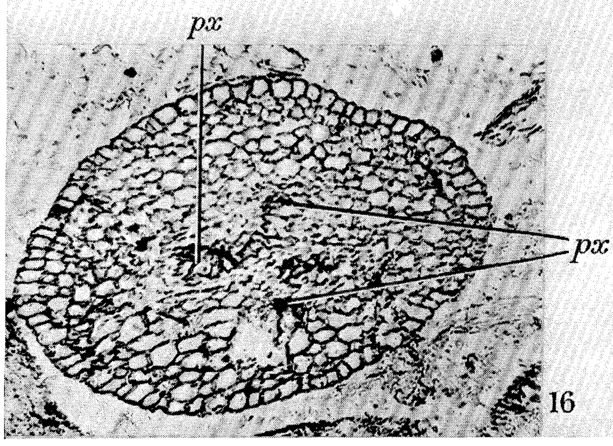

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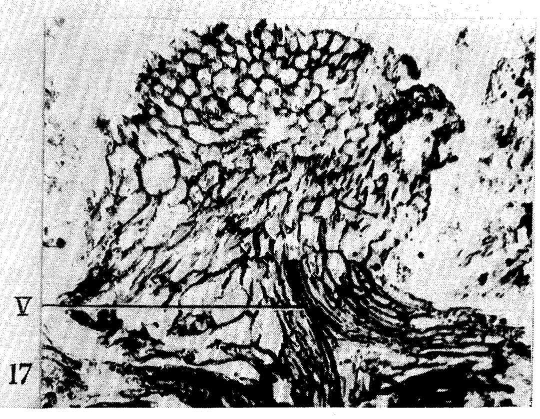

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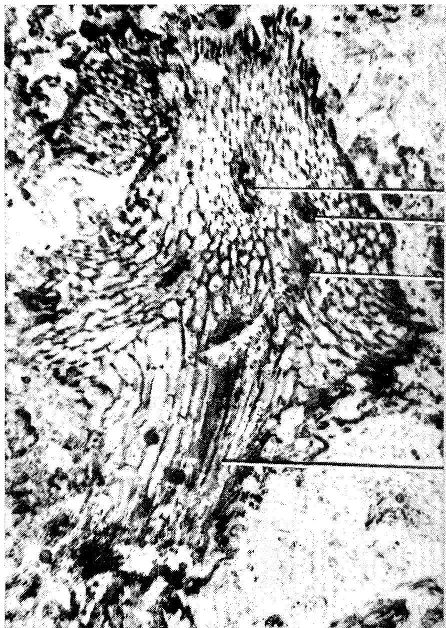

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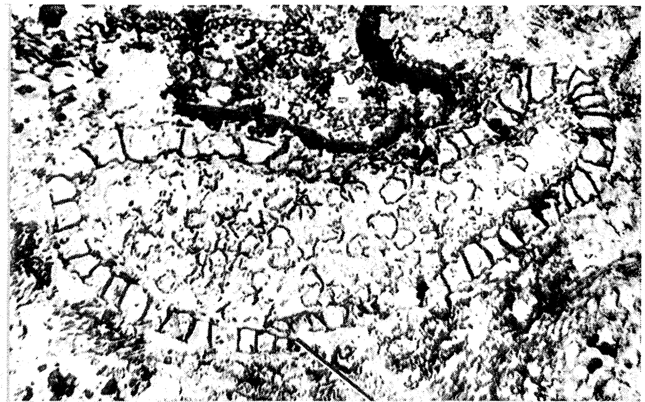

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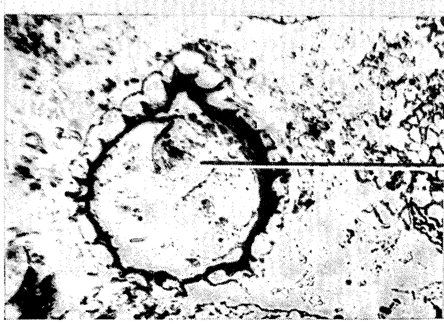

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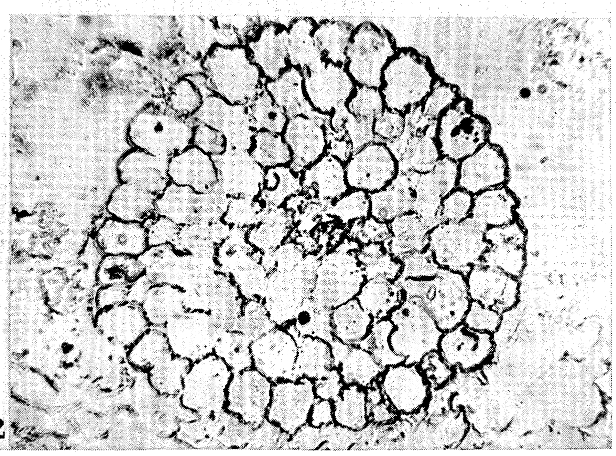

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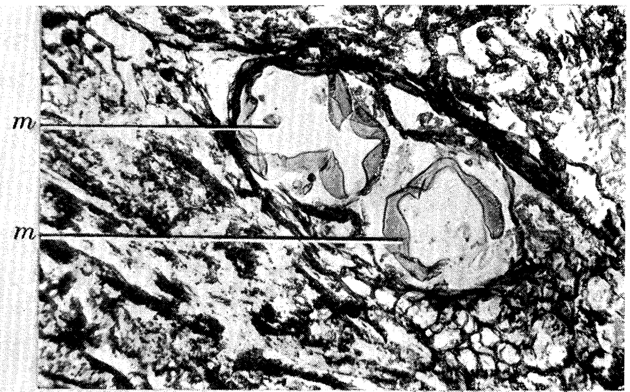

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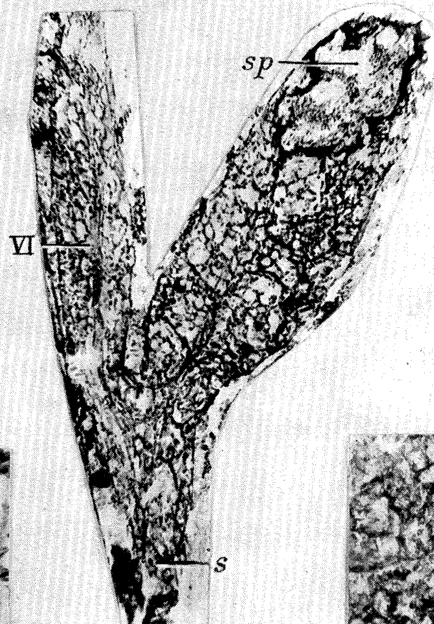

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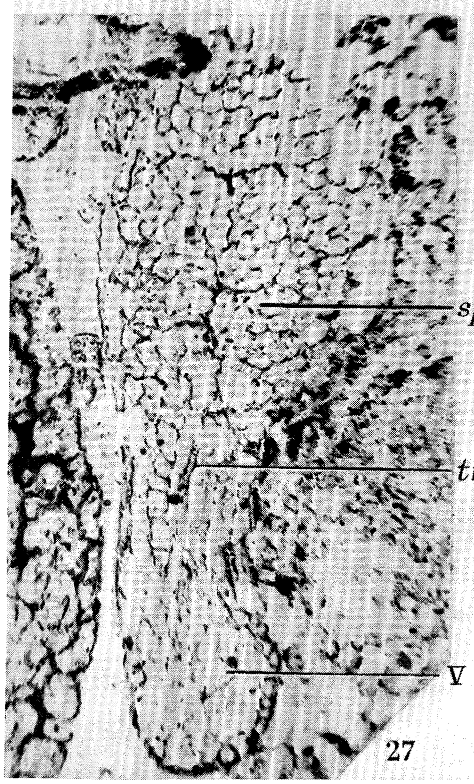

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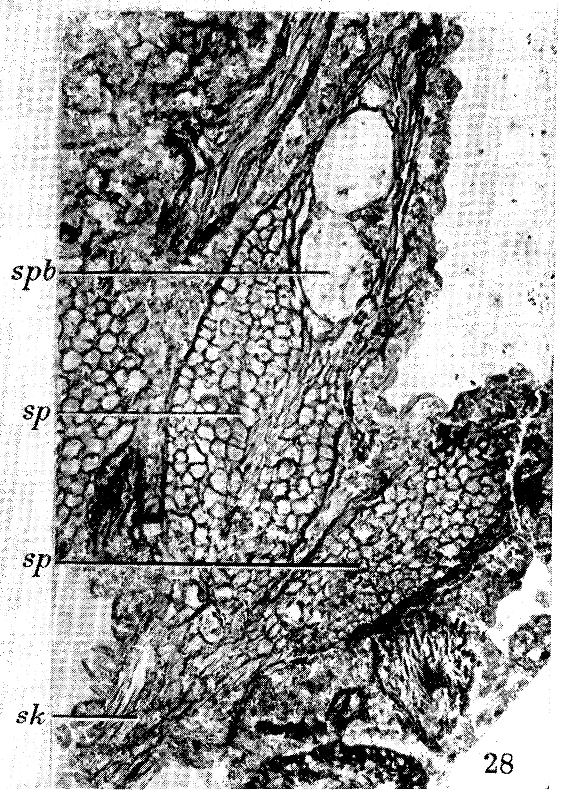

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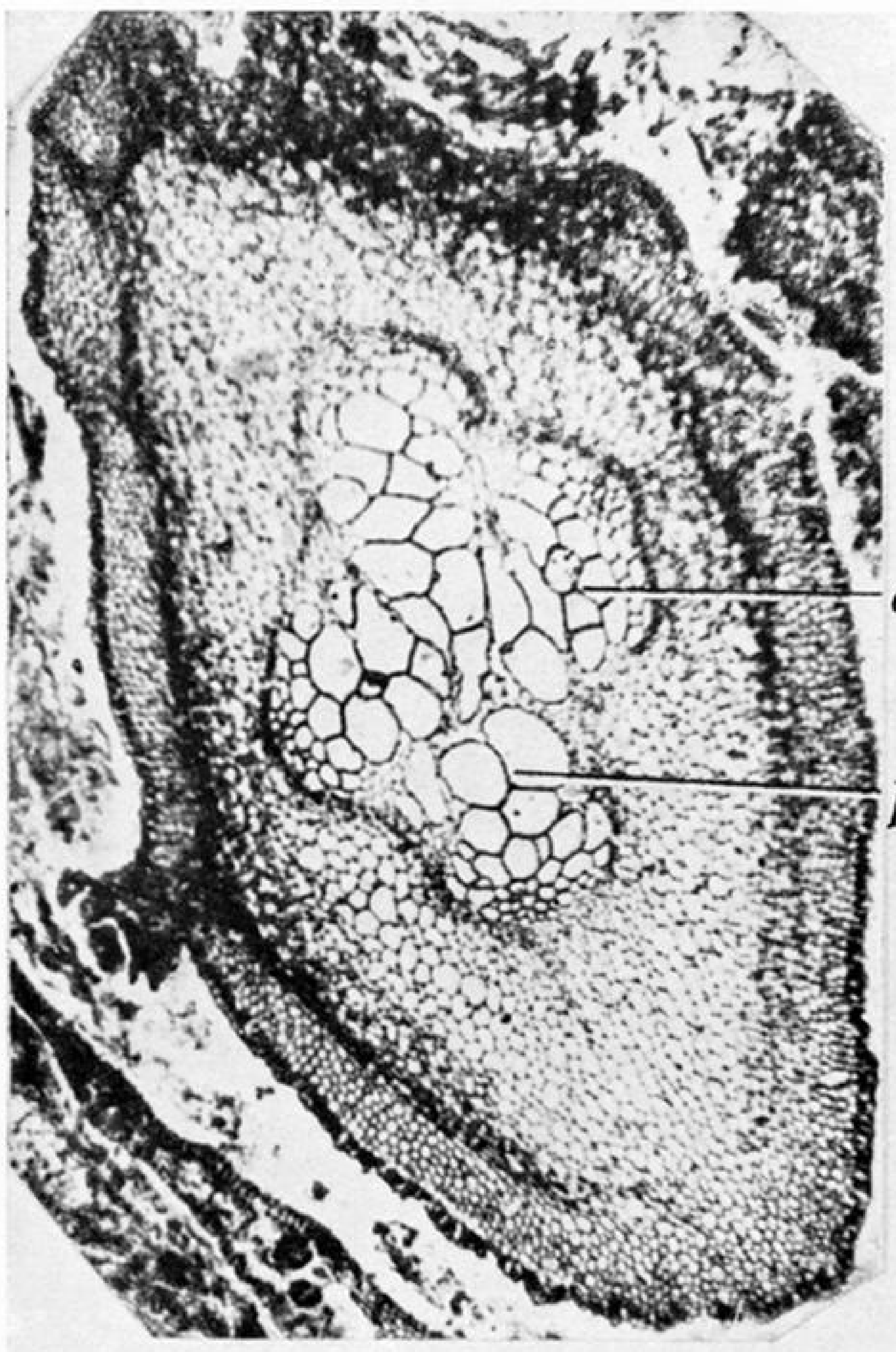

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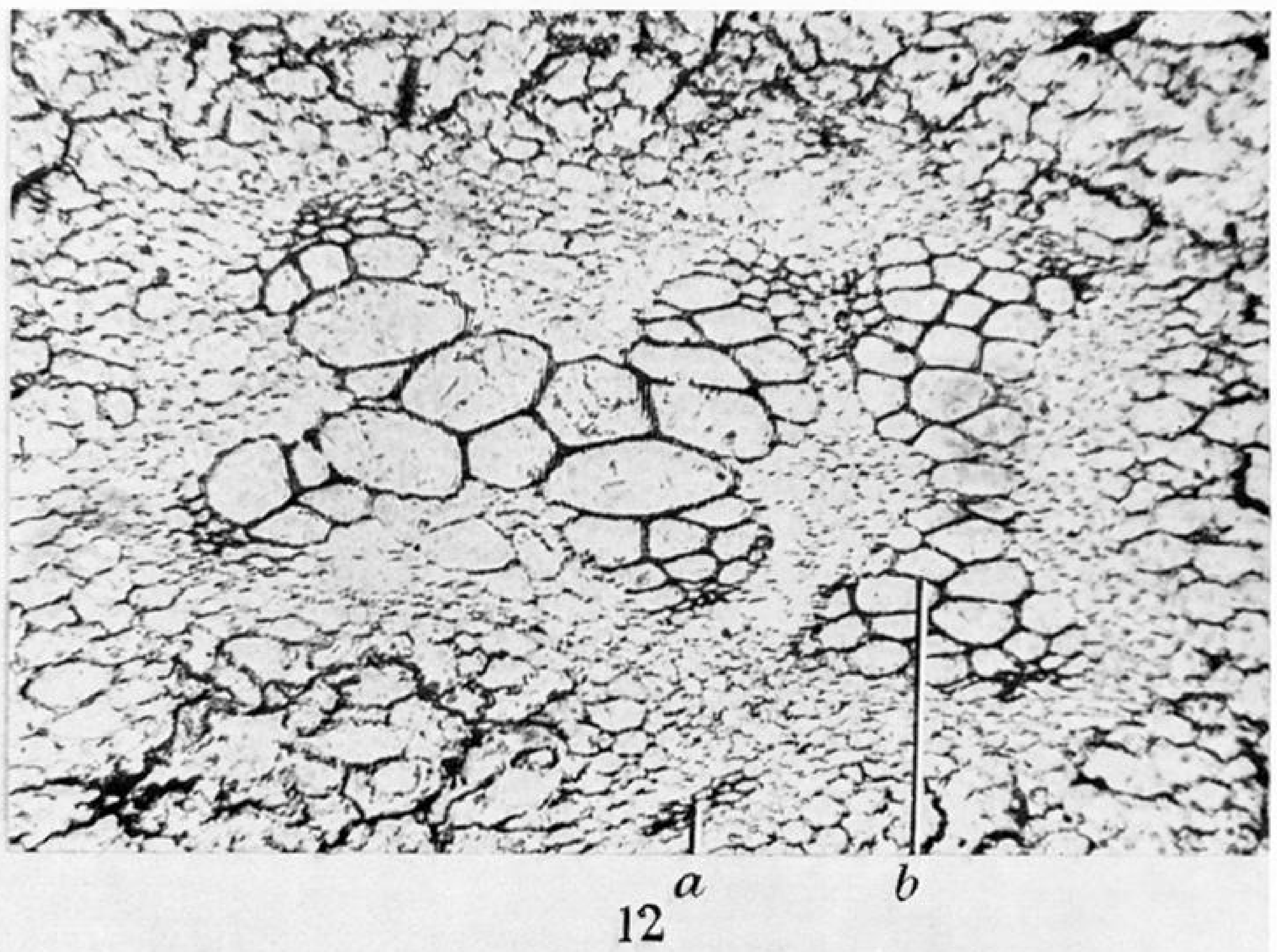

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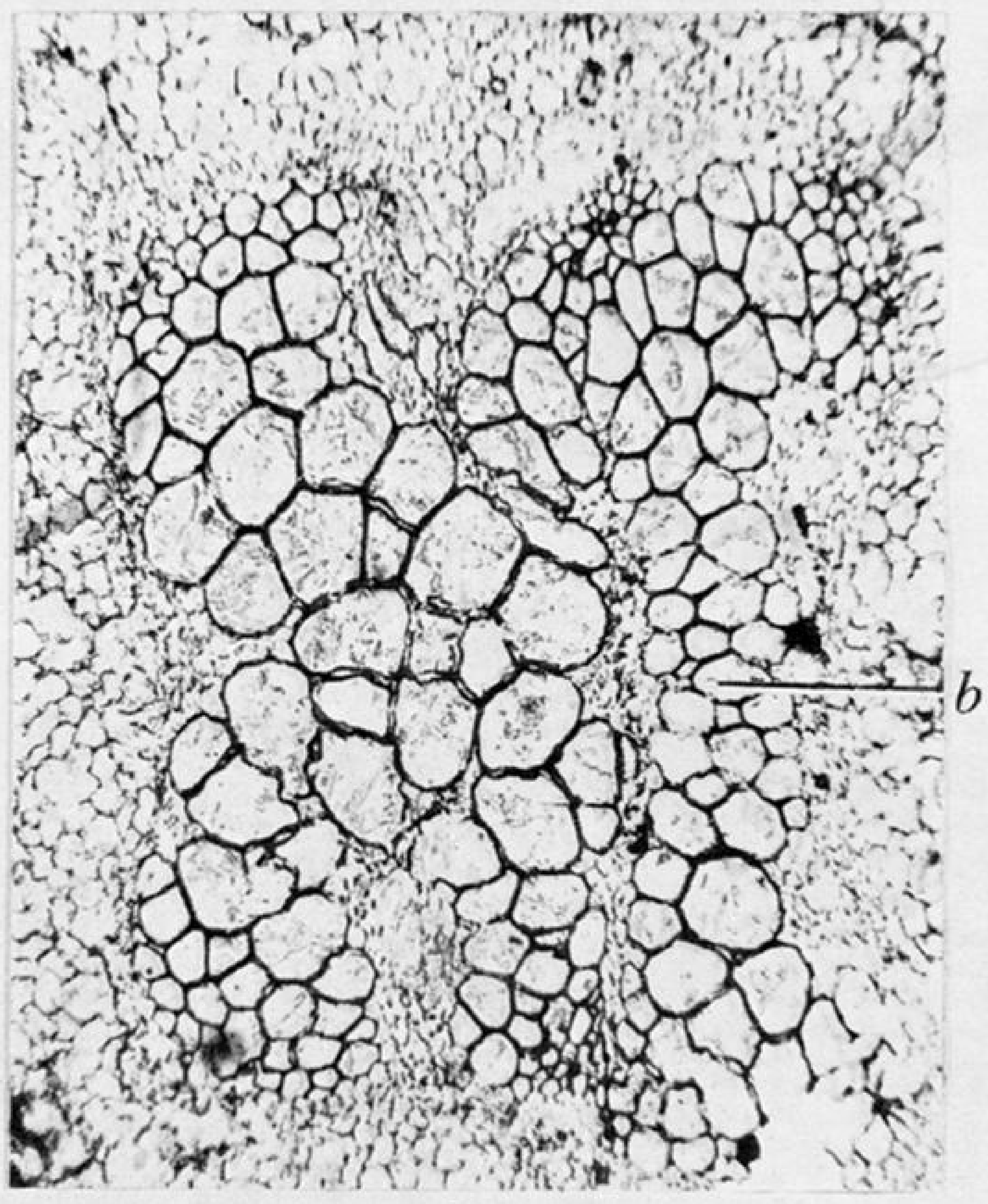

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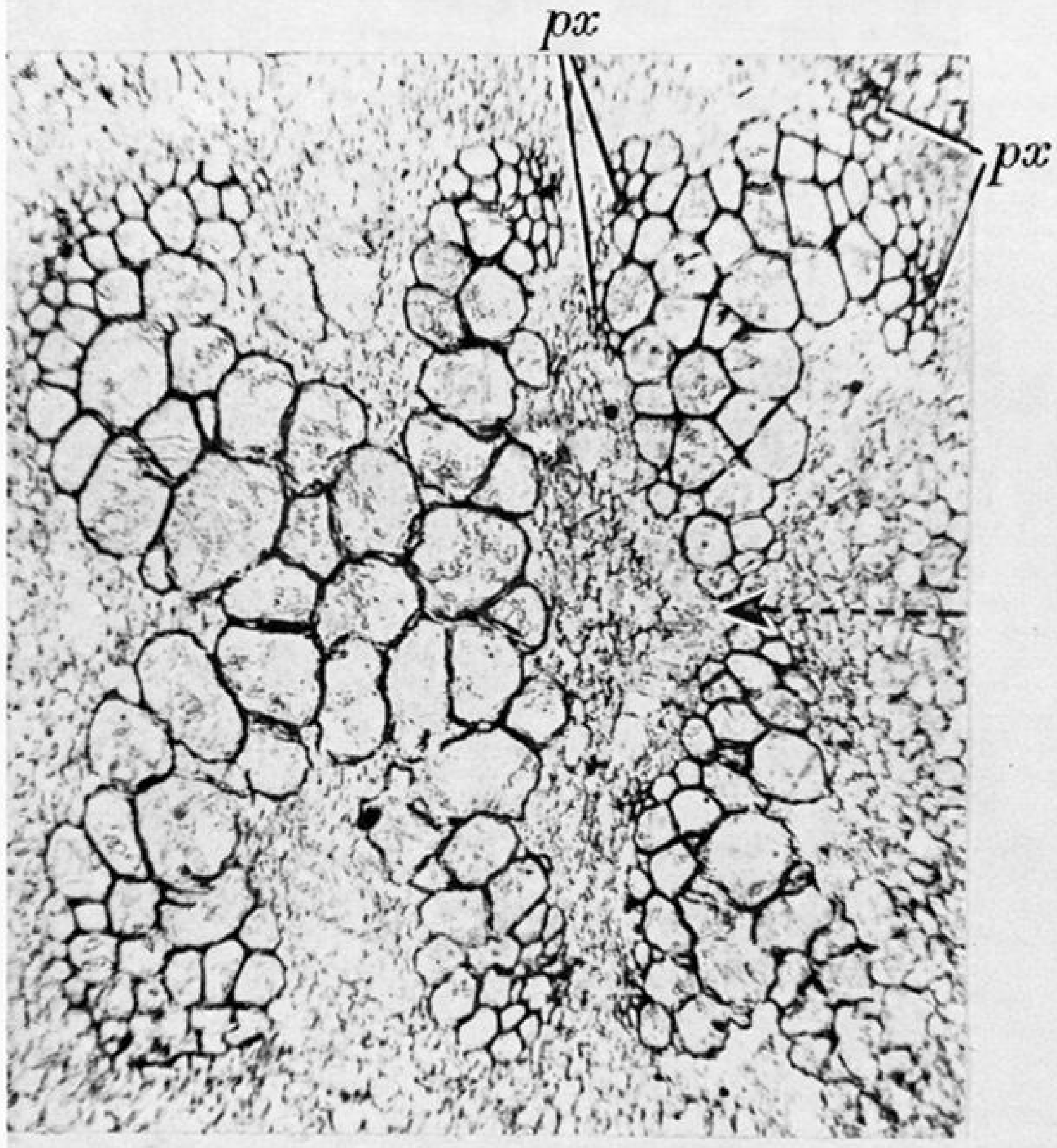

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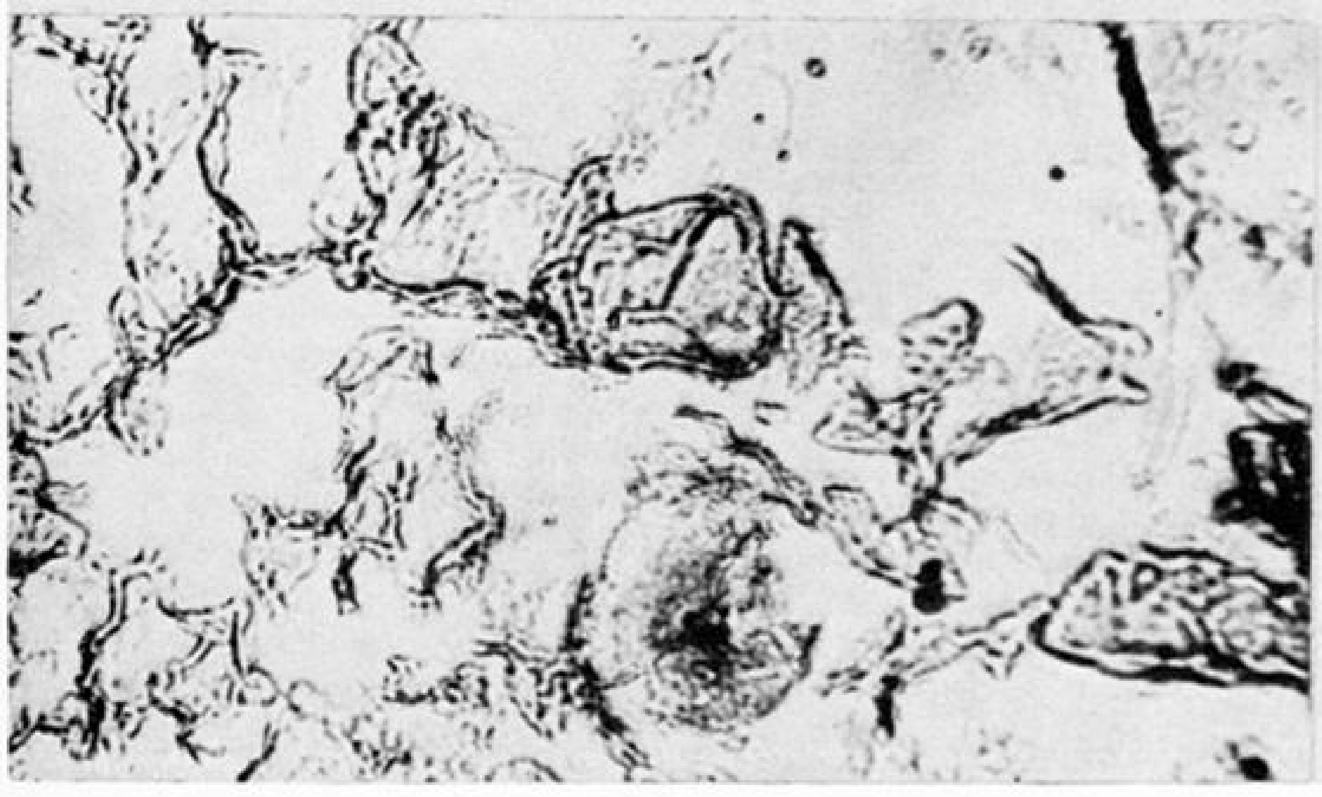

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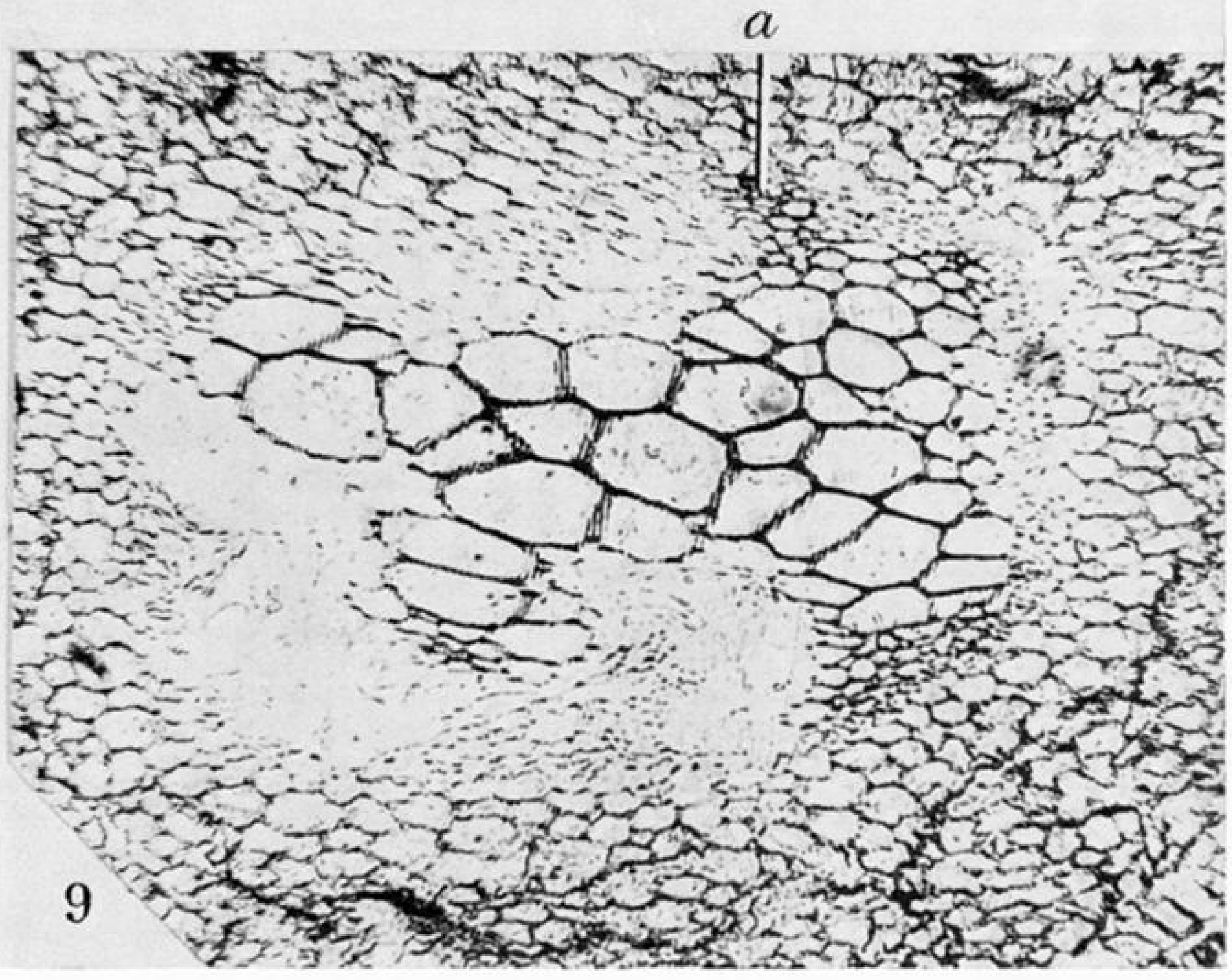

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PLATE 1

FIGURE 8. Transverse section of a petiole. The cortex is distinguishable into outer and inner parts. The xylem is H-shaped with two anterior (*al*) and two posterior lobes (*pl*). *Sl. no.* 483. (Magn. ×31.)

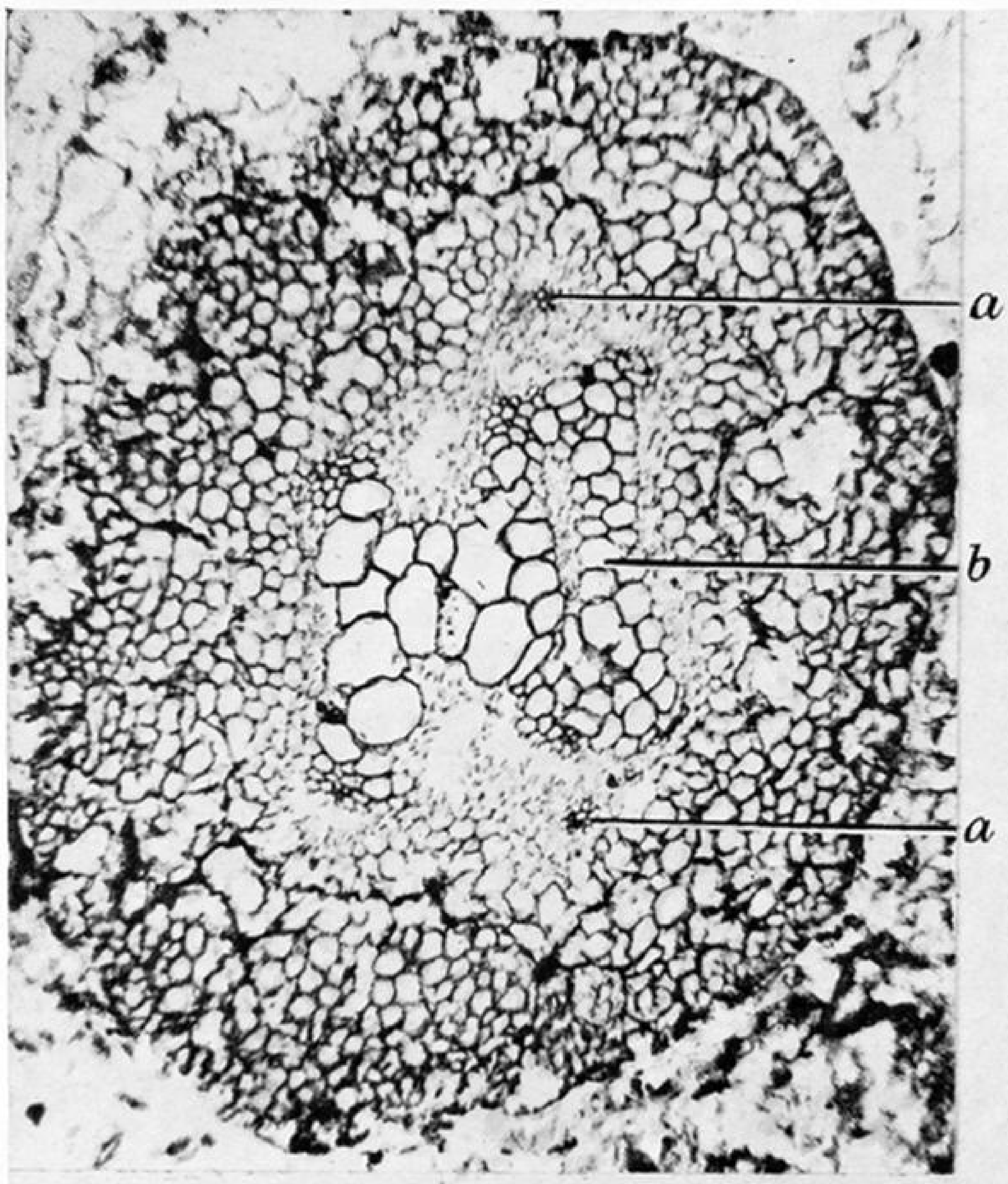
FIGURE 9. Shows the second phase in the branching of a branch of the Ist order. The two lobes of xylem on the right side have fused to form a broad plate which carries the first outer protoxylem of the daughter stele. The main protoxylem has given out an aphlebia trace (*a*). *Sl. No.* 484. (Magn. ×72.)

FIGURE 10. A joint-trace-bar (*b*) has formed in a petiolar stele. The outer protoxylems on the bar have already bifurcated. *Sl. no.* 491. (Magn. ×59.)

FIGURE 11. The same joint-trace-bar seen at a higher level. It has separated from the petiolar stele and has itself divided by equal dichotomy (see arrow) into two daughter steles with four protoxylems (*px*) each. The petiolar stele has again become tetrarch. *Sl. no.* 490. (Magn. ×59.)

FIGURE 12. A joint-trace-bar (*b*) formed by a branch of the Ist order in the process of detachment. Inner side of the bar carries two and outer side only one protoxylem at each end. *a*, aphlebia trace. *Sl. no.* 456. (Magn. ×66.)

FIGURE 13. A microspore showing triradiate mark, from a microsporangium assigned to *S. burnt-islandica*. *Sl. no.* 507. (Magn. ×396.)



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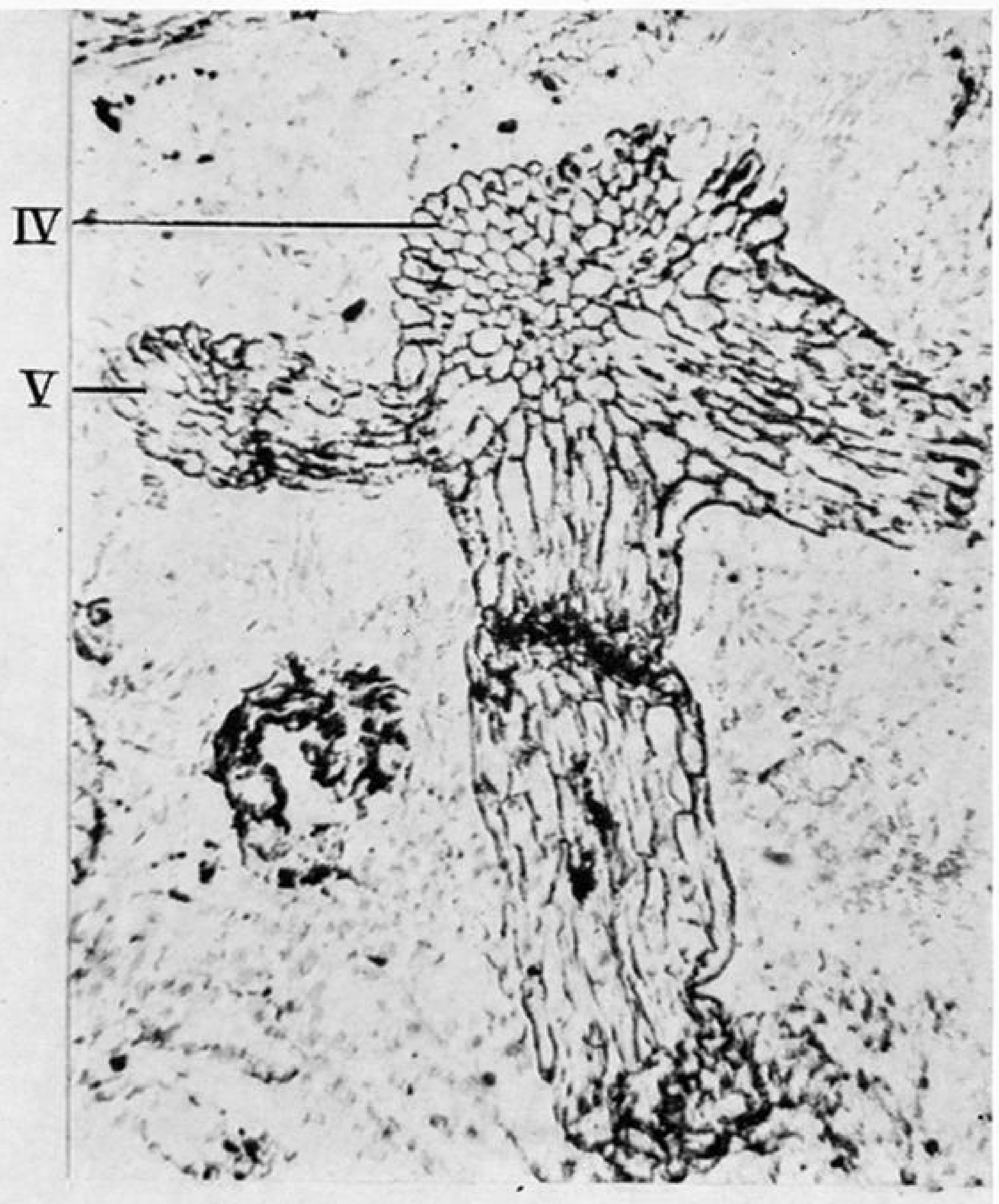

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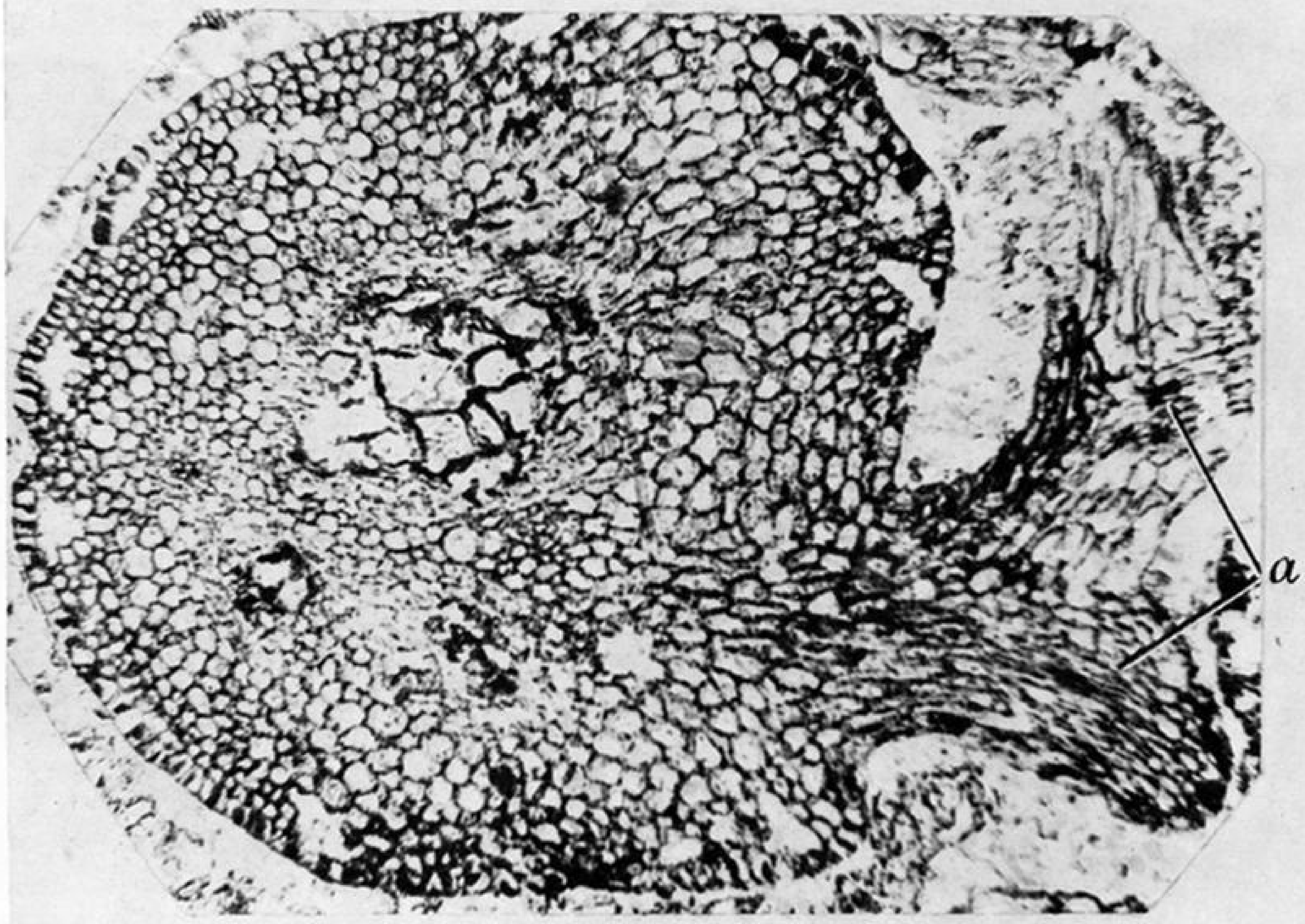

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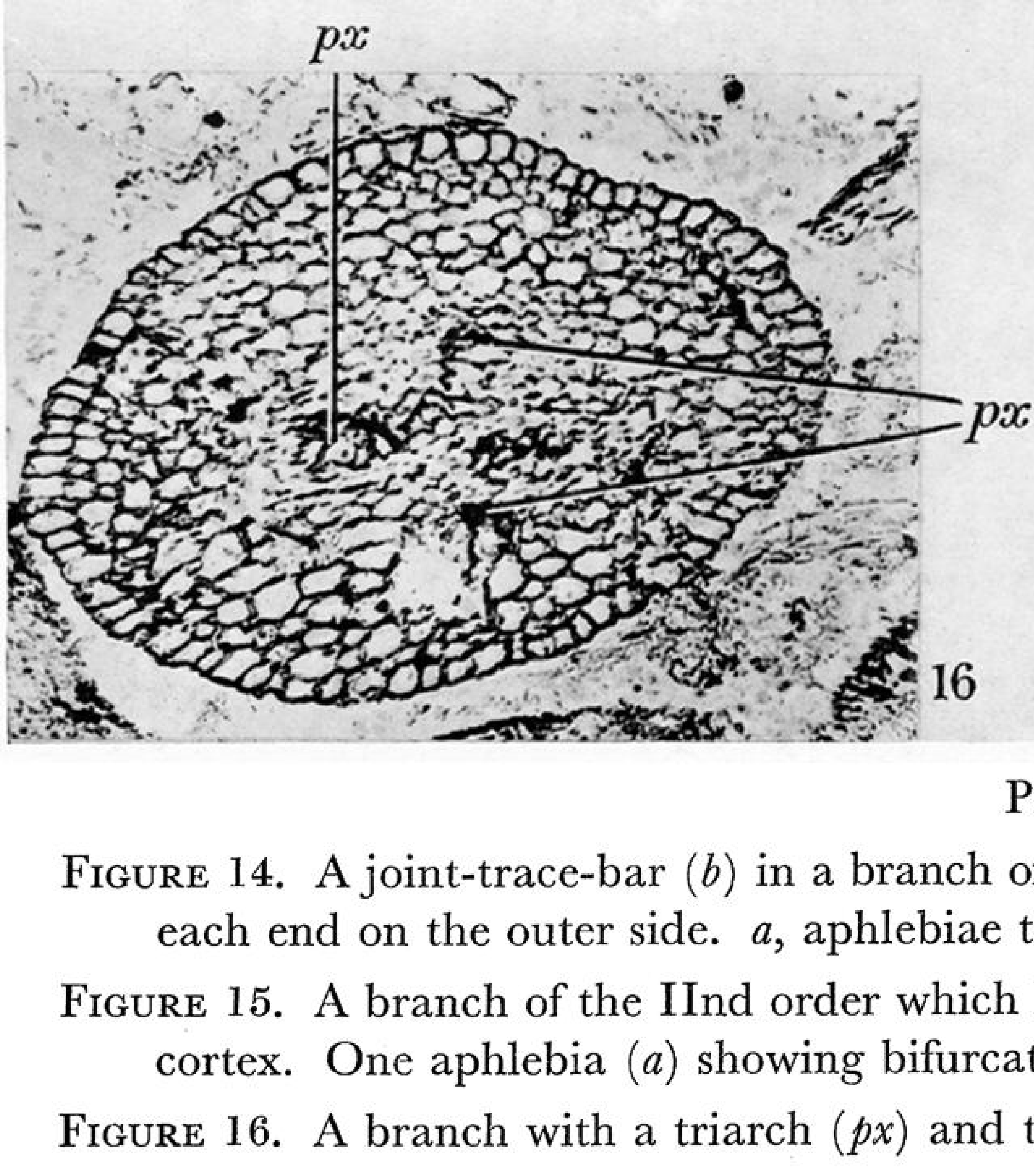

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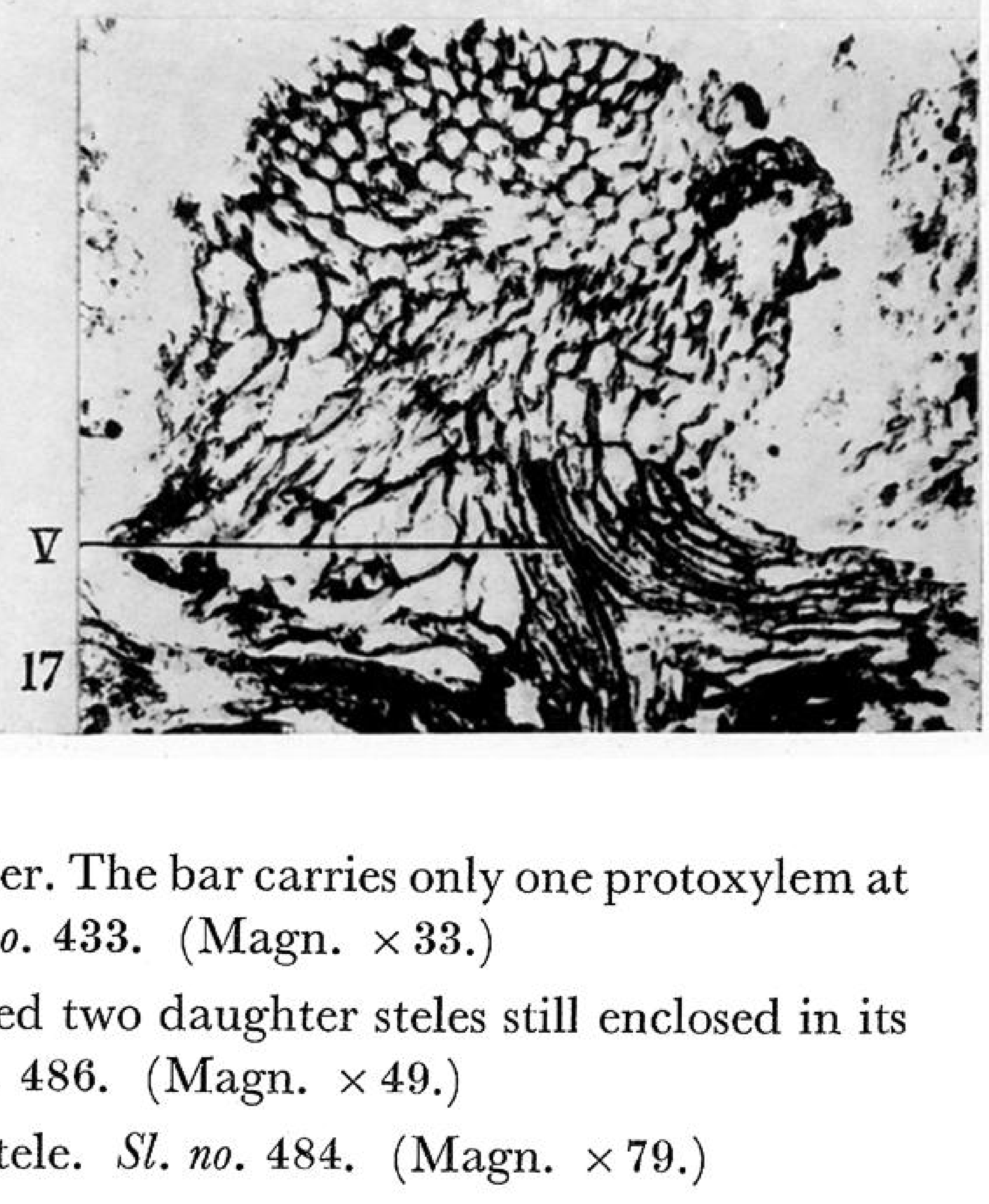

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Plate 2

Figure 14. A joint-trace-bar (*b*) in a branch of the Ist order. The bar carries only one protoxylem at each end on the outer side. *a*, aphlebiae traces. *Sl. no.* 433. (Magn. ×33.)

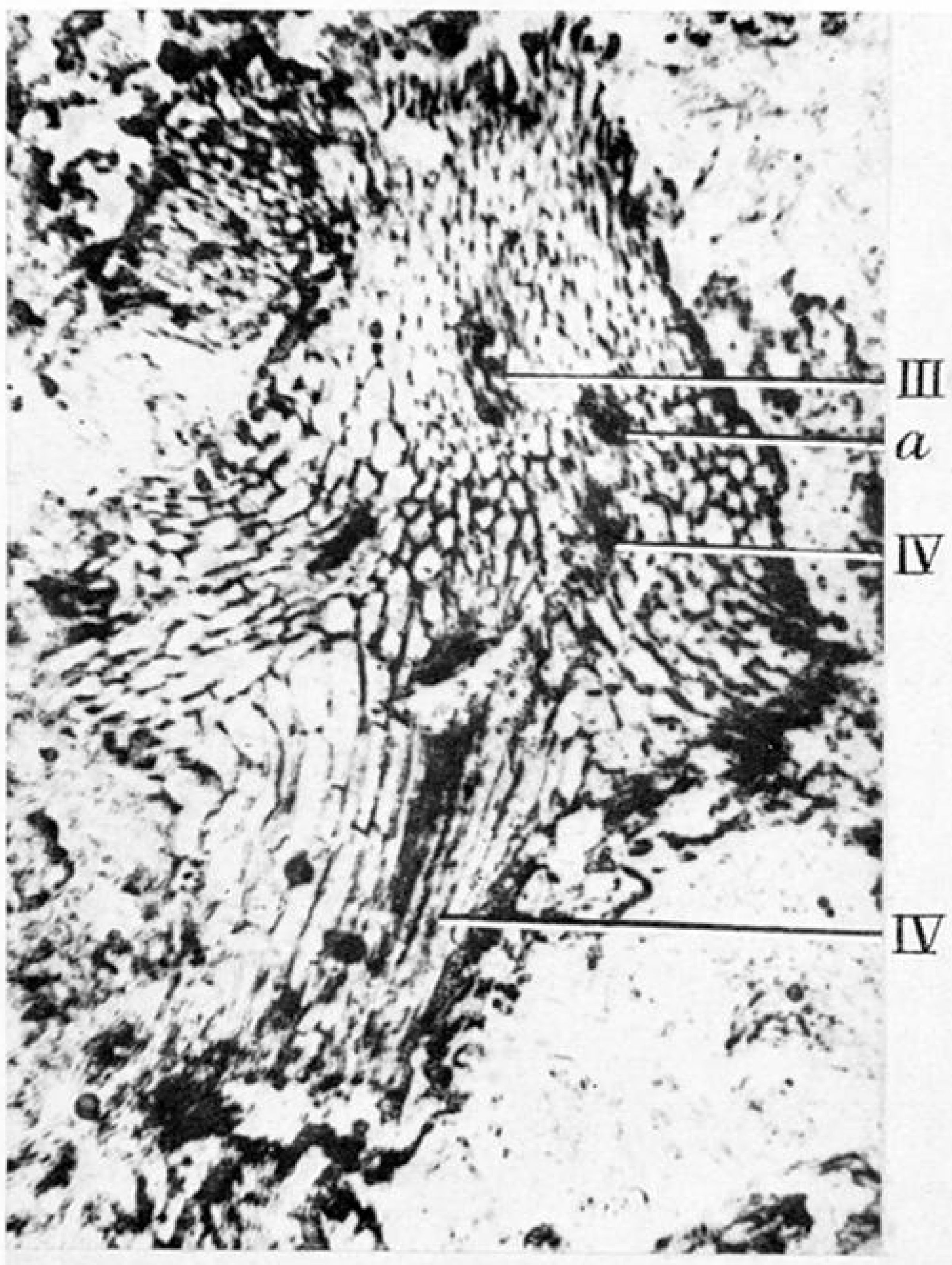
Figure 15. A branch of the IInd order which has produced two daughter steles still enclosed in its cortex. One aphlebia (*a*) showing bifurcation. *Sl. no.* 486. (Magn. ×49.)

Figure 16. A branch with a triarch (*px*) and triangular stele. *Sl. no.* 484. (Magn. ×79.)

Figure 17. Shows immediate bifurcation in a lateral branch (Vth order) produced by an axis 0·32 mm in diameter (IVth order). *Sl. no.* 141. (Magn. × 123.)

Figure 18. A branch of the IVth order (0·32 mm) giving out opposite pairs of daughter branches (Vth order). On the top right-hand side forking of the daughter branches is commencing. *Sl. no.* 463. (Magn. ×79.)

Figure 19. A stoma from a minute branch seen in surface view. (Magn. ×814.)



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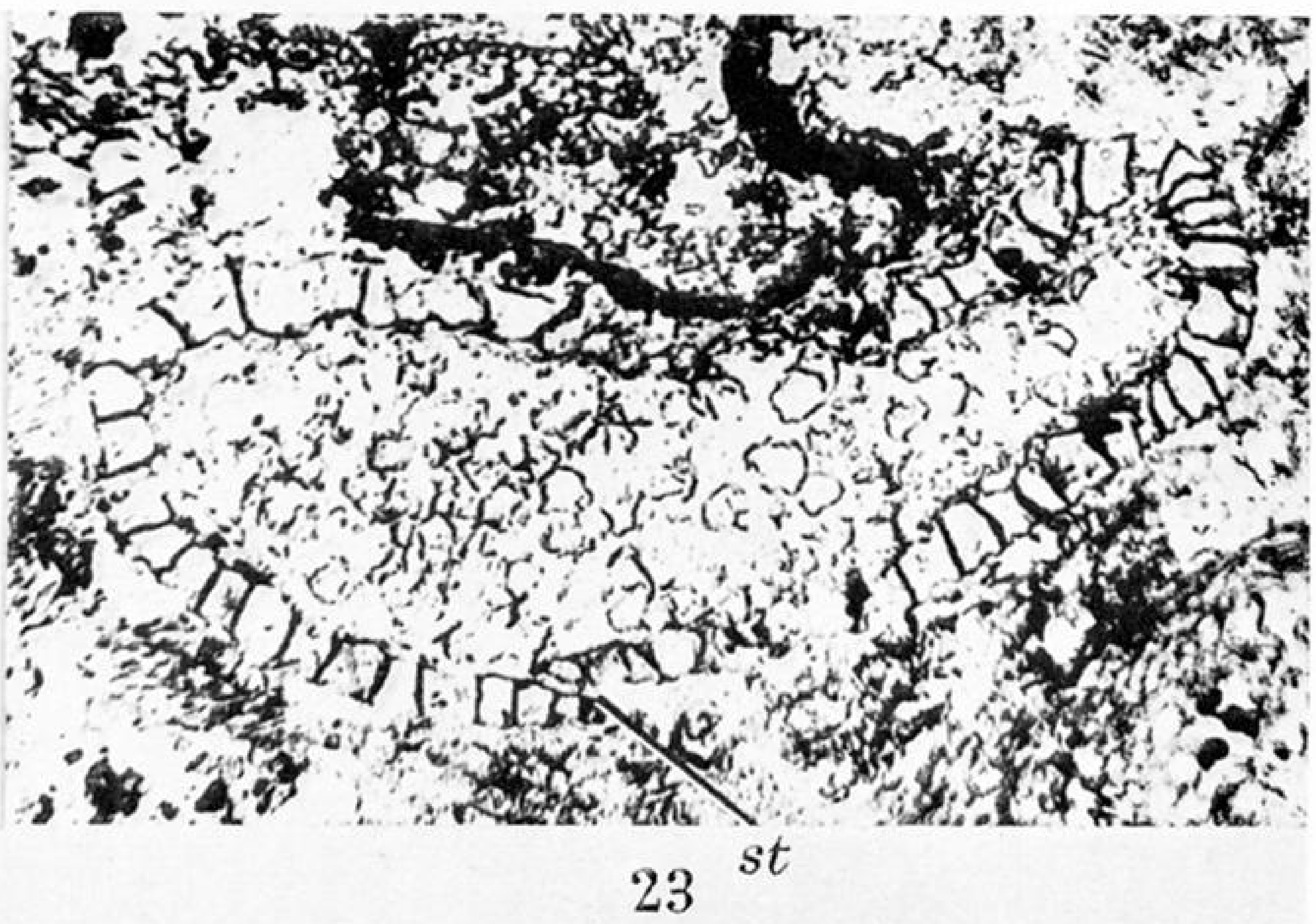

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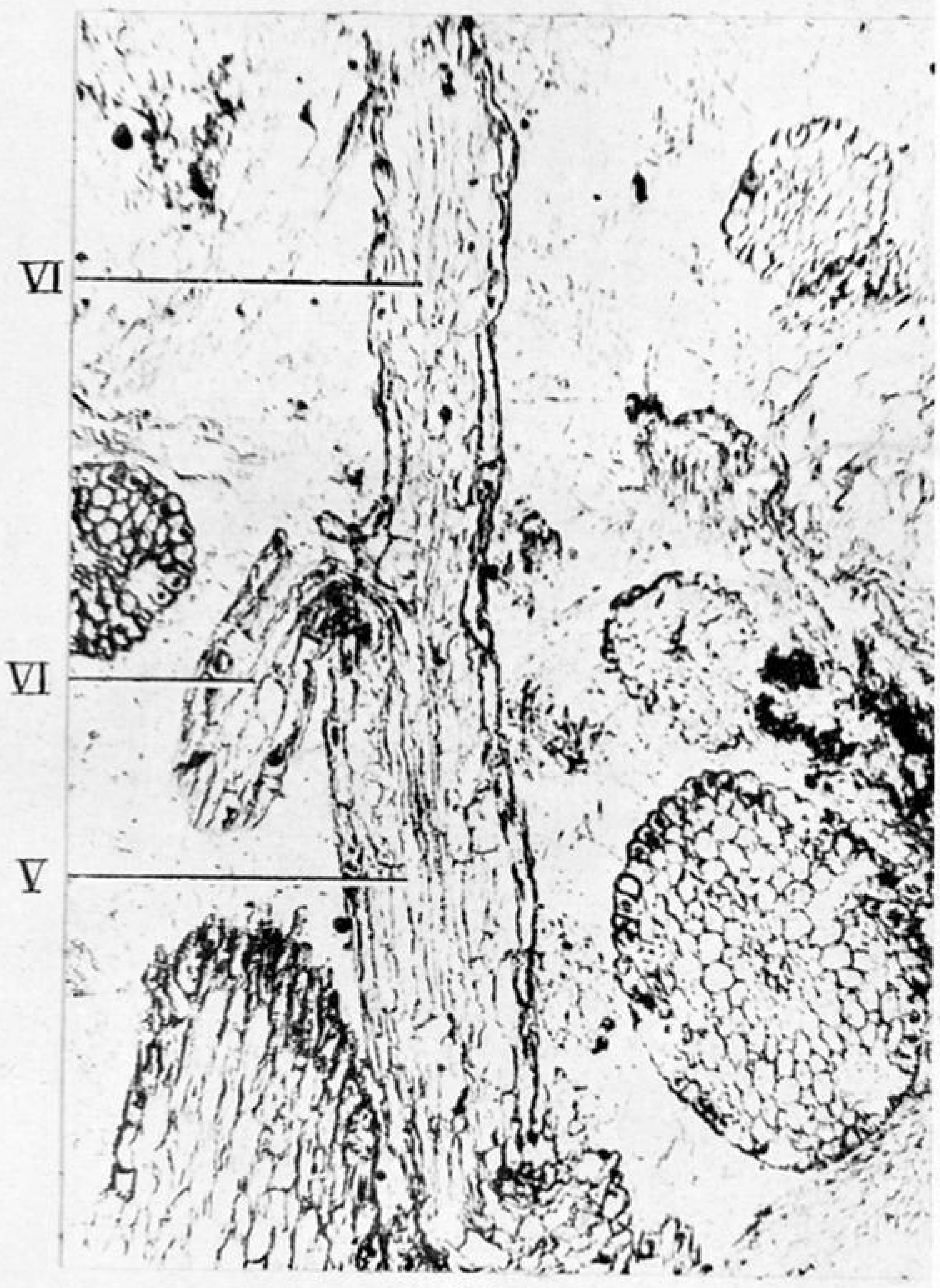

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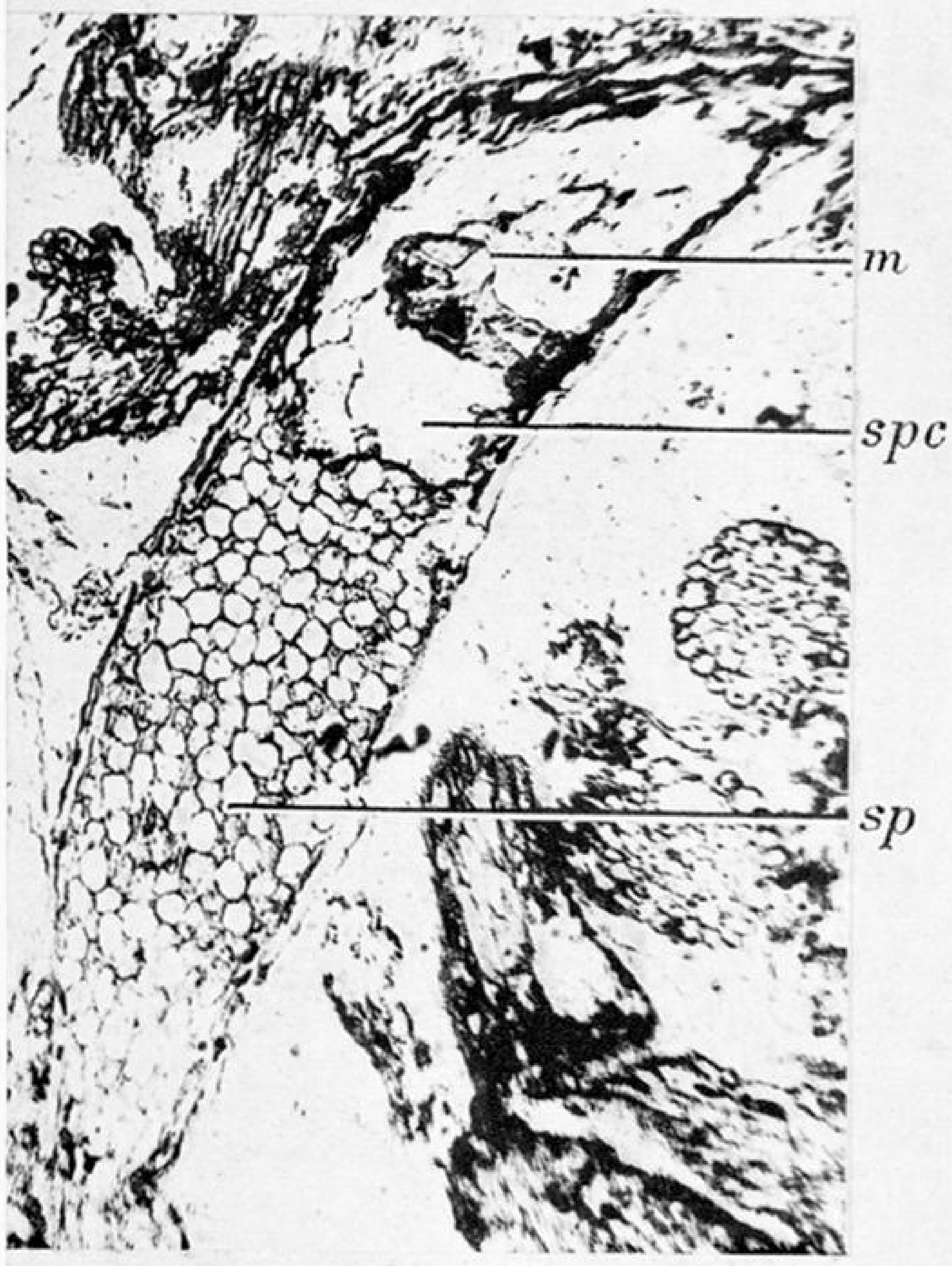

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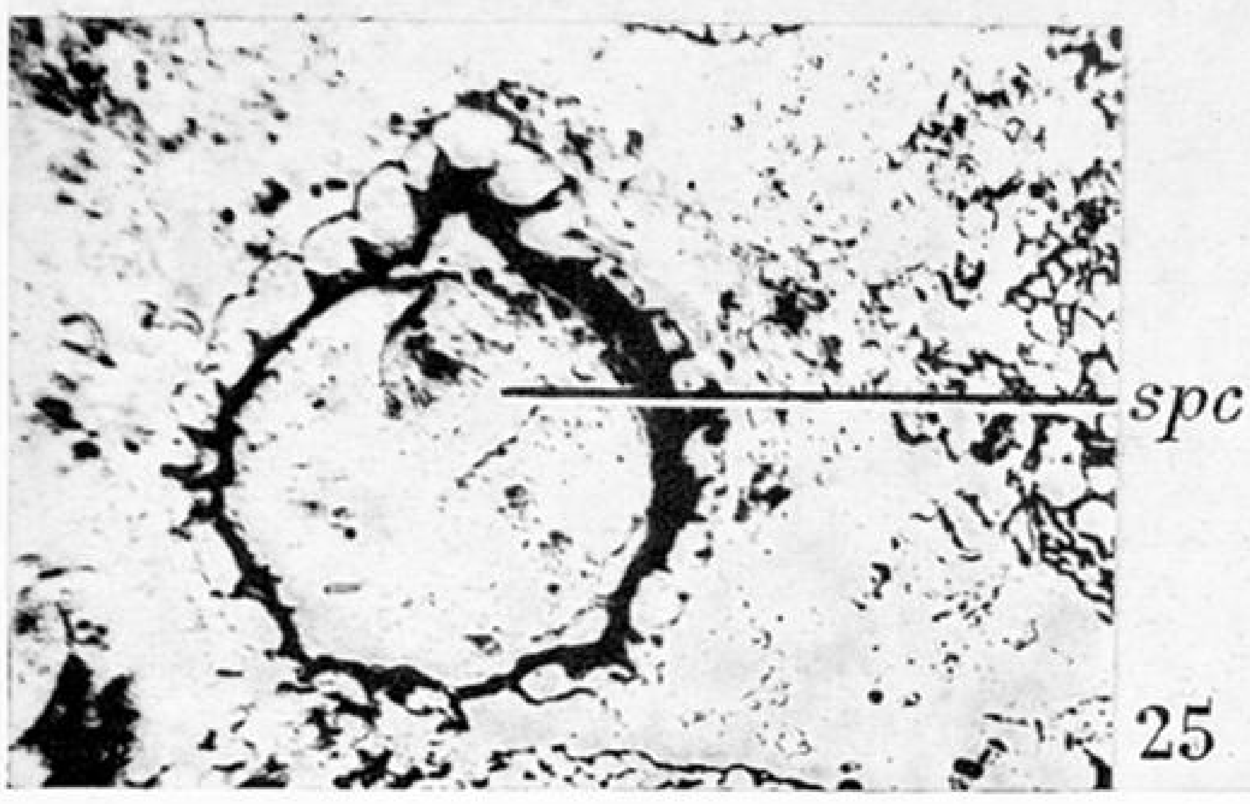

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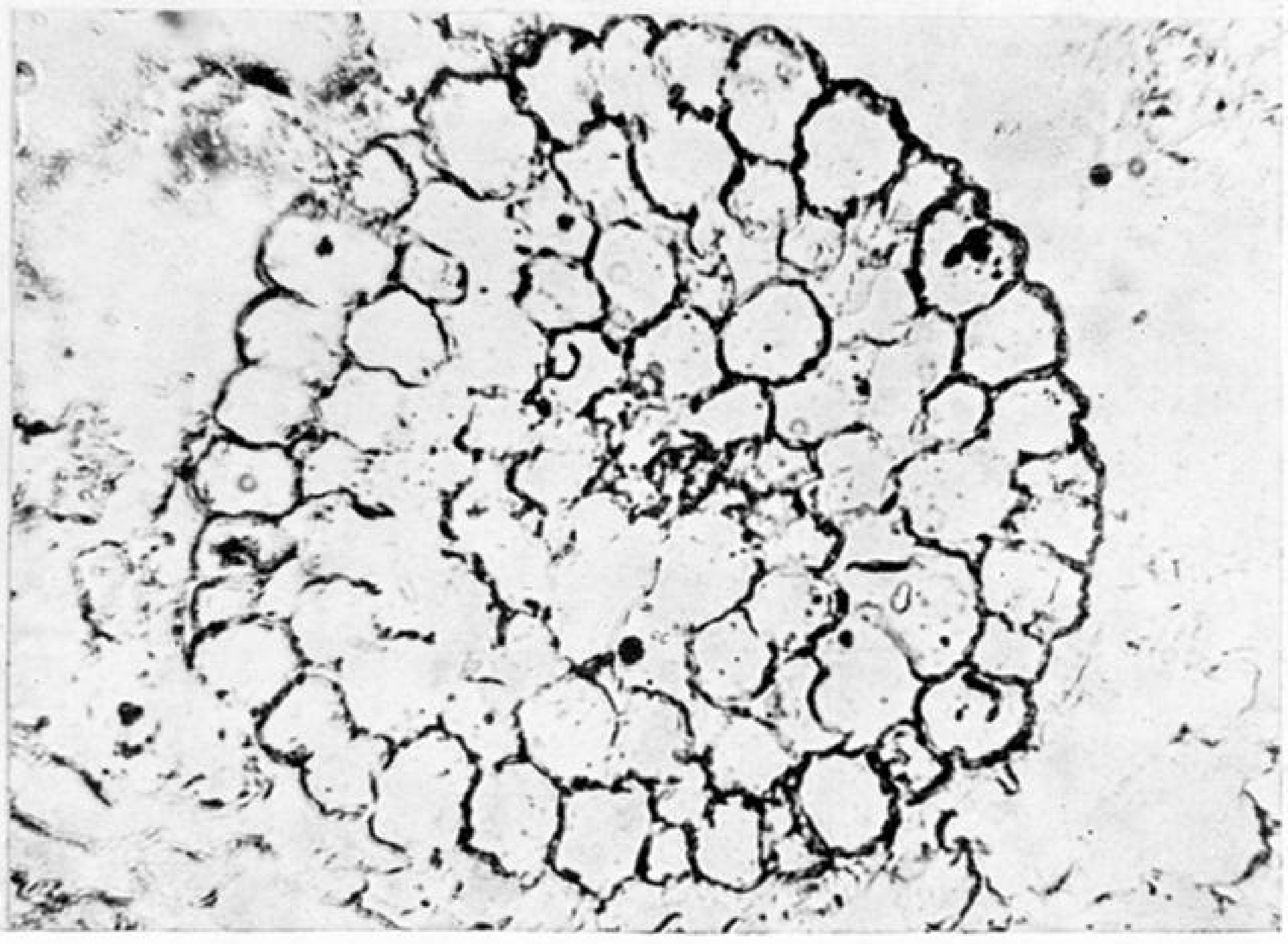

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PLATE 3

FIGURE 20. A branch of the IIIrd order (0·5 mm) giving out two branches of IVth order and a pair of aphlebia traces (*a*). The triarch stele of the main branch has disintegrated into three monarch steles, two of which pass out into daughter branches (IV). *Sl. no.* 471. (Magn. ×70.)

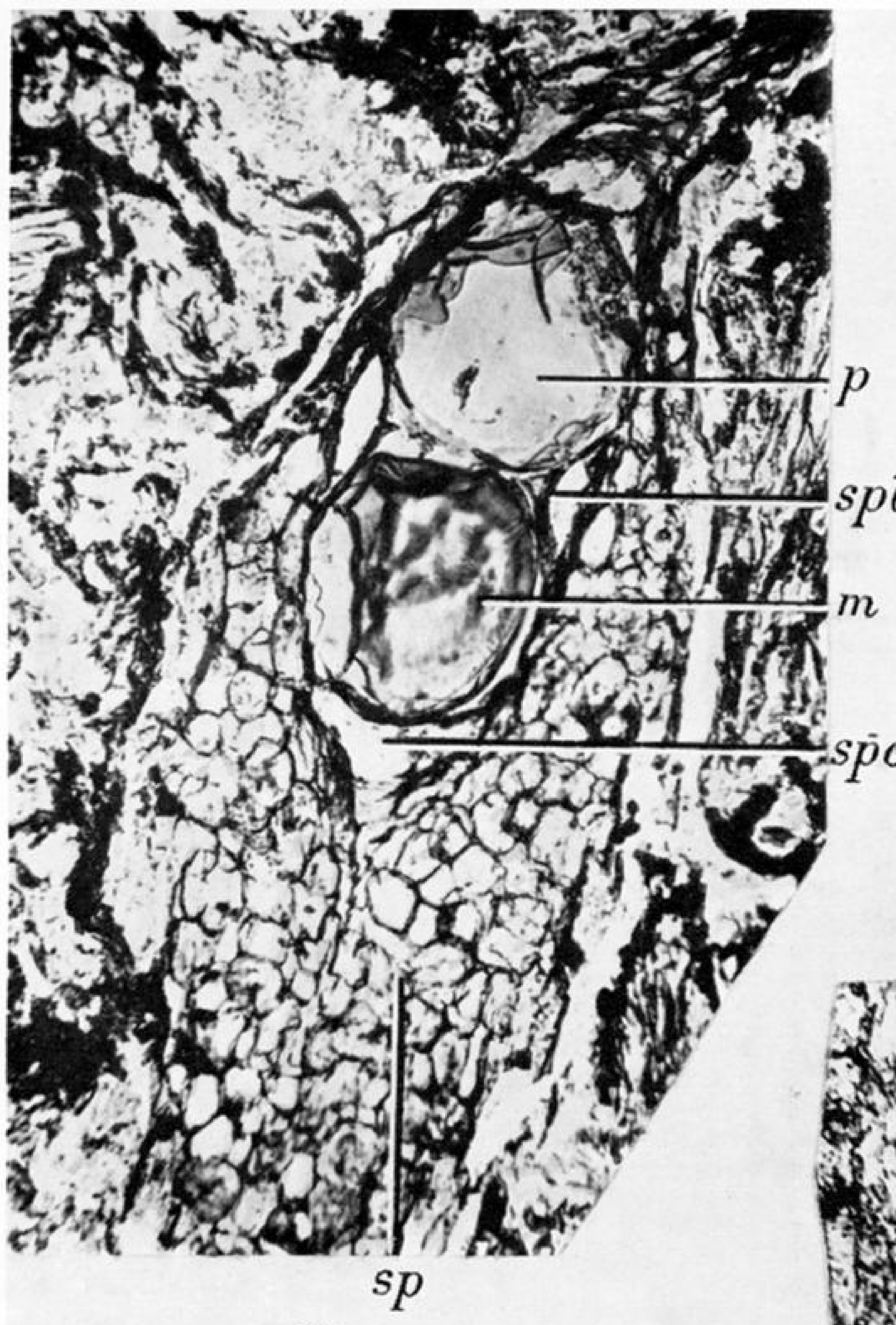
FIGURE 21. Bifurcation (VI) in a branch of 0·16 mm size (Vth order). Sections of other branches of different orders are also seen in the photograph. *Sl. no.* 484. (Magn. ×94.)

FIGURE 22. Transverse section through one of the penultimate branches (Vth order) of the frond showing big epidermal and cortical cells and a delicate vascular strand in the centre. *Sl. no.* 459. (Magn. ×374.)

FIGURE 23. Transverse section through a microsporangium assigned to *S. burntislandica*. The wall of the sporangium has large uniformly thickened cells and a stomium (*st*). *Sl. no.* 506. (Magn. ×95.)

FIGURE 24. One megasporangium (= *Bensonites fusiformis*) in longitudinal section, showing the cellular body (*sp*) at the lower end, and sporangial cavity (*spc*) with one intact megaspore (*m*) at the upper end. The megaspore shows a triradiate mark. *Sl. no.* 500. (Magn. ×78.)

FIGURE 25. A transverse section through the sporangial cavity showing U-shaped thickened cell walls. *Sl. no.* 505. (Magn. ×106.)



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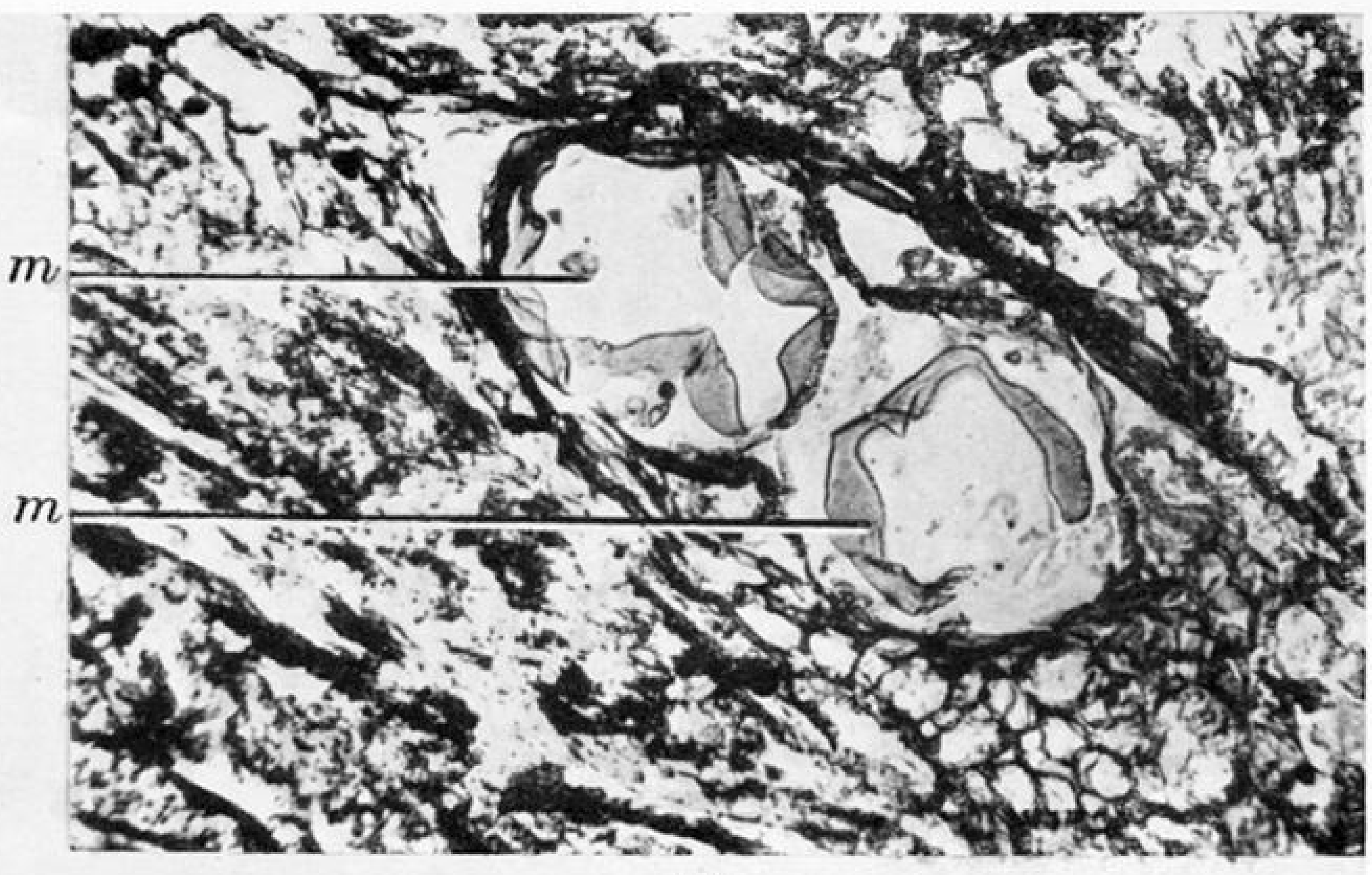

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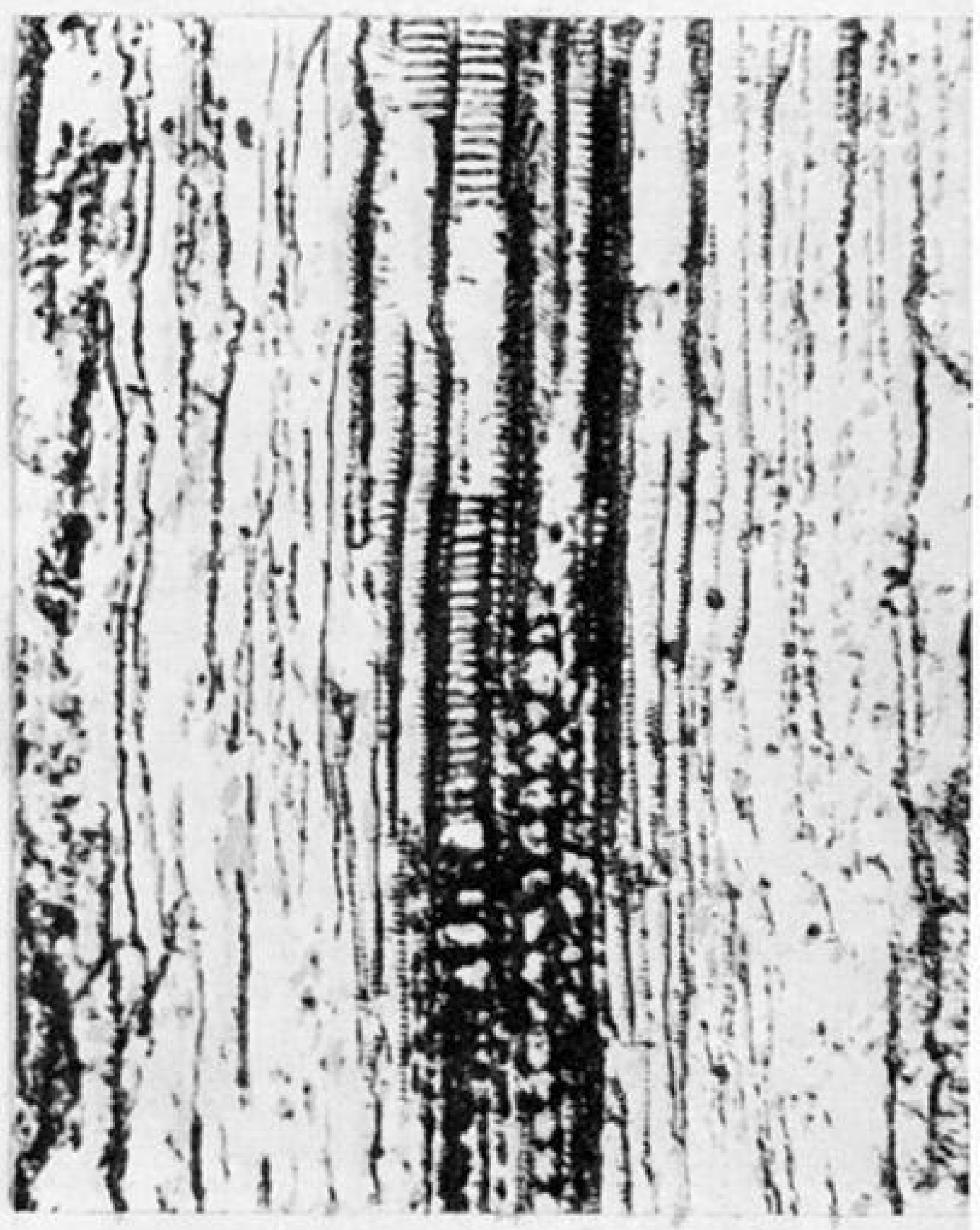

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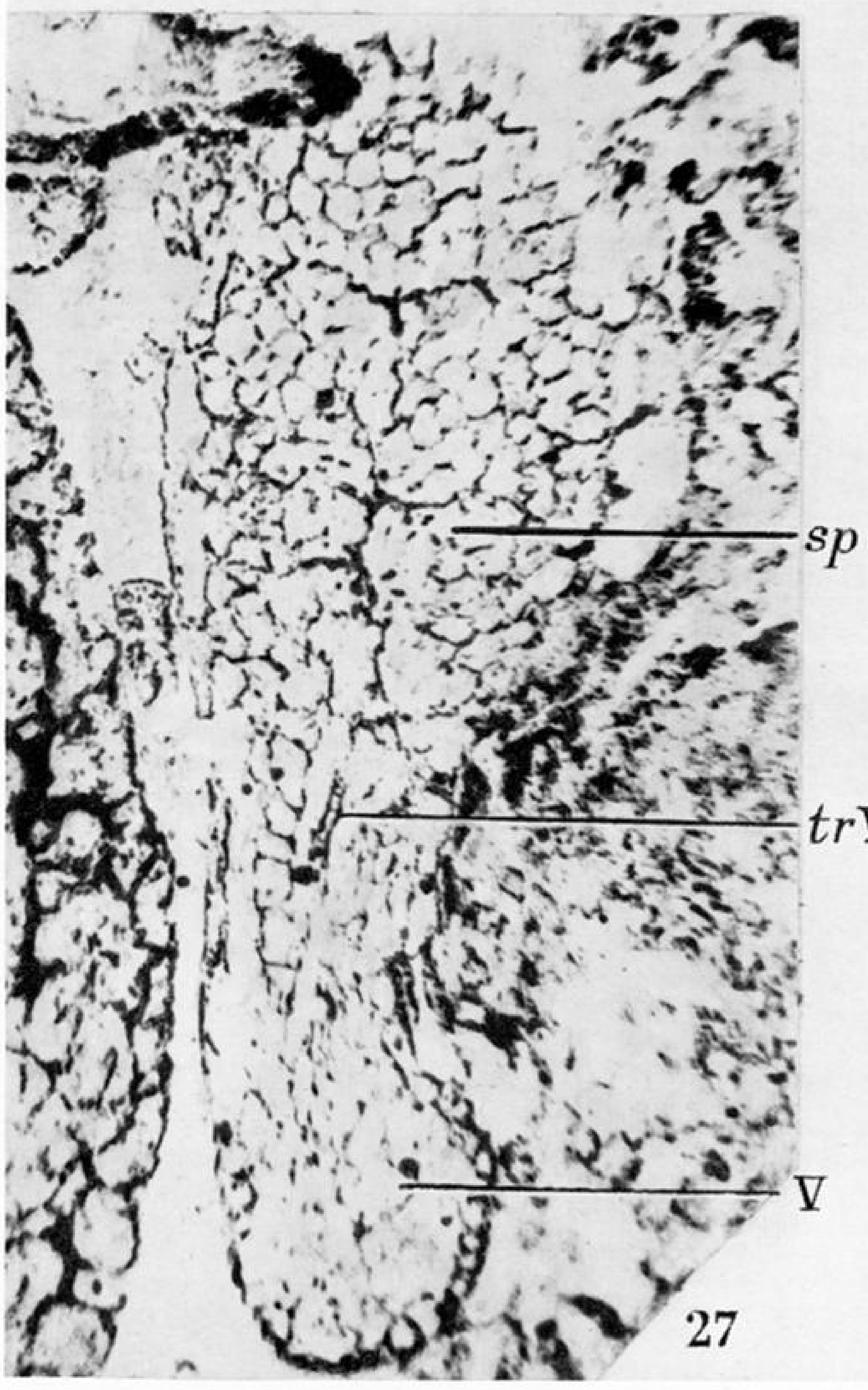

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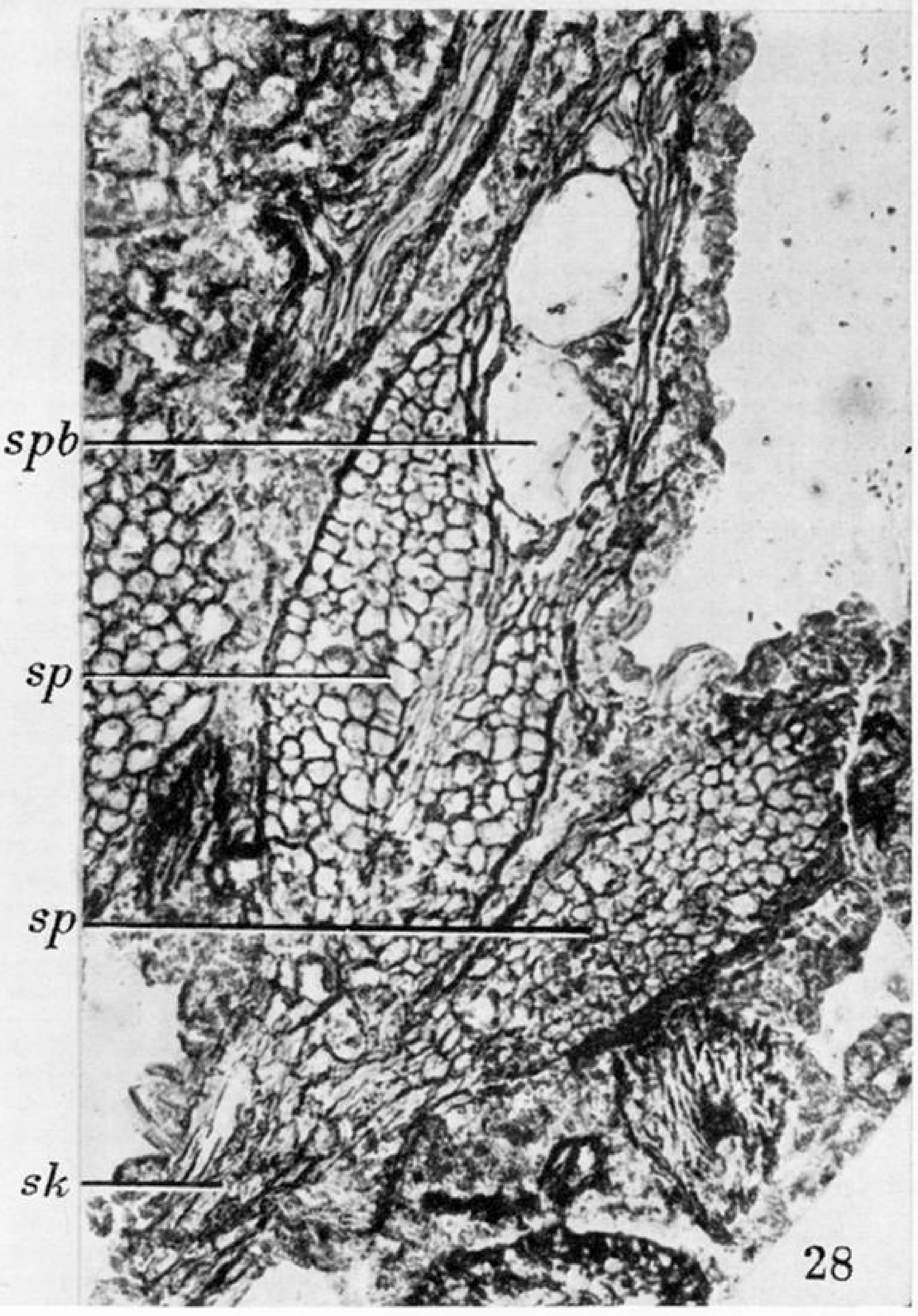

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PLATE 4

FIGURE 26. 0·16 mm penultimate branch bearing a megasporangium (*sp*) on one of its very short lateral branches. The former shows a stoma (*s*) which is identical with the stoma shown in figure 19. *Sl. no.* 499. (Magn. ×55.)

FIGURE 27. A 0·16 mm branch (V) of *S. burntislandica* seen in connexion with the megasporangium (*sp*) through its lateral branch (VI) which shows a tracheid (*tr*). *Sl. no.* 503. (Magn. ×97.)

FIGURE 28. Two megasporangia (*sp*) borne on a single stalk (*sk*); *spb*, spore bag. (Magn. ×100.)

FIGURE 29. Oblique longitudinal section through a megasporangium showing the cellular body (*sp*), sporangial cavity (*spc*), spore bag (*spb*) and two megaspores. In one megaspore (*m*) almost the entire cuticle is seen while the other shows a spore print (*p*) with a few bits of cuticle attached. (Magn. ×149.)

FIGURE 30. The megasporangium which is drawn in serial sections in figure 6. Two megaspores (*m*) show bits of cuticle of the wall. (Magn. ×142.)

FIGURE 31. Spiral and scalariform thickenings in the tracheids of a petiole. *Sl. no.* 488. (Magn. ×140.)