III. *Resin Canals in the Canadian Spruce* (Picea Canadensis (*Mill.*) *B.S.P.*)—*An Anatomical Study, especially in Relation to Traumatic Effects and their Bearing on Phylogeny.*

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[Plates 8–14.]

Contents.

I. Introduction.

Every student of conifer wood structure is familiar with the importance that in modern anatomical work is attached to the occurrence and distribution of resin canals. It is apparent in classification, identification, and, above all, in discussions of phylogeny. For example, the Pineæ are said to be distinguished by the normal occurrence of resin canals throughout the secondary wood, the Abieteæ by their occurrence practically only in response to wounding. The canals in the latter case are considered by some as being "revived" by injury and by others as in the process of acquirement. However, important though resin canals undoubtedly are, too little is known with regard to them to warrant many of the prevailing conclusions. There has been no systematic study of their origin and distribution, even in a single species. It was to make a beginning towards the filling in of this gap in our knowledge that the present study was undertaken.

The spruce was chosen partly because of the abundance of local material, both in nurseries and in the wild state. In fact, although nursery stock was ultimately made use of to perhaps a greater extent than the material from the woods, the study could probably not have been completed on this material alone, so obscure did the principle underlying the distribution of the resin canals seem when viewed merely from a study of nursery plants. There were, however, additional reasons of a scientific nature for the selection of the genus Picea. The resin canals, occurring apparently normally in the wood, are not nearly so abundant as they are in the pines, and are more irregular in distribution. Two low-power photographs have been made to illustrate these points. In Picea sometimes resin canals are completely lacking in an annual ring, whereas in the adjacent area they are fairly abundant (Plate 8, Photo. 1), but not so numerous nor so evenly distributed as they are in the pine, where every ring of the section shows several (Photo. 2); nor is their radial distribution in the year's growth uniform. They occur at various regions in either spring or summer wood, even to the very borders of both, although usually they are more abundant in the earlier part of the season's growth. The distribution of what are ordinarily considered normal resin canals is thus very sporadic in Picea. Again, in the region of wounds, tangential series quite like those so frequently figured as typical of Abies, are plentiful (*cf.* Photos. 23 and 24, Plate 9, the former of Picea, the latter of Abies).

Because of both these features, which were later found to be correlated, the genus Picea was chosen for intensive study. This study has included the wood from the various regions of the plant, root, stem and branch, and embraced the seedling, the young and the old tree. Some undescribed features of the primary resin canals of the cortex of the stem and of the secondary system in the bast have also been included.

2. Methods.

Fortunately for the anatomical student, the structure of seedling wood can be studied in perennials of the tree type by sectioning plants which are several years of age, the wood of the seedling being overlaid by that of the later growth. This, besides affording facility for the comparison of seedling and older tissues, provides a convenient support for sectioning.

Our procedure was to secure young trees such as could be sectioned in all parts, with the root system as complete as possible. From these a set of transverse, free-hand sections was made for preliminary study. The sections were taken at various levels, the decision as to the exact location depending largely on external features. For example, sections were made of each year's growth in length, either in the middle or at both top and bottom, and also at equal distances above and below external evidence of wounding. The sections were kept in order on large slides by numbering, and the parts of the tree, similarly numbered, were preserved for future reference, should preliminary examination reveal features requiring further investigation.

In preparation for the more detailed study of smaller material, series of sections were made by means of a Jung sliding microtome of the rigid wood-cutting type.* For the larger material, an inch or more in diameter, a Spencer Lens Company "special" was used with good results. To keep the series of sections in proper orientation a V-shaped groove was cut in the outer growth from top to bottom of the tree. Most of the serial sections were made from fresh or partially-dried material, without preliminary soaking in alcohol except in the case of young plants, where such treatment is expedient in rendering the tissues more rigid. For general study the sections required no staining, but were simply placed in series on the slides without cover-glasses. A little glycerine added to the alcohol used in sectioning kept the sections from drying out and curling, anchoring them to the slides and leaving them in good condition for microscope examination. Sections for purposes of illustration were selected from these series, stained and mounted for photographing, or simply treated with phloroglucin and hydrochloric acid for ordinary study and camera-lucida drawings. The phloroglucin was dissolved in alcohol and the hydrochloric acid mixed with equal parts of glycerine to ensure sufficient body for mounting. For charting the resin canals of large specimens, temporary mounts of sections so treated were made between two large slides bound together with string or elastic bands. These were put into an ordinary lantern and projected on a drawing easel, which was placed at a definite distance (about 10 feet) from the lantern, to ensure uniform magnification. A string attached to the focussing wheel of the latter put the control of the focus into the hands of the draughtsman. Verification of the number and arrangement of the resin canals was made afterwards by the microscope. In the case of the smaller sections and the details of larger ones, ordinary camera-lucida and photographic methods were used. Only when especially good sections were needed for detailed photographic illustration was the part embedded in celloidin.

The making of the numerous long series of sections and their study was a laborious task, but the results warranted the work, and as only the sections that were wanted

* The type used was described in the 'Bot. Gaz.,' vol. 50, May, 1910, pp. 148–149.

for permanent record were mounted, there was no serious drain on slides and covers. By the use of the lantern a set of phloroglucin sections from a small tree could be viewed practically all at once, thus facilitating the study of the series of changes. Charting the resin canals of these sections in important cases was found valuable, either as a basis for further intensive study or for purposes of illustration and permanent record. Many charts were made, accompanied by drawings of the plants to scale, showing the location of the annual scars from the winter buds and the distances between successive sections. Such a chart is seen in fig. 4, p. 88, and will be referred to later.

3. Systems and Character of Resin Canals.

In speaking of the character and distribution of resin canals in the conifers, Coulter and Chamberlain* state: "In Pinus, Picea, Larix and Pseudotsuga they form an anastomosing system in the secondary wood and cortex of both shoot and root, and also occur in the outer margin of the primary xylem of the root." As this statement occurs in connection with the presentation of Jeffrey's views on the resin tissue of conifers, it is probably based on the following sentences from the summary in his article†: "The Pineæ are characterized by the invariable presence of resin canals, forming an anastomosing system in the secondary wood and cortex of root and shoot. Resin canals are present in the outer margin of the primary wood of the root." In the above quotations it would seem that the term "cortex" is used in the way that De Bary‡ defined it, as including both the "*bast zone, bast* or *liber* (phloem) which, limited internally by the cambium, includes and is characterized by all the phloem-groups of the ring, and the *external cortex,* Duhamel's *enveloppe cellulaire,* lying outside this." At any rate, this is the ordinary interpretation of the above statements, and is the logical one, from the fact that otherwise reference to the well-known resin canals in the outer and primary cortex of the stem is omitted from what would seem to be a general statement regarding the resin canals. Not only are the quotations not explicit with regard to the cortex, but they involve fundamental misconceptions, as our study of the conditions in Picea, by series of sections, has revealed.

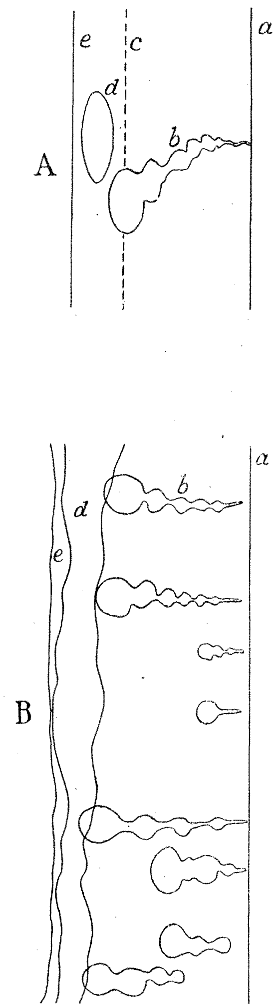
The resin canals of the bast and primary cortex of the stem will be considered first. Photo. 3 (Plate 8) is from a transverse section and shows a primary resin canal of the cortex, to the middle left, while obliquely above is a structure (only part of it shown in the photograph) of similar appearance, but belonging to the bast. From a consideration of the individual transverse section there would seem to be justification for inferring that, if one is a vertical resin canal, the other is also. Most radial sections might be similarly misinterpreted, but Photo. 5 from a more fortunate section of a radial series affords a clue to the true condition. Moreover, the more or less circular contour

* 'Morphology of the Gymnosperms,' 1917, p. 233.

† "The Comparative Anatomy and Phylogeny of the Coniferales—Pt. 2—The Abietineæ," 'Mem. Boston Soc. Nat. Hist.,' vol. 6, No. 1. January, 1905.

‡ '*Comparative Anatomy of the Phanerogams and Ferns,*' 1884, p. 458.

invariably seen in such tangential sections of the bast as those in Photos. 12–14 makes it quite clear that we are not dealing here with vertical canals. Fig. 1 consists of two composite drawings which illustrate the situation. The drawings were made from series of sections, the location and size of the bulbs being determined by micrometer measurements, and the outlines plotted to show the shape of canals and bulbs as seen in median section, *i.e.*, at their greatest diameters. Fig. 1A is from a series of transverse sections through the canal shown in Photo. 3.* The cambium was taken as a base line, and is shown to the right of the figure at *a*, while the dotted line *c* indicates, as nearly as could be determined, the boundary between bast and primary cortex. The line to the left *e* is the innermost layer of the periderm, the oval structure within *d* being a portion of a cortical resin canal. It is worthy of note that the horizontal bast canal has grown radially, in addition to its local increases in both vertical and tangential diameters in the region of the bulbs, and extends somewhat into the primary cortex.



TEXT-FIG. 1.—*Picea Canadensis* (Mill.) B.S.P. Diagrams of horizontal resin canals in the bast of the stem—A from transverse sections, and B from radial sections. *a*, cambium; *b*, bulbous horizontal canals of the secondary bast; *c*, junction of primary and secondary cortex; *d*, vertical resin canal of primary cortex; *e*, periderm.

At first the bulbs are more or less spherical in outline, but later they increase more rapidly in the tangential direction, becoming first elliptical (see Photo. 12 for a tangential view and the outer cysts of the series in fig. 1A for transverse), and afterwards much more elongated, as older bast reveals. Fig. 1B from a series of radial sections, plotted to the same scale and in the same manner as A, indicates similar series of bulb-like structures as seen from this angle. The boundary between bast and cortex is more indistinct in radial sections than in transverse, and the dotted line indicating its position has been omitted in this figure. To the left are three lines, the outermost one, as in the previous diagram, indicating the position of the periderm, while the next two form the boundaries of a vertical resin canal of the primary cortex. From the two diagrams it will be evident that the multiseriate medullary ray extending into the bast opens out into a horizontal canal, which repeatedly enlarges into bulbs or cysts, which grow in size as their distance from the cambium (and consequent age) increases.

Once the true condition is known, it is more readily realised that an appearance as of vertical canals in the bast may be seen in the transverse sections passing just above or below the constricted portions of the ray and including only the cysts, and also that many radial sections might present a similar appearance.

* In the photograph the orientation is reversed, top to bottom, from that of the drawing.

The true condition is, however, so apparent in any tangential section that it is difficult to see how it has escaped the notice of recent anatomists.* Perhaps this is because so little attention is now devoted to the study of bast as compared with the concentration of effort on wood.

The increase in size of the bulbs is accompanied by divisions of the medullary ray cells which form their walls. This is shown from the number of the lining cells in radial row in successive bulbs. For example, the upper wall of the inner bulb in Photo. 7 has two, rarely three, layers of cells in radial rows, whereas the outer one (to the left) has three and sometimes four. Again, in Photo. 4 of an older and larger bulb, there are five to six layers, the layering being continuously increased as the bulbs get older. It is also evident from a comparison of these figures that the lining cells become relatively thinner as the bulbs age. Anticlinal divisions also occur, increasing the number of rows, and this, together with an extension of the individual cells in the periclinal direction, provides for the increase in area of the walls of the growing bulbs. The cells of the inner layer, though thin, are rich in content, and in this respect are comparable to the epithelial cells lining corresponding structures in the pines. Photo. 6 shows these cells in face view.

Photos. 11 to 14 illustrate certain other details of the conditions found in a study of tangential series of sections through the bast. Photo. 11 shows in its upper part a multiseriate ray in the bast close to the cambium. In this region the lumen of the horizontal canal entirely disappears. That a like condition obtains in the wood near the cambium is evident in the lower ray shown in the same photograph, though a tiny schizogenous pore is just forming here. In the cambial region and for a short distance on either side, the ray is biseriate and solid, though a distinct lumen soon appears in both wood (Photo. 10) and bast. There is thus no anastomosis between the horizontal system of the bast and wood at the cambium of the stem, but only a continuity of the tissues. In Photo. 13 from a section of the bast a little distance farther out, probably in two-year-old bast, four of the multiseriate rays are shown. The canals have formed and the bulbs are in evidence though not yet of large size. In this plane they are circular in outline, and traces of the uniseriate part of the ray are in evidence above and below them, the ray cells with their dark contents being especially evident in the case of the two smaller central canals. In Photos. 12 and 14, from sections still further toward the circumference, a more adult condition is attained. Here the bulbs are large and, the uniseriate "tails" having apparently been absorbed into the expanding epithelium, represent the whole multiseriate ray. Neighbouring uniseriate rays preserve their identity throughout. Many of these may be seen in Photos. 13 and 14, distinct because of their dark content.

* It is probable that DE BARY knew at least part of the true condition as he speaks of the "blind ends of the horizontal passages . . . which extend into the bast" (*op. cit.*, p. 526). He further states that these "are not in communication with other canals of the wood and bast" (p. 490).

The growth of the bulbs in the horizontal canals of the bast helps to provide accommodation for the increasing girth of the stem. The parenchyma cells of the bast, however, are the main factors in this connection. In their early history these are longer in the vertical direction (see Photo. 13 for tangential views of these and Photos. 8 and 9 for radial), but later enlarge and expand tangentially (Photo. 14), most of them appearing with rather attenuated contents and with very thin walls which are easily broken in sectioning (see Photo. 9 above and below the bulb). Later this tissue appears in distinct horizontal rows in the tangential section (Photo. 12), which is an evidence of division to meet the needs of expansion. Pairs of cells of similar size occur at various points in the horizontal rows, indicating that division is not confined to one region. In most cases larger and more vigorous looking cells are in contact with the old sieve tubes, as may be seen to the left in the photograph.

With respect to anastomosis between the primary and secondary resin canals, this cannot occur in the stem except between those of the bast and the primary cortex. In the diagram, fig. 1B, the course of a vertical primary resin canal has been outlined, and those of eight horizontal canals with their series of bulbs extending to varying distances toward the primary system. In the case of the fourth canal from the bottom the two systems overlap to as much as a third the diameter of the primary canal. And yet, though there were certainly abundant chances for the anastomosing of the two systems, no single instance of such an occurrence was observed. In some sections it appears much more likely that these canals would combine with one another than that the different parts of the primary would join. For example, in Photo. 8 the upper and lower parts of the primary canal, to the left, are more separated than the lower portion and the secondary. This photograph shows the nearest approach of the two systems that has been observed in the series of sections. The lack of connection between the primary and secondary sets is the more surprising when one finds that the same type of lining cell is present in both, *i.e.*, a cell that is really the product of secondary growth, since it is produced in radial rows (see Photo. 4, where the primary is to the left and that of the bast to the right). The only difference here is that the primary has a few more layers of cells, but, when the relative age of the primary and secondary is considered in the light of what has been shown above in connection with the layering of the secondary, this is readily understood.

The peculiar feature of secondary growth exhibited by the resin canals of both bast and cortex, and the secondary accommodation-growth of the parenchyma cells of the bast, deserve further attention. It is customary to give too much credit to the primary growing point and the cambium for the formation of the tissues of a plant and to forget that there are subsequent alterations in these that cannot be accounted for except on the basis of later cell multiplication. Botanical students are usually made familiar with the well-known periderm type of secondary growth in the tree forms of monocotyledons—the dracænas, yuccas, etc. This condition, however, is treated as a very exceptional thing, and the point usually so emphasised that the student gets an idea that secondary cell division in primary tissues is extremely rare. The two instances noted above should serve as a helpful antidote. The condition in the case of the resin canals is perhaps an extreme example, but it serves well to indicate their peculiarly individualistic character, these structures finding no homologue except perhaps in the laticiferous tissue whose peculiarities of growth have long attracted the attention of plant anatomists.

In concluding our description of the cortex in the stem we wish to state that from our observations of a large number of series of sections it does not seem probable that there is ever any natural connection between the primary and secondary systems of resin canals. Even in the case of injury where a secondary connection might be thought likely, judging from the great external accumulation of resin, the study of series of sections through such areas reveals no trace of it.* The erroneous idea of the occurrence of anastomosis may have arisen partly from the mere probability of such a connection and partly from the deceptive appearances already referred to, especially in transverse sections, when studied individually, as is the usual practice.

In the bast of the root of Picea the horizontal system is so similar to that of the stem that no illustration of the root condition is necessary. There are, however, two exceptional features to which special reference must be made. In the primary cortex of the root we have not found any resin canals, an observation in agreement with those of anatomists of the older school.† For example, in the outer parenchymatous tissues of the root from which Photo. 67 (Plate 13) was made, though there are five vertical canals shown in the first year of the secondary wood, in addition to the two in the primary, no appearance of such structures was to be found in the primary cortex. We have also investigated this region before periderm formation begins, in some instances to as far back as 10 cm. from the growing point of old roots, and found no resin canals. Nor have we found any in the hypocotyl of the young plant. In the stem cortex, on the other hand, they are present from a very early stage in the differentiation of the cortical tissues. We have not specially illustrated this well-known feature of the stem, but some of these canals, as yet small, may be seen in the portion of the cortex included in Photo. 66 (Plate 13). One has only to remove the thin outer tissues on a young stem to disclose the course of these canals from one end of the year's growth to the other. Later they become cut off by periderm formation, a fate which likewise ultimately befalls the outer cysts of the horizontal system of the bast of both root and stem.

The second point to be referred to in the root is in connection with the resin canals in the primary wood. These are well-known structures, the external position of which

* Not only is there no anastomosis between the primary and secondary systems in the region of wounds, but an increase of the former in connection with the great local increase in the latter is entirely lacking. We have found since, however, that the primary tissues can be made to produce more resin canals, but only by stimulating the tissues when active, *i.e.*, in the primary growing point.

† De Bary, A., *op. cit.*, p. 443.

in each arc of the protoxylem of the Pineæ, in contrast to the central location (in the metaxylem) of the single one in the Abieteæ, is used to distinguish the root wood of these two sub-divisions of the Abietineæ. One is shown at either end of the primary wood in Photo. 67. When the root is triarch, a third canal occurs. In the case of these canals of the primary root, though there is a connection with horizontal canals passing through the secondary wood (to which reference will be made later), there is nothing in the nature of a connection between primary ligneous and cortical canals, since none of the latter are present in the spruce. Primary cortical canals are found, however, in the root of the Araucarians and Cycads, and on this account, in describing such features, it is imperative to distinguish clearly between primary and secondary cortex, as we have already indicated in connection with the quotations at the beginning of this section.

The resin system of the secondary wood presents many differences from that of the bast. In it there are two distinct types of resin canal, belonging to the horizontal and the vertical series respectively. The horizontal system of the wood is the correlative of that of the bast with which its tissues are continuous, while the vertical, according to our results, has no corresponding type in the latter.

An examination of the system in the stem brings out several points of interest. Each horizontal ligneous resin canal is formed from a solid biseriate ray, which, at a short distance from the cambium, opens up (Photo. 10, Plate 8) as in the bast, forming a hollow structure. The corresponding canals in the wood and bast are thus closed at the cambium and their lumina separated in this region (Photo. 11, Plate 8), as noted above. In the wood there are no later bulb-like growths as in the bast, the fusiform ray adding only slightly to the number of its cells a short distance from the cambium and continuing uniformly for many years if the tree is old and the horizontal canal originated early in its life. However, though the size continues uniformly the lumen of the canal does not, but is occluded at places, so that the horizontal system of the wood is a series of cysts with solid ray tissue intervening. To make certain that this is correct we examined series of tangential sections, as the condition with regard to the lumen is more distinct in these. The great similarity between the different fusiform rays presented a difficulty, which was satisfactorily overcome by cutting from a small block and locating the particular rays by means of a micrometer eye-piece.

There is also a difference in character between the cells composing the fusiform ray in the bast and those in the wood. In the bast they have thin walls of cellulose, while in the wood most of them are lignified and comparatively thick-walled, although a few have thin cellulose walls. The thin-walled cells are usually more abundant in the neighbourhood of the vertical canals, but are not confined to this region. In Photo. 15 (Plate 9), for example, there is a thin-walled cell to the left of the outer vertical canal, and again there is another in the ray a little farther on, unassociated with a vertical canal. The presence of these thin-walled cells may also be seen in the uniseriate ray (Photo. 20) between two canals. The uniseriate upper and lower parts of the fusiform rays are never lost in the wood, and have ray tracheids associated with them just as the ordinary uniseriate rays have. The horizontal system of the wood has thus just as distinct an individuality as that of the bast and is as definitely a part of the ray as is the latter, though its individuality does not show so strikingly in one respect, that is, in the ability to increase its size by secondary division of the original ray cells. The reason for this may be that the ray in the wood is subjected to uniform pressure by the firm tracheary elements by which it is flanked, and has no " accommodation " space for expansion as in the bast.

The other system of the wood, the vertical series, has a different origin and is without counterpart in the bast. This system, as was pointed out by one of us in 1912, is derived from the modification of potential tracheary elements.* Some stimulus applied to the cambium causes certain initial cells in this region to deviate temporarily from their ordinary course of development. Instead of forming tracheids, they form resinous tracheids, or divide by horizontal walls, producing either septate tracheids or thick and thin-walled parenchyma.† An illustration of the abundance of the septate tracheids and the extent of their distribution tangentially may be seen in Photo. 22 (Plate 9), where the characteristic bordered pitting on the septa is visible even at the low magnification of the photograph. The radial extent is not so great (Photo. 18), indicating that the stimulus was acting on a considerable area of cambium but only affecting normal production of tracheids for a comparatively brief time. The thick and thin-walled parenchyma is closer to the cavities than these septated tracheids. The thin-walled cells are fairly long at some places and very short at others. Two of the long type may be seen in the middle of Photo. 21. A very short one that appears stretched in the radial direction is visible with its distinct nucleus just above the second cavity from the bottom in Photo. 18, which is from a radial section. Views of these thin-walled cells in transverse section are to be seen in Photos. 23 and 25, the latter at a greater magnification, about two and one-half times the other. It is regretted that these sections are not reproduced in colour, for with the hæmatoxylin and safranin stains used they stand out very distinctly. Their walls, being of cellulose, took on a purple colour with the former stain, while the lignified walls of the more sclerenchymatous ones and of the tracheids were stained red with safranin.

A comparison of the cells of this vertical series with those of two other types of conifer is of interest. Photos. 24 and 26 (Plate 9) are from *Abies balsamea* stem, and show a tangential series believed to be produced by the spruce bud-worm. The section was put at our disposal for illustration by Mr. C. H. McLeod, who is making a special study of this feature. Septate tracheids are just as abundant between the canals here as they

* Thomson, R. B., 'On the Comparative Anatomy and Affinities of the Araucarineæ,' 1912.

† Penhallow, in his well-known work, 'A Manual of the North American Gymnosperms' (1907), noted and described the various transitional elements, but considered that they were derivatives of the parenchyma, in the processes of transformation into tracheids, the reverse of the present conception. In conformity with this idea he names the septate tracheids, referred to here, " parenchyma-tracheids."

are in Picea. The parenchyma cells which surround the canals are all thick-walled and lignified, as is the case with the majority of the cells in Picea. The important difference is the entire absence of thin-walled parenchyma in Abies. Even the tylose-like cells that project into the lumen, which are nearly always thin-walled in Picea, are thick-walled in Abies. Several of these are included in the photograph. They often have a nucleus quite as distinct as the thin-walled ones of Picea, whose bulging inner walls are in many cases made to look much thicker than they really are by the approximation of the nuclei and cytoplasm to them.

Photo. 27 (Plate 10) shows the condition in the pine. Here there is no thick-walled, lignified parenchyma at all, and the whole structure is composed of cells with abundant content and prominent nuclei. There is, however, a differentiation in these, the cells lining the canal, the so-called epithelium, being separated from the outer set by a ring of collapsed cells. When longitudinal sections, either tangential or radial, are cut through such canals very few septate tracheids are found. The pine has thus few vestiges of the original transformation of tracheids into parenchyma, either in the form of thick-walled parenchyma or of septate tracheids, and has reached a very advanced stage in the formation of ligneous resin canals, as may be inferred from their greater abundance here than in any other genus of the conifers.

The cavities in the vertical ligneous series of Picea are first seen shortly after the stimulated areas of the cambium are turning again to the normal production of tracheids. We have seen evidence of both schizogeny and lysigeny in their production. The cavities are irregular in shape, especially in wound areas, where they are numerous, fusing tangentially or branching, and forming more or less vertical irregular series of cysts (Photos. 18 and 19, Plate 9). The cystose character is always present, even when the canals are few and scattered. The spruce in this respect resembles the balsam, a feature which PENHALLOW* stressed when accounting for the origin of the corresponding canals of the pine, regarding the latter as the culmination of the process of fusion. With his conclusion our results are completely in accord.

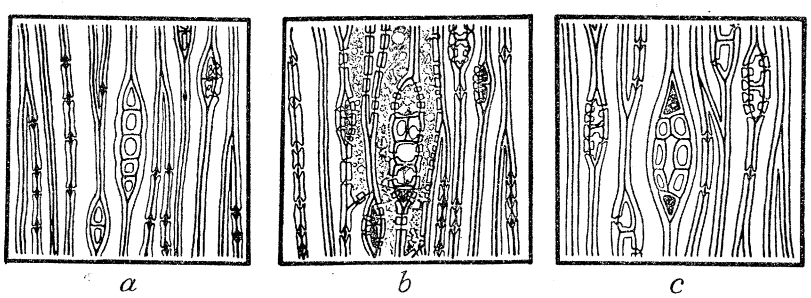
In the course of these cysts, as seen in tangential section, they often appear pierced by uniseriate rays, so resistant is the ray structure and so independent of the surrounding resiniferous tissue (Photo. 19). Even the fusiform ray with its resin canal pursues its course undiverted through or beside the cavities of the vertical series. Two of these from Photo. 19 are shown at a higher magnification in the centres of Photos. 21 and 22. The first is from the upper left and the second from the upper right of the preceding figure. The sections took the hæmatoxylin stain very heavily in the region of the fusiform rays, and though the cavities are clear, the details of the tissues are indistinct. The independent course pursued by both types of ray may be further illustrated from the photographs of transverse sections. In the upper part of Photo. 15 a fusiform ray is seen passing alongside, and in Photo. 16 between the vertical structures, while

* 'North American Gymnosperms,' 1907, p. 134.

in Photo. 20 the course of a uniseriate ray is depicted. They are not diverted to a perceptible extent, and the only modification that they show is a local increase in the thin-walled parenchyma. Though the tissues of the horizontal and vertical systems remain histologically distinct there is certainly every possibility of anastomosis, and no doubt, on wounding, the resin supply of the one supplements that of the other.

However, that there is normal anastomosis between the horizontal and vertical systems in the spruce stem we have not been able to demonstrate. Though the material we studied was carefully embedded in celloidin, the walls of the cells in the region of what might be the junction point were so thin that they might be broken easily and certain of the delicate cells pulled away in sectioning. This and the fact that we have often found the two systems with their cavities separated have made us doubtful as to the occurrence of normal anastomosis. For example, Photo. 18 (Plate 9) illustrates a common condition. Here the small horizontal cavity, above, is separated from the vertical by a long thin cell which is more or less broken towards the right. If natural anastomosis ever does occur in the stem of the spruce, the habit is certainly not well established. As will be noted later there is more evidence that it may be present in the looser tissues of old root, where the cystose character of the canals is less marked.

Though the two systems of the wood seem so persistently distinct, they owe their origin to a common stimulus, as we shall see later, and their association is not a matter of chance. In Photos. 15, 16 and 17, three horizontal canals are seen arising from three vertical, the first two in the first year wood and the third in the second. Not only do the fusiform rays always originate from the vertical system, but many uniseriate rays also. In order to illustrate the mode of origin of each type more definitely, three sections of a tangential series, arranged from within outwards, have been drawn (fig. 2) from the



TEXT-FIG. 2.—*Picea Canadensis* (Mill.) B.S.P. Camera lucida drawings of three sections of a tangential series through the region of a vertical resin canal of the wood of the stem : *a*, from the side of the canal next the pith, showing four uniseriate medullary rays ; *b*, through the outer tissues of the canal—a new uniseriate ray has appeared to the left of the central one which has become partly biseriate ; *c*, from farther out, showing the five rays, the central one with a horizontal resin canal.

stem of a young plant of *Picea canadensis*, covering a radial distance of about 120μ. In the first figure *a* there are four uniseriate rays, the central one the largest. In the second figure *b* a fifth uniseriate ray appears slightly to the upper left of the large central one which has become partly biseriate. The cells with simple pitting and contents, surrounding the latter, belong to the vertical system. The third figure *c* shows the new uniseriate and a central fusiform ray established amid normal conditions in the surrounding tracheids. One uniseriate ray has turned into a fusiform, one has been formed, and three others have continued through the region.

Turning again to Photos. 15 and 17 of transverse sections, it will now be evident that there are indications in each of the transformation of a uniseriate ray to one of the fusiform type. A uniseriate ray strikes the vertical cavity in each case centrally and is continued outwards as a fusiform. It must not be inferred, however, that every "central strike" produces a fusiform ray (see Photo. 20), or that all fusiform rays originate in such contacts; for while we have never found a fusiform ray originating except from a uniseriate and at the place where the latter comes in contact with a vertical resin canal, this contact is, in some cases, lateral rather than central.

The relative antiquity of the horizontal and vertical resin canals of the secondary wood of conifers has been a contentious point. The evidence of their origin disclosed in the study of Picea, both stem and root wood, favours the greater antiquity of the vertical series. Since horizontal canals never precede the vertical in development, either in the stem or in the root, and are always associated in origin with vertical canals, it would seem a reasonable inference that they are therefore not an earlier acquirement.

Photos. 15–17 illustrate a further point. Around the pith there are multiseriate primary rays. These are leaf and branch gaps, as the classic work of JEFFREY has revealed, and are present not only in all conifers, but throughout the seed plants. In the Cycads and Araucarians such large primary rays contain canals, a condition that certainly does not hold in Picea. There is clearly no homology between this type of canal and that of the secondary ligneous rays, and only confusion can result from any phylogenetic argument based on such an assumption.

We have not specially illustrated the details in the root, as in general the conditions are similar to those of the stem. A difference, however, that is quite in keeping with general root structure may be mentioned. Conifer roots, with exceptions in the case of those produced early by young seedlings, have a structure noticeably more lax and open than that of the stem. The tracheids have larger cavities and comparatively thinner walls, and the zones of summer wood in the growth rings are narrow and abrupt. The resin canals reflect this laxity in the greater breadth of their lumina, as compared with those of the stem. In addition the lumen of a horizontal canal in such a position is often found open in the cambial region, and connecting freely with the lumen of a vertical canal as well. Whether the anastomosis of vertical and horizontal resin canals in the root is due to the breaking down of some of the very thin-walled cells in this region we have not satisfactorily determined. In many cases, however, the appearance is that of a normal free anastomosis.

The chief difference, then, between secondary ligneous resin canals in root and stem is their more open character in the later-formed roots of more mature trees. It is to be noted, in this connection, that in addition to what has already been said, the parenchyma partitions dividing the canals into cysts are either absent, or much more widely separated in this region than in the stem.

4. Food Supply or Vigour of Growth and Resin Canal Production.

There has been no inconsiderable amount of discussion with regard to the importance of food supply, or, as it is sometimes put, vigour of growth, in connection with the production of resin canals. Jeffrey* has subscribed to the theory with reservations, believing that abundance of food in forms with comparatively few resin canals induces the formation of these structures by producing reversion to an ancestral type where they were more plentiful. A quotation will make this attitude clear :

> "Where there has been reduction from a more luxuriant ancestral type, experimental conditions, which bring about a greater determination of nutrition to the parts in question, are apt to cause a reversion to ancestral structure. . . In the case of Sequoia, as I have pointed out in the first memoir of this series (Jeffrey, 1903), injuries to the phloem and the cambium, which bring about a damming up of the products of assimilation in the region of injury, cause a hypertrophy of the woody tissues. In this hypertrophied wood more or less typical resin canals occur."

Kirsch,† on the other hand, has held that resin canals are formed in regions of abundant food supply, not as reversions to ancestral habit, but to provide increased translocation facilities for the elaborated food.

In considering these hypotheses, the difference between physiological conditions in the wood and the bast are pertinent, since the relative availability of food supply might reasonably be thought to exert a corresponding influence on the production of resin canals in these two regions. Thus, one might expect the stimulus to the formation of the canals, which acts on the cambium,‡ to produce greater results on the side where the food supply is ordinarily conceded to be greatest, that is, in the bast. The facts, however, are the reverse. The stimulus produces a result only in the ray cells of the bast, the sieve tube initials and other bast elements proper not being affected,

* "The Comparative Anatomy and Phylogeny of the Coniferales—Part II—The Abietinæ." 'Mem. Boston Soc. Nat. Hist.,' vol. 6, No. 1. January, 1905.

† "The Origin and Development of Resin Canals in the Coniferæ, with Special Reference to the Development of Thyloses and their Correlation with the Thylosal Strands of the Pteridophytes," 'Trans. Roy. Soc. Can.,' vol. 5, Section IV (1911).

‡ It is just possible that the stimulus acts on the young products on the tracheary side of the cambium, our reason for stating this being the fact that we have just recently found that formic acid when inserted into a wound travels far up the tissues, evidently in the upward current in the wood, and results in production of resin canals many times farther above the seat of injury than below it. However, the stimulus does produce a result on both sides of the cambium, and our conclusion holds independently of this debatable feature, which has, however, a very distinct bearing on the "damming up" theory, probably being the true explanation of the greater response above than below.

while, on the other hand, in the wood it affects the tracheary as well as the medullary ray cell initials, resulting in two distinct types of resin structure, that of the horizontal and that of the vertical series. One would think that even if the sieve tubes were irresponsive to the stimulus to produce resin canals, the heavily food-laden parenchyma cells of the bast might respond, but as has been shown above, these do not add to the series of cells surrounding the resin-bulbs, which are wholly of ray origin. Moreover, it may be added that the food supply theory fails to explain adequately the character of the distribution of resin canals resulting from wounding. When a tree trunk produces resin canals as a result of wounding, they centre not only in the region above the wound, but also directly below it. In fact, there is no indication of a bifurcated arrangement below the wound, as would be expected if the downward current of food were responsible for their occurrence. In wounding of the root a similar condition obtains. These are significant facts, indicating the existence of a stimulus acting apart altogether from increased food supply.

From these more or less theoretical viewpoints, it would seem that the food supply has little bearing on the problem of the production of resin canals. It must be conceded, however, that the relative availability of the food material on the bast and on the wood side of the cambium is a difficult matter to determine, and that it is perhaps better to connect the food supply aspect with "vigour of growth." The latter, however, is a lax term that its users have not troubled to define, and must be considered from as many different aspects as possible. For example, vigour of growth may refer to growth in thickness, when the thickness of the annual ring of the wood, or its area, becomes the standard for comparison. On the other hand, it may refer to growth in the vertical direction, when relative height is the basis. Again, both of these factors may be entailed, when bulk will be the criterion.

On the question of a correlation between the formation of resin canals and the rapidity of growth in thickness, a glance over fig. 4 (p. 88) of *Picea Canadensis* will present some interesting facts. Nos. 5, 6 and 7 of this figure represent three sections through one year's growth in height. These sections in the third annual ring from the outside have 55, 34 and 24 resin canals respectively, in the second none, and in the outside ring 11, 15 and 14. Where area or thickness is considered, it is clear on looking at the figure that the number of resin canals bears no relation to either. The outer ring is about three times as thick as the innermost of the three, and its area many times greater, and yet it has fewer, less than half the number, of resin canals. On the other hand, it must not be assumed that a thin annual ring entails their presence, for the second ring from the outside, which is much smaller than the outer one, though larger than the third, has no resin canals. Furthermore, these same three annual rings contradict the theory, if increase in bulk is considered as the criterion of vigour of growth, for before they were laid down this portion of the trunk had completed its growth in length, and so the areas of the rings are proportionate to the increase in volume of the cylinder for each year.

If increase in height, or length, is used to represent vigour of growth, the result is the same. To illustrate this, we have brought together the following data (Table I) chosen from the results recorded in Tables II and IV.

TABLE I.

——	Year.	Growth in Height.	Number of Resin Canals.*		
			Top.	Middle.	Base.
		Cm.			
Picea Canadensis III (from Table IV)	1922	7·7	—	0	—
	1921	3·5	1	—	1
	1920	3·2	—	5	—
	1919	3·2	—	4	—
	1918	3·4	—	2	—
	1917	3·9	—	0	—
Picea mariana X (from Table II)	1922	17	1	—	1
	1921	5	—	0	—
	1919	13	3	—	2
	1918	8·5	—	0	—
Picea mariana XII (from Table II)	1922	6	—	0	—
	1921	3·5	—	0	—
	1919	3·5	—	0	—
	1918	3·5	—	0	—

* A dash indicates that no section was taken.

A brief consideration of this table is all that is necessary to dispose of any claim that rapidity of growth in length is the determining factor in the production of resin canals, in so far as Picea is concerned.

The results illustrated are typical of those obtained throughout the work, and such conditions are in our opinion sufficient to negative any theory that considers vigour of growth the controlling factor in resin canal production. If further illustrations are desirable, they may be found in Table II (pp. 80 and 81), where the complete resin canal production of *Picea mariana* X and XII is disclosed, together with their annual growth in height, and the greatest and least diameters of the stem at the height of the various sections. It may be noted in passing that though No. X is nearly twice as tall as No. XII and about the same thickness, it has considerably fewer resin canals.

There may, however, still be the proverbial grain of truth in the vigour of growth theory. It is well known that wounding increases the number of resin canals, and undoubtedly plants when vigorously growing are more susceptible to injury than when they are passing through their more or less dormant period. A rub on a trunk of a tree that in the spring would remove the tissues to the cambium might only abrade the bark in the winter. Again, the current year's growth of either stem or branch is especially susceptible to injury when its tissues are forming and soft, and the more rapid the growth the more this factor would count. There is also a strong probability that the plant would respond to wounding to a greater extent in a season of rapid growth, both because of the greater amount of its tissue in the plastic condition, and because of the probably greater responsiveness of the cambium when active than when in its dormant condition. We have a series of experiments to determine the season when the response is greatest, which will not be complete for another year, but there are already indications by the appearance of the over-growth that the response is directly related to cambial activity. Thus vigour of growth may provide conditions favourable to wounding and the production of resin canals, but the direct responsibility does not rest here.

Since, then, neither food supply nor vigour of growth can, as such, be directly connected as the causal factor with the production of resin canals, theories based on such accessories only distract attention from the main issue and prevent a proper interpretation of the facts. With such misconceptions cleared away, we may now turn to a more detailed study of wounding and its results in Picea.

5. Preliminary Investigations and Experimental Work.

The sporadic nature of the occurrence of resin canals in mature spruce wood at once suggested that the causal agency might prove to be some external accidental factor such as wounding. The abundance of apparently normal canals in such wood, however, prevented the definite delimitation of the effects of individual wounds, and so it did not prove so favourable a field as that of the young plant for preliminary investigation. Especially valuable in this connection were some seedling black spruce (*Picea mariana*), found growing wild in a peat bog in Muskoka, where no domestic animals interfered with them. These showed very little external evidence of wounding, although concealed wounds of the type to be described later were found to be present. Twenty-three specimens were examined and "tables of counts" similar to that shown in Table II (p. 80) were made as records of resin canal distribution. Several of the seedlings attained the age of seven years without a trace of resin canals in their secondary tissues. Photos. 28 and 32 (Plate 10) are from the cotyledonary and primary root regions respectively of one which, as determined by the external growth scars, was six years old. It is interesting to note that in Photo. 32, although the wood shows the arrangement typical of a root, not even the canals in the primary wood have yet made their appearance. As all other sections from the seedling were as free from secondary resin canals as these, it will be readily seen that the making of a "table of counts" in this case would not be a difficult procedure. Very often the tables show no resin canals in the first four or five years, though in some instances they appear earlier, and in one case they are present in the second year's growth. In the fifth year, 52·4 per cent. of the

Table II.—*Picea Mariana* (Mill.), B.S.P. (*P. Nigra*, Link), Black Spruce.

A. *Resin Canal Production in Young Trees from a Peat Bog.*

The first two columns give the number of each section and its distance above the lowest section. The figures to the right record the number of resin canals per annual ring at the various heights, the first giving the results for the last ring laid down, in 1922, the second for that of 1921, etc. The line at the bottom indicates the age in years of the tree when each ring was laid down.

One to three sections from each year's growth in height were made. A lack of one year's growth in length is recorded in the case of the lower portion of each tree. The uppermost section of X is 5·5 cm. and that of XII 3 cm. from the top.

No. X, Port Sydney, November 27, 1922.

Section No.	Height in cm.	Resin Canals produced each year.					
		1922.	1921.	1920.	1919.	1918.	1917.
1	43·0	1					
2	38·0	1					
3	30·0	3	0				
4	27·0	1	1	0			
5	20·0	1	0	0	2		
6	17·0	1	0	1	3		
7	13·0	0	0	0	6	0	
8	8·5	1	0	0	5	0	
9	5·0	0	0	0	2	0	0
10	2·0	0	0	0	0		
11	0·0	0	0	0			
Age in years		6	5	4	3	2	1

No. XII, Port Sydney, November 27, 1922.

Section No.	Height in cm.	Resin Canals produced each year.					
		1922.	1921.	1920.	1919.	1918.	1917.
1	23·5	0					
2	20·0	0	0				
3	17·5	5	0				
4	16·0	11	0	0			
5	13·0	20	0	0	0		
6	11·5	19	0	0	0		
7	9·0	17	1	0	0	0	
8	6·5	13	10	1	0	0	0
9	4·5	16	6	1	0	0	0
10	1·5	2	1	0	0	0	0
11	0·0	1	0	0	0		
Age in years		6	5	4	3	2	1

specimens have resin canals, so that among plants five years old there are about equal chances of finding specimens with and without resin canals.

An unexpected irregularity was found in the case of the seedling root of the black and other spruce species. On making sections, as we did at short intervals in preparing the charts and tables for the preliminary investigation, we found that the plant suddenly dropped several annual rings in a very short extent of its height just above or in the region of its most profuse development of lateral roots. This is due to the fact that in the case of the young plant it frequently happens that the primary tap root is lost at a

TABLE II (continued).

B. *Micrometer Readings of Major and Minor Diameters of Sections.*

No. X, Port Sydney, November 27, 1922.

Section No.	Major and Minor Diameters at end of each year.					
	1922.	1921.	1920.	1919.	1918.	1917.
1	34×33					
2	46×43					
3	70×65	20×19				
4	87×84	47×45	30×27			
5	105×102	70×68	54×51	34×32		
6	110×105	80×75	62×58	42×39		
7	130×118	97×90	82×75	52×52	22×22	
8	109×91	70×69	56×53	40×35	20×19	
9	93×78	62×59	51×46	47×37	33×27	14×14
10	50×48	30×27	26×24	17×15		
11	45×43	22×21	11×11			

No. XII, Port Sydney, November 27, 1922.

Section No.	Major and Minor Diameters at end of each year.					
	1922.	1921.	1920.	1919.	1918.	1917.
1	23×20					
2	53×50	16×13				
3	69×58	20×20				
4	89×78	56×53	26×26			
5	95×89	65×64	39×38	20×20		
6	95×93	67×67	40×39	20×20		
7	99×96	80×73	50×47	42×41	20×19	
8	113×106	97×88	55×51	41×36	30×27	15×14
9	124×123	109×94	57×52	42×42	39×37	23×20
10	80×64	70×60	42×32	36×27	21×20	12×10
11	50×50	40×35	30×24	10×10		

C. *Growth in Height (in Centimetres) for each of the Last Five Years.*

Year.	1922.	1921.	1920.	1919.	1918.	Total.
No. X ...	17·0	5·0	1·5	13·0	8·5	45·0
No. XII ...	6·0	3·5	3·0	3·5	3·5	19·5

comparatively early stage. Such drops are illustrated in Tables II and IV. The former (p. 80) shows a loss of two years in each of the six-year-old plants, and the latter (p. 90) one of seven and another of four in a specimen seventeen years of age. This condition is the more surprising since the plants still have, to all outward appearance, a true primary tap root with no indication of its secondary origin. Had the phenomenon occurred in the upper part of the stem, one would have suspected that the tree had had one to several years of its leader cut or broken off and that a dormant bud had continued the vertical growth.* With the root the probability of the occurrence of similar, or, indeed,

* The following statement with regard to this feature is from a recent Wisconsin text-book, and is the only one we have found : "Frequently, as in the pine, the primary root dies early and a secondary root takes on the appearance of a tap root." ('A Text-book of General Botany,' by SMITH, OVERTON, GILBERT, DENNISTON, BRYAN, ALLEN, 1924, pp. 23–24.)

any type of injury did not at first present itself. However, the common occurrence of breaks in the number of annual rings in the whole root system, together with the enormous loss of lateral roots and rootlets that we later found during the investigation of older plants, proves the severity of the conditions under which the root grows, and shows that the root is not, as is commonly held, a much more protected and consequently more permanent organ than the stem. No doubt heaving and other frost phenomena play an important rôle in connection with the injury of the root, but a discussion of the influence of such œcological factors is deferred till the distribution of resin canals in the root is considered. In passing, however, it may be pointed out that the great loss of roots in both young and old plants should not be without interest to forest pathologists, because of the resulting possibilities for ingress of various timber-destroying fungi, especially those of heart-rot type.

The difficulty concerning loss of the tap root in the young plant proved of minor importance, for, by searching among the abundant material available, we succeeded in finding specimens without the defect. In the case of concealed wounding, however, the solution was not so simple. Not only did the young plant show little external evidence of wounding, but even series of sections failed, in many cases, to disclose any break in the tissues and subsequent overgrowth, which we had been accustomed to think of as a necessary indication of wounding (*see* Photo. 57, Plate 13, and fig. 6, No. 5, p. 98). There was, however, always evidence of a physiological disturbance in the annual ring containing the resin canals, which showed itself in a more or less definite false annual ring or rings. Such a condition is illustrated in Photo. 31 (Plate 10). The first year's growth is thin, and contains no resin canals, while the second is thick and has two false rings with a series of resin canals associated more or less closely with each. Although the magnification is low, it can be seen that the rings vary in distinctness and in radial extent. The inner ring is much thicker and more diffuse on the side of the stem opposite the part where its resin canals are located, and more definite and limited where these are most abundant. The outer one is less distinct and double along the left side, but still evident. When examined under a high power it is seen to be more like a root annual ring, *i.e.*, the change is abrupt on both sides. In fact, false annual rings may take on a variety of form. Part of one that may be termed the "inverse" type is shown at a higher magnification in Photo. 29.* Here, if the lower tissues were cut away, it would be almost impossible to tell the true from the false, or to know, except by the inclination of the rays, in what direction the cambium lies. Its resin canals are just beyond the upper limits of the field of the photograph in the diffuse portion of the ring. The lower power photograph (Photo. 31) shows the resin canals a little beyond the false ring. This is their usual position when they are abundant and arranged in tangential series. Certain of the Photos. of Plate 13 may also be examined to advantage in this connection. The definiteness of this position of the resin canals with regard to the false ring largely disappears when the canals are

* See also Photo. 62 (Plate 13) for a complete ring of a similar type, from another section of the series.

scattered (Photo. 65, Plate 13). On examining the wounds of the open type we found also a similar association of resin canals and false annual rings. This and the invariable presence of a false annual ring in connection with resin canals not referable, at some part of their vertical extent, to open wounds, led to investigations planned to discover the origin of the false annual ring and to ascertain whether it and the resin canals had a common cause. Experiments were begun on young spruce in our garden nursery. We used pliers for local temporary pressure or bruising, and spring clothes-pegs for continuous pressure. In other cases we simply bent branches sharply, but without producing fracture. Ligatures were also applied and formic acid used as a chemical stimulant. In all cases similar branches or parts free from any evidence of wounding were kept for controls.

These experiments were begun late in the season—June 20–22, 1923—and some of the material was collected August 9–11, 1923. Photos. 33 and 34 (Plate 10) indicate the results of clothes-peg wounds, the former of a branch and the latter of a root of *Picea Omorica*. In the case of the branch, which was in its second year, the peg was applied so as to put the pressure on vertically—above and below. On examination of this spot it was found that the tracheary elements on the upper side of the branch were crushed, distorted and mixed with parenchyma and resin canals. The growth on the upper side was also very limited, while on the lower hyponastic side, where the tracheids are normally thicker-walled, there appeared to be little or no disturbance of the wood elements. The response in the production of resin canals corresponds with the evidence of injury. It is greater above, where there is a slightly tangential arrangement, while below the canals are few and scattered. Of the false ring, however, the reverse is true, it being more developed below than above. Unfortunately, the branches were from the upper part of a tree old enough, being a garden plant of about ten years of age, to have some other resin canals in it, and so less valuable for demonstration. However, the traumatic series and false annual ring arose from the wound area, and extended for a considerable distance above it. In fact, the photograph was taken from a section about a centimetre above the peg.

The root has not made so much growth as the branch after the application of the peg, and so the result is more difficult to represent in a photograph (Photo. 34), since only a few of the canals have opened up, and there is much parenchyma associated with them. The root, like the branch, was in its second year, but we have only included a small portion of the tissues because of the necessity of a high power photograph to indicate the details. The cambium is to the right and some of the normal wood elements to the left. Below there is one big open resin canal, and above it a line of parenchyma extending directly to the irregular lumen of a second canal. In the centre of the photograph and one row of tracheids to the right of the line of parenchyma is a mass of such cells, whose splitting apart has just begun, forming a tangentially broadened small canal. Above this is a solid mass of dark parenchyma, without doubt an additional canal in the process of formation, as it is within the level of the outer border of the wood. Had the root been left growing longer, it is clear from the examination of the sections themselves that it would have organised two series of resin canals—a feature which is not uncommon in the spruce, where we have observed as many as four series in one year. (*See* Photos. 60 and 61, Plate 13, with two, and fig. 6, No. 5, p. 98, with four, the outermost very short.)

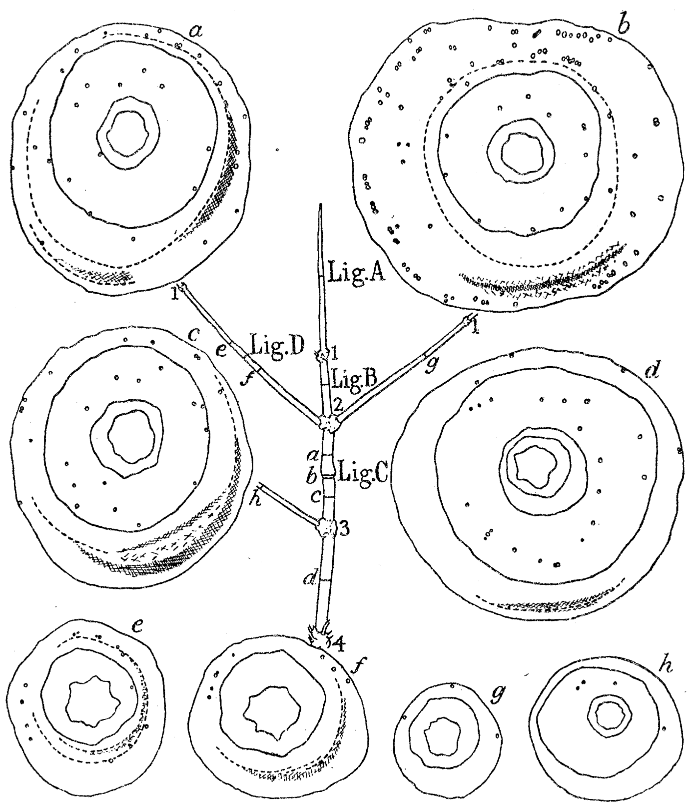
The last photograph on Plate 10 is from a plier-wounded *Picea pungens*, four years of age, which was growing vigorously. Plier pressure was applied at the middle of the current year's growth of the leader, and again at the middle of the next year below. The photograph is from just above the latter. The pressure was a little too great in both cases, the part above the upper one being killed, and the cambium being destroyed to a slight extent in the lower. There were, however, no complications here in connection with the presence of resin canals in the previously-formed tissues, and the result is very striking. We have also examined the bent forms and found a clearly-developed false ring and a few resin canals, but this kind of strain does not seem to be so effective as either type of pressure.

The ligaturing experiments were made on the lower branches of *Picea Omorica*.* The ligatures were of fine copper wire, and were applied midway between the winter bud-scars, where the twigs were in their first, second and third years. Certain of the results are illustrated in fig. 3, in which the canals are represented by small circles and the false rings by broken lines where their boundaries are distinct, and by cross-hatching where diffuse. The results for the third year—ligature C—are indicated in *a*, *b*, *c*, *d* and *h*. At *a*, 1 cm. above the ligature, there are twenty-two resin canals ; at *b*, just above the ligature, ninety-four, and at *c*, 1 cm. below the ligature, eleven. In each section there are well-developed false annual rings. Control *d* is from 3·5 cm. below *c*, about the middle of the fourth year, and has five canals (two joined) and a slight false ring. Control *h* is from the middle of the third year of a lateral branch and has one canal and no false ring. This branch came off 2 cm. below the ligature C on the main branch, and the section *h* is at a distance of 3·4 cm. from the junction point. We found that ligature B, on the second year of the main branch, had been inadvertently placed over a concealed wound and had to be discarded, but the conditions in the branch to the left, where ligature D was applied, were normal. At *e* and *f*, 1 cm. above and below this ligature, there are respectively twelve and eight canals and well-developed false rings. The section *g* of the corresponding branch at the right, which was kept as a control, has three canals, but no false ring. The ligatures on the young twigs of the current season's growth did not produce any result. As we found no canals in these or in the controls the point has not been illustrated, but the general lack of canals in the first year can be judged from the other figures, where not a single one is present. At first we were inclined to think that the ligatures had been too carefully applied, though we knew that we had tried to tighten them to the same extent as on the older twigs. We thought also that

* In this case the ligatured branches were allowed to remain on the tree from June 22, 1923, to May 29, 1924.

perhaps the twigs had not increased sufficiently in size. However, when we examined the point of application, by series of sections, and compared them with the older ones we found that neither supposition was right, and consider that the feature is significant of the general lack of response of the inner year's growth of young plants, as compared with the corresponding years of mature trees.

The formic acid treatment of Picea was too severe, as the young treated twigs all died, and we have no results from this genus to report. The treatment of older branches



TEXT-FIG. 3.—*Picea Omorica*, Bolle. Effect of ligaturing in producing false annual rings and resin canals. Centre—sketch of branch: Ligs. A, B, C, D indicate positions of ligatures; *a*, *b*, *c*, *d*, *e*, *f*, positions from which the sections similarly marked were taken, and 1, 2, 3, 4, the age in years of the adjacent parts. Right and left—diagrams of sections: solid lines indicate the boundary of the pith and the outer limits of true annual rings; small circles show the position of resin canals; broken lines and cross-hatching indicate false annual rings.

of Abies and Pinus, however, resulted in an enormous increase of resin canals, accompanied by false annual rings, the response extending to a distance many times greater above than below the point of application.

Though the evidence in some of our experiments has not been as clear as we could have wished, on account of the occurrence of canals whose presence we did not suspect, yet in every case we have found that the number of canals is increased and that this increase is accompanied by a false annual ring. As we had no contradictory results, we consider the evidence sufficient to prove not only that resin canals are produced by the concealed type of wounding, but that the canals and false rings are associated phenomena, both due to a common disturbance of the normal activity of the cambium. Moreover, wounding of the concealed type has been recognised and its striking results noted, although its general importance and significance have been overlooked in the greater attention given to the study of wounds of the open and more evident type. For example, instances are on record of the enormous production of resin canals induced by frost and by gall-forming insects. In the latter case, however, there is no doubt a slight disturbance of the external tissues in the oviposition. The response in these two instances is of such magnitude as to indicate that greater results can be attained by stimulating the whole cambium than by its local destruction.

With regard to the particular significance of the false annual ring, we are inclined to consider that it represents the weaker type of response on the part of the cambium. It is curious to note in this connection that the thick-walled tracheids of the false ring often have contents, and are really resinous tracheids, the most primitive type of ligneous resiniferous structure. Associated with these there is often parenchyma in the parts near the resin canals, this being also the extreme type of response to slight injuries. From this view point, the precedence in time that the false ring shows might be interpreted as the shock period or the interval between wounding and maximum response. Whatever the explanation, it is clear that we have in the false ring a valuable criterion for the diagnosis of wounding of the concealed type, where the cambium is stimulated but not destroyed, and the woody tissues show no subsequent overgrowth to mark the presence of the wound.

Our experimental results have thus confirmed, not only the importance of the concealed or non-overgrowth type of wound in the production of resin canals, but also the value of the false annual ring as an indication of the presence of such wounds. With this knowledge we may now turn to the consideration of the young cultivated plant and the older form.

6. Nursery Seedlings and Older Plants.

Picea Canadensis IV from the Government nursery at St. Williams illustrates our results with young cultivated stock, though many others were studied for comparison and confirmation. This specimen was six years old, and had an unusual number of resin canals for a white spruce of that age. Indeed, we have found wild forms of the same age without a single resin canal. Table IV, p. 90 (a record of the resin canals in another specimen of *Picea Canadensis*, growing under natural conditions), may be taken to illustrate this rather extreme condition. The plant was seventeen years old, and for the first six years of its life had no resin canals.

The contrast between this plant and the cultivated form we are about to consider will be clearer from a study of the table for the latter (Table III, p. 89). From this it will be seen that the resin canals come in at the second year (1917) and continue from that time with only slight lapses. They even occur in the terminal growth from 1918 onwards, that is, from the time the plant is in its third year, while in the other they are not present in the terminal growth until 1918, when the plant has attained the age of thirteen years. Here there are two at the bottom and none at the top of the year, while in the St. Williams specimen at the age of four years there are nineteen in the lower part and four in the upper. The great number in the cultivated seedling of six years of age may be accounted for when the conditions of growth in the nursery are realised.

These are set forth concisely and clearly in a letter from Mr. F. S. Newman, who is in charge of the station : " Our procedure is as follows : Seed sown broadcast ; beds hand-weeded two years (breakage might occur here in isolated cases) ; lining out at two years of age ; lines during third year hoed and hand-weeded ; lifted and planted out permanently at end of third year or following spring." The possibilities of accident in the nursery may be contrasted with those of the peat bog in which the black spruce, referred to on p. 79, grew.

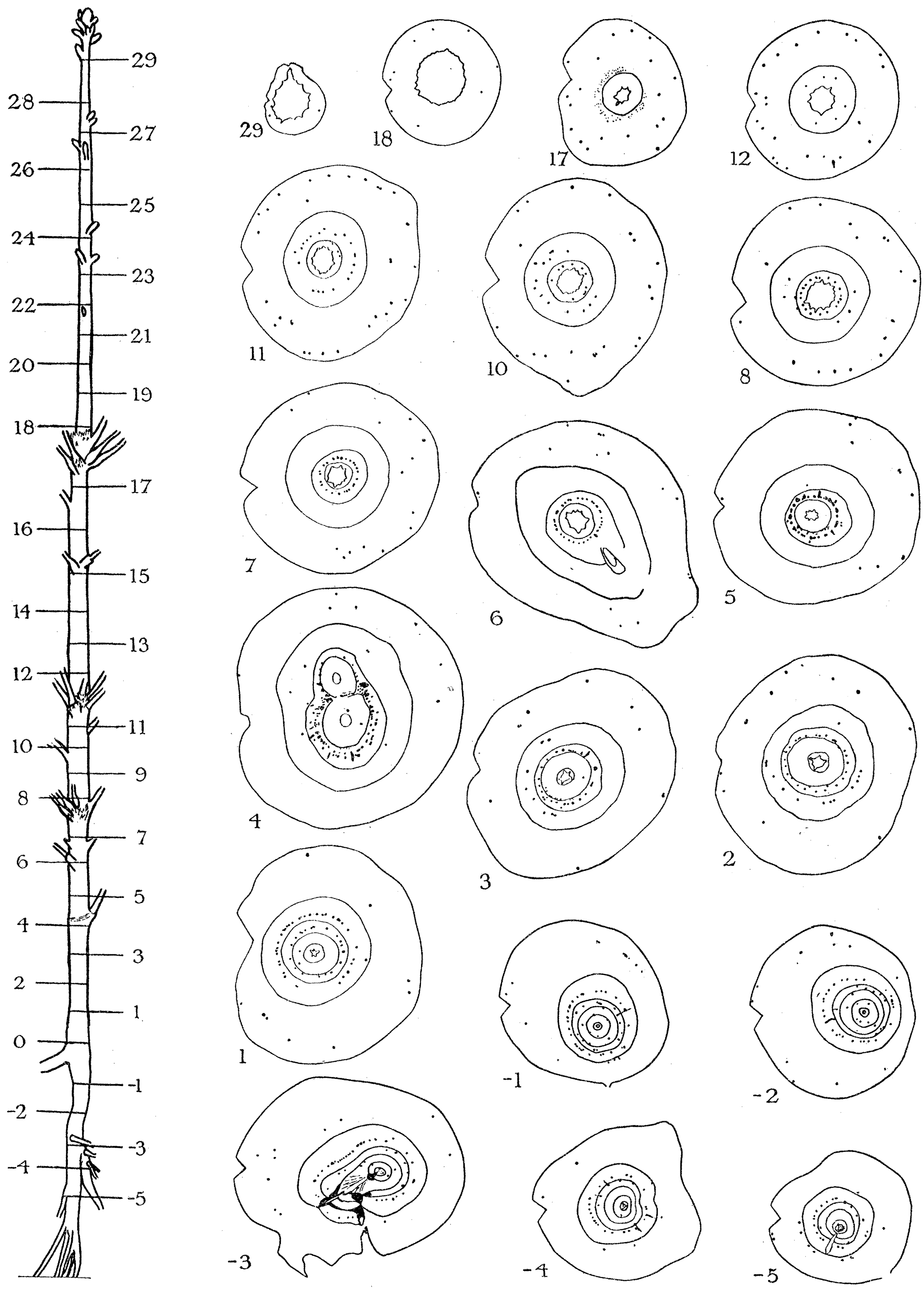
A drawing of the nursery plant about half natural size is shown on the left in fig. 4, in order to indicate the level at which the various sections studied were taken. In all, twenty-nine of these were drawn, but many that are not necessary in presenting the explanation of the distribution of the resin canals and the principle underlying it, have been omitted. Series of sections were also cut from regions requiring further investigation, and some of these have been photographed to illustrate important points.

We shall look first at the general distribution in the second year from the outside, *i.e.*, in the 1920 growth. In No. 17 near the top of the part of the stem, where it has two years of growth in thickness, there are no resin canals in the inner year (1920), and this condition continues, as other sections show, nearly to the base (No. 12), where there are six, which one would never suspect of being other than normal because of their scattered arrangement. In No. 11, where the section shows three years of growth, there are twenty in a rather scattered series, while in Nos. 10 and 8 there is a further decrease to fourteen and then to eight (one double). In Nos. 7, 6 and 5, where the sections have four rings, there are none. There is thus a local set of resin canals in the above region, and in order to find the cause of it, we cut a series of sections through the region of which the branch node between 11 and 12 is the centre.

We have photographed certain sections to illustrate how the serial sections helped in locating and determining the character of the wounding of which there was no external evidence, and the presence of which was only suspected from the local abundance of resin canals. In Photo. 36 (Plate 11), which is just above No. 10,* the resin canals are quite scattered in this second year from the outside, but there is evidence of some physiological disturbance from the presence of a false annual ring about the middle of the year's growth.† This is rather diffuse on the right, but narrower and more definite

* To compare the distribution of the resin canals in the drawing and the photograph, one or other must be reversed in both directions.

† In the drawings of fig. 4 the false annual rings have not been represented.



TEXT-FIG. 4.—*Picea Canadensis* (Mill.) B.S.P. Nursery plant about seventeen inches tall. Left : sketch of the plant, showing the positions of sections made in the preliminary study. Right : diagrams of selected sections to illustrate the distribution of resin canals. The boundary of the pith and of each annual ring is indicated by heavy lines. Dots show the position of resin canals. The numbering of the sections corresponds to that on the sketch of the plant.

TABLE III.—*Picea Canadensis* (Mill.) B.S.P. (*P. Alba,* Link) White Spruce. No. IV, St. Williams, October 20, 1921.

Numbers of resin canals per annual ring at different heights. In this case several sections per year's growth in height are recorded, the section numbers corresponding to those in text-fig. 4, from the same tree.

Section No.	Resin Canals produced each year.					
	1921.	1920.	1919.	1918.	1917.	1916.
29	3					
28	4					
27	5					
26	2					
25	2					
24	2					
23	1					
22	2					
21	4					
20	6					
19	5					
18	9					
17	19	0				
16	21	0				
15	20	0				
14	22	0				
13	23	0				
12	23	6				
11	29	20	4			
10	21	14	10			
9	16	24	11			
8	18	8	19			
7	14	0	24	0		
6	15	0	34	0		
5	11	0	55	0		
4	7	7	106	6		
3	10	9	31	8	0	
2	11	14	28	1	0	
1	9	35	20	2	0	
—1	16	29	14	4	4	0
—2	10	28	9	3	5	0
—3	11	40	8	4	2	0
—4	5	23	6	0	1	0
—5	12	16	5	0	0	0
Age in years ...	6	5	4	3	2	1

TABLE IV.—*Picea Canadensis* (Mill.) B.S.P. (*P. Alba*, Link) White Spruce. No. III, Port Sydney, August 20, 1922.

Numbers of resin canals per annual ring at different heights. At the bottom of the table the growth in height for each of the last nine years is indicated.

Height of Section.	Resin Canals produced each Year.																
	1922	1921	1920	1919	1918	1917	1916	1915	1914	1913	1912	1911	1910	1909	1908	1907	1906
cm.																	
54·0	0																
51·0	0																
47·0	9	1															
45·5	16	1															
44·5	19	6	0														
42·5	27	5	5														
41·0	28	15	6	0													
39·0	30	11	2	4													
38·0	38	26	1	11	0												
36·0	42	31	0	7	2												
33·5	45	33	0	1	1	0											
29·5	25	44	0	5	1	1	0										
25·5	31	27	2	2	1	1	1	0									
23·0	25	37	2	1	1	1	3	0	0								
20·0	15	39	0	3	0	3	0	0	0	0							
18·0	10	35	1	6	0	3	0	0	0	0	0						
15·0	33	40	0	7	2	0	2	0	0	0	0	0					
13·0	29	37	1	5	2	0	8	0	0	0	0	0	0				
10·5	30	39	1	5	0	3	5	0	0	0	0	0	0	0			
6·5	65	33	1	3	1	4	11	1	1	0	0	0	0	0	0	0	
4·0	80	37	0	5	3	2	16	1	5	6	1	0	0	0	0	0	0
2·0	50	42	2	4	7	9	6	0	3	0	0	0	0	0	0	0	0
1·0	34	47	3	3	5	1	8	1	0	0							
0·0	15	13	1	0	0	0											
Age in years	17	16	15	14	13	12	11	10	9	8	7	6	5	4	3	2	1
Growth in height in centimetres	7·7	3·5	3·2	3·2	3·4	3·9	4·1	3·5	3·2								

to the left. At a higher level (Photo. 37) the resin canals are seen to be more definitely arranged and associated with the ring, which begins to appear double, these features increasing farther up, as may be seen by the succeeding Photos. 38 and 39. Photo. 37 comes from just below No. 11, and shows the branch that comes off at this level, while Photo. 39 is from the region just above No. 11. These photographs indicate that the resin canals also become gradually grouped into two series, and that these are associated with the two rings. In fact, the two series become so distinct, both in tangential and radial position (Photo. 38), that one suspects that they have different causes. The inner one is more traumatic in appearance and the reason is apparent a few sections farther on. Photo. 39 shows a branch (No. 1) just above the region where the series was most dense in Photo. 38. The pith of this branch does not extend any farther than is shown in Photo. 40, which is at a higher magnification to illustrate the details, *i.e.*, just to the level of the inner series of canals, as the extent of its black pith indicates. It was broken off here, and has been so completely covered by filling-in tissue that there is scarcely any evidence of a disturbance of the tissues beyond this year. In fact, the filling-in tissue becomes fairly normal in appearance in the later-formed wood of its own year. The condition here may be contrasted with that in the normal branch shown in Photo. 37. Here, in following the series of sections, which are in upward sequence, the pith of the branch gets larger as it progresses farther and farther from that of the main stem, the figure showing it about half-way out. As the broken branch (No. 1) has such a limited growth, it must have been broken off when it was very young, possibly when it was not far advanced from the bud stage. If the canals of this inner series are followed in their upward course through the subsequent photographs of this and the next plate, it will be seen that they become gradually scattered and reduced in number until finally there are only five of them left. (Photo. 52.)

Photo. 38 or 39 (Plate 11) is a good starting point for a consideration of the outer series, where its arrangement in close connection with the outer false ring has been noted. We have already referred to its more or less scattered disposition in the preceding figures. Here it has assumed a definite tangential arrangement on the left side. In Photo. 42 branches Nos. 2 and 3 are seen with piths joining that of the stem. The former comes off at an angle of about 90 degrees to the left of, and the latter nearly opposite, the first branch. In Photos. 43 and 45 the two branches are seen in their farther upward and outward course. The series lies chiefly between these two branches but extends a little beyond each, especially beyond the third, the false annual ring being more distinct in the remainder of its course, on the right of the figures, appearing double in this region. In Photo. 43 there is a local increase and fusion of the series in connection with the third branch, which suggests its greater share in the production of the series. When the tissues at the base of this branch are examined critically they disclose some interesting features. In Photos. 39 and 41 the leaf trace subtending this branch is shown. It displays more irregularity in its tissues and their connection with the stem than normal traces, and the centre of this irregularity is just within the series of resin canals. In fact, the trace itself has a resin canal at the level of the stem series. Above the branch a greater irregularity occurs (Photos. 43 and 44). Here a ray is shown sharply diverted to the left, at an angle of about 30 degrees, and the whole branch displaced in its subsequent course. There is also a lack of symmetry in branch No. 2, especially in the upper part of the connection (Photos. 43 and 45), which will be more apparent by comparison with a normal branch, such as that in Photo. 37, where the attachment is practically bilaterally symmetrical.

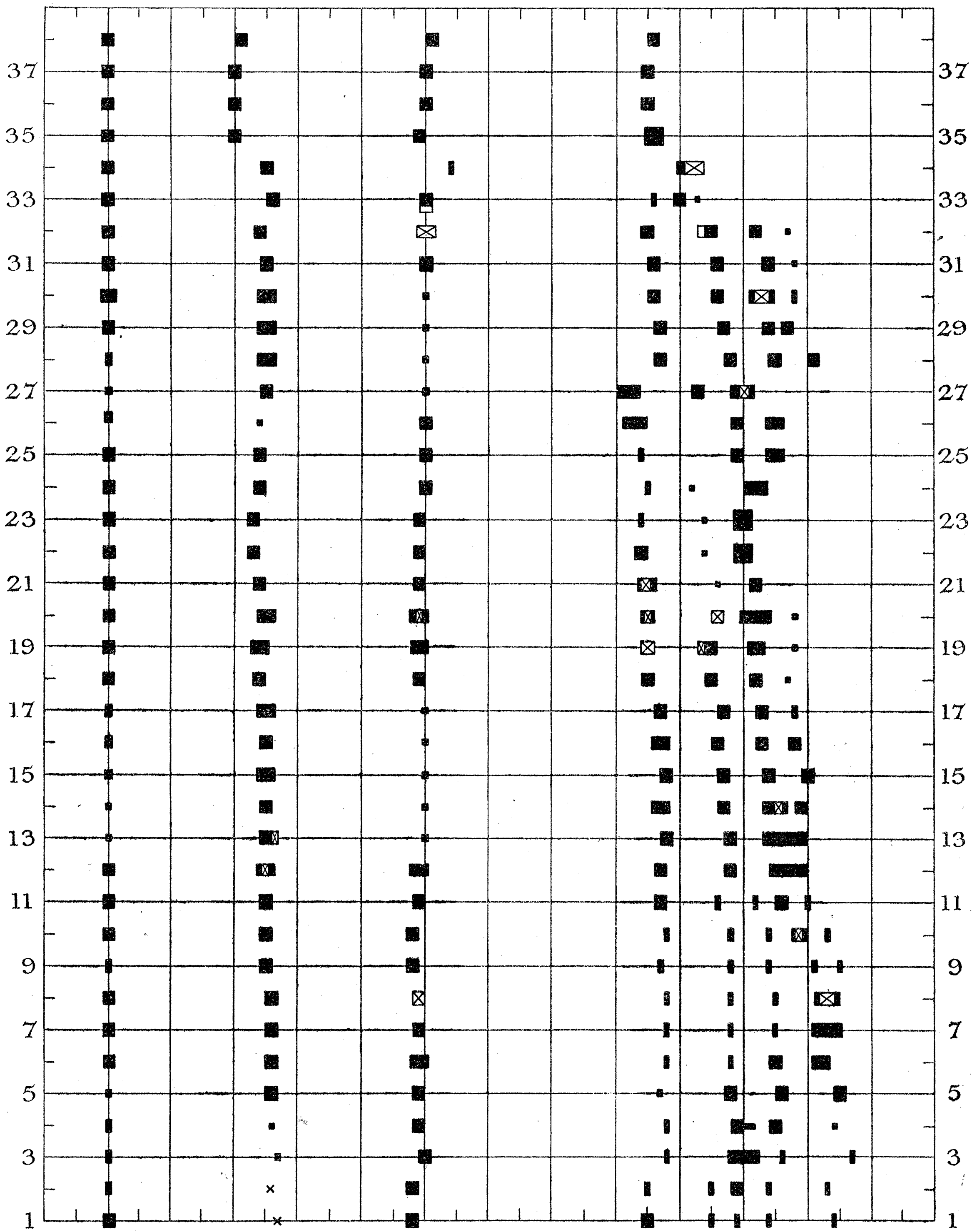
From the features disclosed in the series of sections, it is evident that the branches suffered a lateral downward strain just before the mid-season of their growth, when their tissues were in a soft, growing condition. The agent that injured these two branches, especially branch No. 3, is without doubt responsible for the major part of the outer series of resin canals. In the case of both the inner and the outer series there are small local increases or extensions which are due to minor injuries. For example, the pith of branch No. 4 shows a local disturbance about the level of the inner series (Photo. 47, Plate 12). Since its tissues are very dark brown in colour, the pith especially so (Photo. 48), and since the branch made practically no basal growth either below (Photo. 46) or above (Photo. 49) and no growth farther out except for a short distance, we infer that this branch was injured at the same time as No. 1, and is responsible for the slight extension (to the right) of the inner series that occurs in connection with it. This branch was only injured, and not destroyed as was the case with branch No. 1, on which the major responsibility for the inner series centres. Similarly in connection with the outer series, slight increases to the left, in the middle and to the right, respectively, are associated with branches Nos. 5, 6 and 7 (Photos. 49 and 50). It may be noted also that the resin canals of the stem series extend into the basal region of each of these branches, as well as into those of branches Nos. 1 and 2 (Photo. 42).

There are, in addition, small local increases in both series, especially in the outer, associated with buried leaf traces. For example, the trace of the leaf subtending branch No. 7 (Photo. 47), extended only a little farther out than is shown in the photograph, although others, apparently normal, could be followed to the outside. That the leaves with traces buried early were injured at the same time as the branch and added to the series of canals seems probable, especially since, in contrast to these wounded leaves, normal leaves, and branches as well, are often associated with the elimination of resin canals. An instance of the way in which the normal leaf trace acts is illustrated in Photos. 53–55, taken from a series of sections. Photo. 54 shows the trace extending radially outwards from the pith. In Photo. 55, from a section below, a canal (the lower one about the middle of the inner year) is seen in the region immediately beneath the trace. This canal disappears in connection with the exit of the trace and does not reappear above it as its absence from the section above (Photo. 53) shows. It must not be inferred, however, that normal leaves and branches are always associated with the loss of resin canals, since in many cases the canals simply end blindly at various levels in the ligneous tissues.

Returning to the outer series and following it upwards, the canals are seen to become less numerous and more distant, as shown in Photo. 52, except for one little local series of five above branch No. 7. The course of the false ring is still clear between the scattered canals, however, and although they appear " normal," its presence affords the clue to their traumatic origin.

We have followed this little group of five canals in the series of sections throughout its subsequent upper course in order to determine in detail how a tangential series becomes transformed into the scattered or " normal " condition, and have constructed a diagram (fig. 5) to illustrate the point. The diagram was made from a series of thirty-eight transverse sections from the region above Photo. 52. The courses of three of the scattered series to the left of the five have been added to show how these behave, the left one being used as the base line in measuring the distances between the different sets. A micrometer eye-piece was used for the measurements of both of these distances and of the area of the lumen of each canal in the various sections. This area is plotted in solid black and a medullary ray passing by or through it is indicated by an " X." An " X " in a square or alone indicates parenchyma tissue without a canal. Two measurements of each canal were made at right angles to one another, one radial and one tangential, and the areas plotted accordingly. For example, the base line canal has a large lumen in section No. 1 which is equal in both directions. In sections Nos. 2, 3 and 4 it is only about half the size, the difference being due to lateral contraction. In No. 5 it has contracted to about one-fourth its original size, and this time in both directions equally. The second begins as parenchyma in sections Nos. 1 and 2 and has a small lumen in Nos. 3 and 4, which enlarges and continues so till section No. 12 is reached, when it is pierced by a ray and in the next section has a ray alongside it. The third one of the scattered canals has one peculiar feature. A leaf trace diverted it to the right in section No. 34. With this explanation, the interpretation of the character and course of the short series of five can be followed. It became reduced to four by fusion of two in section No. 3. In No. 9 it became again five, in No. 12 three, etc., until, finally, in section No. 35 it became one and continued so for many sections beyond the series plotted. The changes indicated occurred in less than a millimetre, the sections being about 25μ thick. The irregularity of the courses of the various canals in this series (*cf.* Photo. 19, Plate 9) is perhaps what strikes one most, in contrast to the more direct of the single canals. Once the scattered system is established it usually persists for a considerable distance. Probably it is this fact that has led to the assumption that such canals are normal. They are, however, only the persistent ends of the traumatic series.

Turning again to the diagram, fig. 4 (p. 88), and following the same year's growth (the second year from the outside) below the lapse of canals, as indicated in Nos. 7, 6 and 5, we come to No. 4, where there are seven scattered canals, No. 3 with nine and No. 2 with fourteen, while in No. 1 there are thirty-five which continue through Nos. — 1 and — 2 into the root region, with slight variations, to No. — 3, where a wound is



TEXT-FIG. 5.—*Picea Canadensis* (Mill.) B.S.P. Diagram constructed from a series of thirty-eight transverse sections to illustrate the transition from a tangential series to the " normal " arrangement of resin canals. The canal at the left is used as a base line. Blackened areas indicate the relative size and position of lumina of resin canals in successive sections of the series. Crosses when alone indicate solid parenchyma across the lumen; when accompanied by blackened areas they indicate the passage of a medullary ray across the canal. The five canals in tangential series at the right have united, in a vertical distance equal to the thickness of thirty-four sections, to form a single canal. This extends for a long distance above, following a course similar to those of the three single canals to the left of the figure, which originated previously from similar tangential series.

encountered and the series becomes clearly tangential. This wound was due to a pull exerted by the lateral root shown to the right at the level of No. — 4, possibly caused in the course of transplanting or by frost injury. During the preliminary sectioning this wound was not discovered, but its presence and position were suspected from the appearance of the sections above. A series of sections revealed the wound and its rather severe character. Photo. 57 (Plate 13) is from one of these sections, and shows the tangential arrangement of the resin canals more clearly than the one, slightly lower, from which the diagram was made. The canals occur in more or less close tangential sequence at either side of the wound, and are accompanied by a false annual ring. Especially is the latter easily discernible in the region where the canals of the series become more scattered. The series gets progressively smaller in Nos. — 4 and — 5 (fig. 4), where the single main root divides into several and the canals continue in diminishing numbers into this bunch of roots.

We turn next to the third year from the outside, the growth of 1919, when the plant was in its fourth year, and begin with section No. 11 (fig. 4) with four canals. In No. 10 these are increased to ten, but they are still more or less scattered. In No. 8 there are nineteen, and they show considerable tangential arrangement, while in No. 7 there are twenty-four. In the nodal region, just below No. 8, a series of sections disclosed a concealed wound. The enlarged base of a branch was found in the wood, and though its pith continued farther out than is indicated in Photo. 58 (Plate 13), yet it had several lateral branches coming from it that enabled it to continue its basal growth, which is here quite large. One of these is shown above the break in the branch pith extending to the upper margin of the photograph. Lateral branches have never been observed in nature to come off from normal uninjured branches so close to the main stem, and this and the character of its pith indicate clearly that the branch had sustained a severe injury, which did not, however, prevent subsequent basal growth. Again, the resin canals in the branch are at the same level as those in the stem and continuous with them, as other sections of the series show, making it clear that the branch and stem responses were contemporaneous and establishing the relationship between them. That the wound did not extend into a normal branch is shown by the photograph (Photo. 59) of one of the five branches of the nodal set (between Nos. 11 and 12) that remained on the stem when the specimen was received. This photograph is taken as nearly at the base of the branch as possible, and though there were many canals in the stem, none extended into the branch. We did, however, find a few canals in the basal region of one of the other branches. These branches were cut off before making the series of sections of the nodal region, and, unfortunately, no record was kept of their relative position on the stem, so that we cannot state definitely that the branch with the canals in it is the injured one, though we strongly suspect that this is the case.

A peculiar feature of this nodal region may be referred to here, since it indicates the extent to which nursery stock may suffer from wounding. It is the presence of a local area of secondary growth in the pith, shown at a low magnification in Photo. 58, at one side of the pith. Photo. 64 is at a higher magnification and a little higher up. Here traces of cambium may be seen to the right (outer side) and clearly marked medullary rays, with rows of secondary wood between them. The walls of the wood cells are lignified and have bordered pits on their radial faces. Two bordered pits are to be seen in the middle part of the photograph and some in face view to the left, where the course of the tracheids is oblique. Farther down, in the stem, this medullary growth of wood becomes circular and has a pith of its own (Photos. 62 and 63). In the former the elements are elongated tangentially, while in the latter they run more normally. The origin of this peculiar feature is at present obscure. It may possibly be that a lateral bud or a local portion of the main axis has been pushed into the pith and overgrown. As it is more clearly associated with the branch gap of the buried branch than with any of the others, we are inclined to consider it connected in some way with the wounding of the latter.

Returning to the diagram (fig. 4) and following, downwards from No. 7, the traumatic canals whose cause we discovered in the series of sections through the node between Nos. 7 and 8, we see that the series becomes more dense in Nos. 6 and 5, the explanation of which is seen in No. 4. Here the partial splitting away of a branch is the cause. A series of sections through the part above No. 4 disclosed the details of the wound and its severe character. The wound on the main axis is shown in Photo. 60, to the lower right, between the ends of the series of canals and the displaced branch at the bottom. The stem cambium was destroyed for about one-third of its extent. This resulted in a double series of resin canals and a false annual ring, which partakes somewhat of the " inverse " type, distinct at its inner border and more diffuse along its somewhat irregular outer boundary. Photo. 61, at a higher magnification, shows the overgrowth from the upper end of the wound and a portion of the series of canals and the false ring, the latter in this portion of the section not being so distinctly of the " inverse" type as in the remainder of its course. If we turn again to the diagram (fig. 4), it will be seen that the outer series we are following diminishes in Nos. 3, 2, etc., to No. — 5, where only five canals remain.

In the whole vertical extent of this third year's growth we have thus two wound centres, one just above No. 7, and the other at No. 4. Unlike the two of the next outer year, as already described, the two in this inner year produce overlapping series of resin canals. A reference to the " table of counts " will be instructive in this connection. Table III (p. 89) gives a summary of the resin canal condition in the different years at the level of the various sections. For example, the gap between the two series of the second year from the outside is shown in the 1920 column, whereas in the column for the 1919 growth every section has canals, and though the fourth section with one hundred and six canals is significant of a wound area, there is no indication in the number of canals at Nos. 7 and 8 that a wound was located below the latter, the location of this wound being obscured by the overlapping of the upper series and the one from below. The table, however, makes it more easily evident than do the sections why in 1919 the last year's growth in length produced so many more resin canals (nineteen at the bottom and four at the top) than the corresponding growth of 1920 (six at the bottom and none at the top). The contrast in these two years is the more striking because one would naturally expect the top year's growth when the plant is five years old to have more resin canals than when it is a year younger.

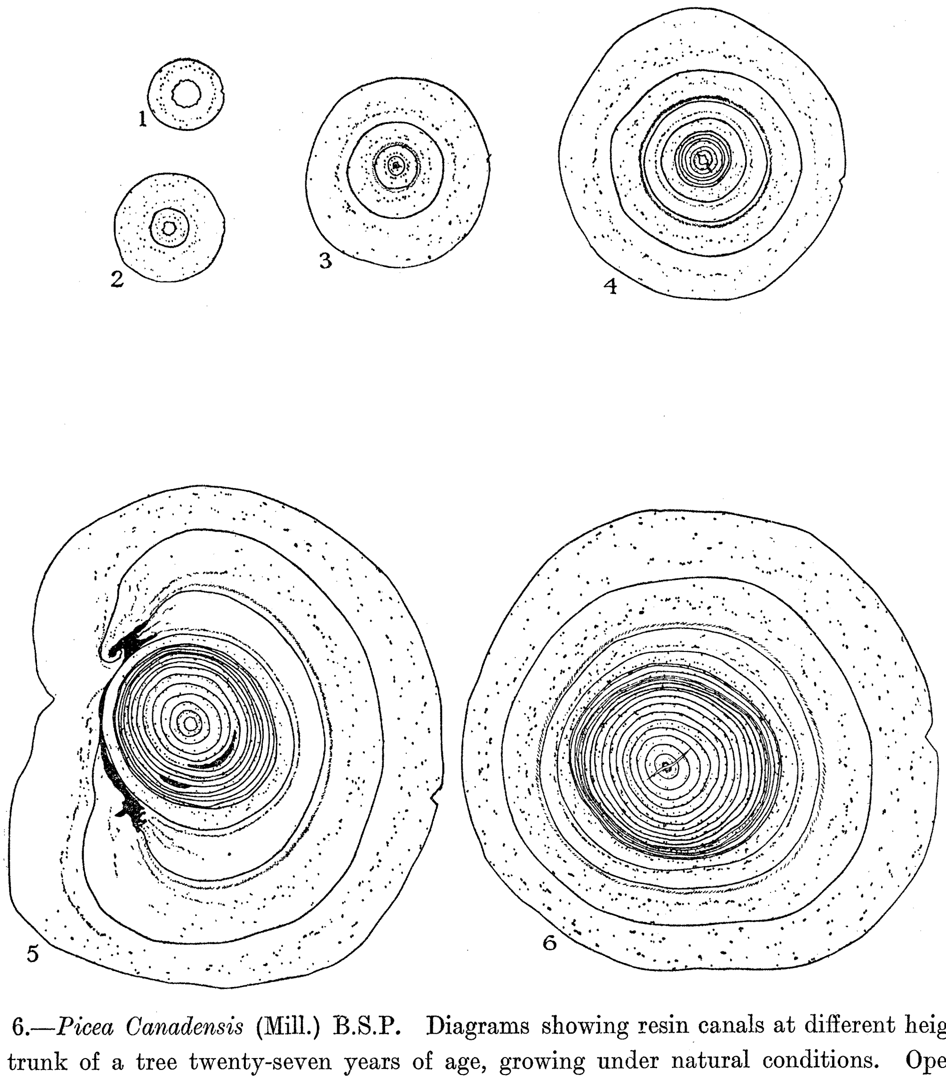
After having seen how the resin canals behave in a young much-wounded nursery plant, we may next consider an older plant, one seventeen years old, of the same species and taken from the open. Table IV (p. 90) shows that this plant had no resin canals in its first six years—a rather striking contrast to the one we have been considering which was just six years of age, but more comparable to the black spruce from the Muskoka bog, which we have already described (p. 79, Photos. 28 and 32, Plate 10). However, our specimens of white spruce were not, as a rule, free from resin canals to so advanced an age as those of *P. mariana*. They came from pastured woods, and we did not secure any from an environment comparable with that in which the other species grew.

To indicate certain features of the difference between the nursery plant of the white spruce and the wild form of the same species, we may refer again to the "table of counts" for these two forms (Tables III, p. 89, and IV, p. 90). It will be noted that there are more sections from each year's growth in height in the case of the nursery plant, the sections being taken at closer intervals and the yearly growth in height of the plant having been greater. This feature does not, however, interfere with the comparisons we are about to make. From Table IV it will be seen that it is not until the wild form is in its thirteenth year that it has any resin canals in the season's growth in height, and here only two at the bottom and none at the top. Nor did this condition persist, for there are none again in the season's vertical growth of 1922, *i.e.*, when the plant was seventeen years old. In the cultivated plant they came in during the third year, with six at the bottom and none at the top, and persisted, there being in the fourth year nineteen at the bottom and four at the top, in the fifth year six at the bottom and none at the top, and in the sixth year nine and three in the corresponding regions.

Again, if the growth in thickness be considered, it will be seen that it is only in the two outermost rings of the seventeen-year-old plant that there is any approach to the number of canals in the three outermost rings of the younger plant. Table IV shows not only how few relatively the resin canals are, but how very sporadic their occurrence s. In the seventh year there is only one in the cotyledonary region, and none in the five years above and in the hypocotyl below. In the eighth year there are six in the latter region and none elsewhere, even in the year-old "secondary" root that has replaced the primary one. In the ninth to the fifteenth years perhaps the most interesting feature is the occurrence of local series. This is characteristic of all the forms we have studied, being especially marked in their earlier years. Its interpretation is sufficiently evident to need no comment. It should be noted, however, that although the presence of local wound centres is masked in the two final years' growth, the sixteenth and seventeenth, by the overlapping of the more abundant canals in these years, yet some centres are still evident. For example, in following the last year's growth upwards, we see that there were fifteen canals at the level of the lowest section which increased to eighty, 4 cm. farther up, again dropping to twenty-nine at 13 cm., etc.

The study of still older plants, moreover, disclosed features that proved most interesting and valuable. The one upon which we spent most time, and of which we made most diagrams, was a white spruce twenty-seven years old. This plant was about eight feet high and two inches in thickness at the base. The diagrams indicating the distribution are so large and so numerous that only a few that illustrate best some further points have been reproduced.

Nos. 1 and 2 of fig. 6 are from the top of the tree where its leader has only one and two



TEXT-FIG. 6.—*Picea Canadensis* (Mill.) B.S.P. Diagrams showing resin canals at different heights in the main trunk of a tree twenty-seven years of age, growing under natural conditions. Open wounds are indicated by blackened areas. No. 1, 1 growth ring ; No. 2, 2 growth rings ; No. 3, 4 growth rings ; No. 4, 10 growth rings ; No. 5, 17 growth rings ; No. 6, 22 growth rings.

years' growth respectively. The presence of numerous resin canals in these provides an interesting contrast to the condition in similar regions of very young plants. In fact, the lower part of this same plant, where there are twenty-seven growth rings, shows an entire lack of canals in the first few years' growth. Photos. 65 and 66 (Plate 13) illustrate sections from the same region as the drawing. The distribution of the canals here is such that they might be considered normal were it not for the presence of the false rings, clearly seen in the photographs.

In No. 5 a severe wound of open type is shown, with the overgrowth features in the year in which it was inflicted as well as in the two succeeding years. The wound area has been blackened in this case to show its extent and the two black areas farther in are faults left by similar wounds. The immediate response to the large wound is shown by the extensive tangential series, continuous from one edge of the wound to the other. Later in the year of wounding it formed short series on either side—four in all, in one year. In the next year out there are series at the sides of the wound, and a slight recurrence of the same thing in the third year. How much longer the effect might have persisted cannot, of course, be stated, but since the overgrowth is complete in this third year, it is not probable that there would have been much of it in the succeeding year. A wound may then effect at least three successive years of growth in thickness with tangential series in a tree of this age. From a study of the character of the response indicated in these three years' growth it is evident, not only that the wound stimulus persists, but that its action is more concentrated and definite in the vicinity of the wound, and more diffuse and sporadic at a distance. Thus in the year of the wound there are very few scattered canals, while the reverse is true of the outer years. So rapidly, and to such an extent, has the scattering in these been attained that, had a piece of the wood including only the two outer years' growth in the region opposite the wound been examined, it is very improbable that the canals would have been suspected of being other than normal by anyone not knowing the facts already disclosed in connection with wounding.

Again, when the complete section is examined it will be seen that there is sufficient evidence in it to demonstrate the controlling influence of a wound, not only on the resin canals produced by it, but on those formed by preceding ones. In the years just before the wound figured there are scattered resin canals. Had this wound not occurred it is only reasonable to infer that there would have been a continuation of the scattered arrangement in the extensive region where consolidation into one tangential series has been effected. It would thus appear not only that the wound stimulus can persist, but that it can be added to and co-ordinated with that of a later wound.

Though the radial persistence and tangential spread of the response to a wound are sufficiently striking, the vertical extent is even more so. When the wound year (third year from the outside) in the sections above and below is examined, the fact that the effect can extend for several years in both directions will be clear. For instance, No. 6 has twenty-two annual rings and No. 4 ten, and yet the evidences of traumaticism are clear in both, more so in the latter than in the former; but this appearance may be accentuated by the exigencies of the diagram, the canals having been represented by the same sized dots, and the circumference being less. However, an examination with the microscope shows that the tangential arrangement of the series in the two is about the same, and it is for this reason that we chose these sections for illustration. The upper section is seven years above the wound and the lower one five below it, the wound being where there are seventeen annual rings. It must not be inferred, however, that the fact of a relatively greater response above than below the wound is essential to the accumulation of canals in the inner years above. The absolute extent and the fact that it passes through the nodal region into the younger years are the determining factors.

The reason for the great extent of the vertical response in comparison with the radial is probably due to the fact that the cambium is active throughout the whole vertical extent of the tree at the time of the wound, whereas in the course of its radial activity the cambium passes through dormant winter periods. There are also greater facilities for vertical distribution in connection with the currents in the tree.

When the young plant is examined for comparison with the older form it will be seen how little evidence of response in succeeding years it shows, and how evanescent here the wound stimulus apparently is. Any of the wound areas in fig. 4 or in the photographs of Plates 10–13 will showt he lack of persistence of the stimulus in the radial direction. Special attention may be directed to Nos. 5 and 7 of fig. 4, and to Photo. 60 (Plate 13). In the latter there are only three canals in the year succeeding the wound, and yet there is a double series of numerous canals in the wound year itself. When the vertical extent is compared, the prevalence of local series in the young plant will be recalled, and the further fact may be instanced that, though the wounding of the young nursery plant (fig. 4) was very severe, none of the response to wounds was carried into the innermost year to any great extent except in the case of the nodal regions between Nos. 7–8, in and below which there were several severe wounds. Even here, after the canals were established at the base of the year (No. 8), their number rapidly decreased, as may be seen in Nos. 10 and 11. (Note the short distance on the stem between these numbers.)

From the comparison of the responses of young and older forms, it is evident either that the plant developes responsiveness to wounding, or that there is an accumulation of the wound stimulus in the older parts. However the cause of greater accumulation of resin canals in the older parts of the plant may ultimately be explained, the fact has a distinct bearing on the phylogenetic interpretation that is sometimes put on the occurrence of resin canals in cone axes, vigorous branches, etc., of mature trees. In the case of Picea at least these are the result of wounding, and we strongly suspect that when the contentious forms themselves are studied more carefully in the light of the present investigations a similar interpretation will be found to hold. Their sporadic occurrence would then be associated with the contingency of wounding, and not with their character as vestigial structures. In fact, their presence would be interpreted as a cenogenetic feature, the forms having them in greatest abundance being the most specialised.

As in the case of the histological structure of the ligneous resin canals, a comparison of the spruce with the pine and the balsam was made, so here we may compare these forms in the gross features of the arrangement of their resin canals produced by wounding. In Abies sometimes several tangential series of canals occur in response to wounding. This indicates that the wound stimulus persists and acts intermittently, as in the spruce, so that Abies has the basic feature of radial scattering. The recurrent stimulus, however, acts more definitely in Abies than in Picea, resulting in another tangential series, while in Picea such subsequent tangential series are confined to the neighbourhood of the wound, and the main response is of the scattered type. Tangential scattering is of limited extent in Abies, but it occurs at the sides as well as above and below the more compact response. Thus a transverse section above or below the tangential series may appear completely "normal." In the pine the presence of tangential series is rare and, when present, of limited extent, while scattered canals are very numerous. The pine thus shows a condition in its response to wounding the inverse of that of the balsam, while the spruce occupies an intermediate position.

Thus far we have practically confined our attention to the traumatic origin of the vertical canals. That the horizontal series owes its presence to the same cause might be inferred from what we have already shown in connection with the origin of horizontal from vertical canals (p. 74). We have traced also their distribution in connection with wounding. To demonstrate this, one has only to take a wounded *young* plant and carefully cut away the outer primary series of the cortex. Then cut carefully a little deeper, and the bulbous expansions of the horizontal canals of the bast will come into plain view to the naked eye. The concentration in the wound areas is so marked and so easily demonstrated that we have not considered it necessary to illustrate the point. Ordinarily air-dried material is best for the purpose, as the tissues are more resistant than when the plant is just brought in. A sharp razor should be used so as avoid tearing the tissues and obscuring the canals.

7. The Root—Special Environmental Conditions and their Results.

The root has come to be somewhat generally considered as a more conservative organ than the stem, largely because of the centripetal growth of its primary wood—a type of growth found in stems, cone axes and leaves of certain more primitive types of plants, but eliminated from such regions in higher forms. While the conception of the root as a primitive organ may be helpful when supported by evidence from other sources, it is well to emphasize the necessity of using it very carefully, for the root has proved itself quite capable of specialization when such is warranted by the conditions of its environment. An example of this facility might be mentioned—the attainment of the specialized rootcap of the Angiosperms with its own initial cells, the calyptrogen. This structure has apparently come into being by a process of evolution whose stages are retained in lower living vascular plants. In the Gymnosperms, the periblem, dermatogen and calyptrogen are not mapped out in distinct regions as in the Angiosperms. The condition in Lycopods is still more primitive, while in horsetails and typical leptosporangiate ferns, a single, conical cell, of the same type in both stem and root, is responsible for the growth of all the primary tissues, the apical cell of the root producing from its basal region cells to form a protective covering of limited extent. Indeed, in some species* of Platycerium and Asplenium the apical cell of the root is so undifferentiated that it may form a stem when necessity arises. The plasticity of the root is further emphasized by the fact that the higher forms, under changed œcological conditions, may lose the rootcap, as in Lemna, where "root-pockets" take its place, and in Cuscuta, with its ephemeral root system.

In view of such facts, it is not unreasonable to enquire whether even the retention of centripetal primary xylem and the lack of a definite pith in most roots may not be due to special conditions under which this organ grows and functions. To penetrate soil, a solid core is advantageous, and from this viewpoint the centripetal growth of the primary wood, often meeting in the centre and eliminating the pith, is a decided advantage. Moreover, the functioning root is subjected chiefly to pulling stresses, and the hollow cylinder evolved in stems standing erect in the air where lateral strain must be overcome is a non-essential to the perfect functioning of the underground organ.

With this introduction we may proceed to deal with the resin canals in the root of Picea, considering first those in the primary xylem. Photo. 32 (Plate 10) is from a section of the tap root of a black spruce, just below the transition zone between hypocotyl and root. In this region the primary diarch plate of xylem is well established, and yet here, in every instance examined, we found no primary resin canals present. These come in later, the time of their inception varying considerably in different individuals. At a level somewhat lower than that of the photograph solid masses of parenchyma appear in the protoxylem. These in turn are succeeded by series of short cysts separated by solid portions practically equalling them in length. Still farther below the cotyledonary region the cysts are found to be much elongated, the parenchyma partitions between them shortened, and the typical adult condition established. Throughout the growth of the root, such canals are occluded at intervals by the parenchyma partitions. They are thus cystose, and differ in this respect from the primary cortical canals of the stem, the lumen of which extends throughout the whole season's growth in height. Photo. 67 (Plate 13) shows the canals as established in a peripheral root of the diarch type from an adult tree, and Photo. 30 (Plate 10) in one of the triarch type from a secondary root of a younger plant.

When the origin of these primary ligneous canals is traced from the growing point of the root-tip backwards, it is found that for a considerable distance—as much as 10 cm.

* Rostowzew, 'Flora,' vol. 48, p. 155 (1890), and Goebel, 'Organography,' vol. 2, p. 226.

in some cases, from the primary meristem—they are represented merely by solid masses of parenchyma, although the primary wood is established and even the secondary is often of considerable thickness. If the law of recapitulation be held to apply, one must believe, from their late appearance both in the seedling and in the tips of older roots, that the presence of primary resin canals in the root of Picea is not a primitive or ancestral condition, but a more recent acquirement. Such a conclusion is in agreement with the well-known lack of canals in the root of the fossil ancestors of the conifers, the Cordaitean forms. In view of the evidence brought forward in an earlier section of this paper as to the production of secondary resin canals, and also of the facts stated as to the evolutionary plasticity of primary root meristem, it would seem reasonable to suspect that here also we may have a response to pressure and irritation, resulting from the pushing of the root-tip through the soil. Experiments planned to throw light on this problem are proceeding, but as yet incomplete.

Before dealing with the resin canals of the secondary wood of the root it will be of advantage to review some of the special conditions that render roots liable to injury. The lack of permanence in both the primary and later formed roots, already referred to, indicates the severity of these conditions. The struggle for supremacy that results in the loss of branches, especially of forest trees, is a matter of general knowledge, but the struggle among the roots is confined to a comparatively thin horizontal plane, and is the more intense on this account, a feature the effect of which is not so generally realised. That the struggle results in the loss of roots seems only a fair inference from the parallel with the stem. Factors that have little or no effect on the stem also play an important part in connection with the root. One is the marked pressure that roots exert, not only upon one another, but upon the surrounding soil. The resultant contorted shape and the many fusions, one root with the other, are only exposed to view by chance ; for example, along a mountain path or when a stump is overturned.

A brief reference to a peculiar case of root-grafting in the Douglas fir, to which Mr. PEMBERTON,* of Victoria, drew our attention, may not be out of place here. He found certain stumps capped with an overgrowth of tissue and determined that such stumps have root fusions with living trees. In one case the nearest living tree was distant about fifty yards, but Mr. PEMBERTON had an excavation made and found the root graft. Though this is no doubt an unusual feature, yet fusion of the roots of the same tree is quite common, as may be seen from the examination of un upturned stump, especially near the stem where there is much crowding. Natural grafting of stems is a much less common, indeed a rare phenomenon.

Frost is another factor that probably influences roots more than stems. The well-known " heaving " action of frost may be instanced as well as the splitting apart of roots by ice formation between them. The latter factor is especially in evidence near the stem and where the root forms branches at an acute angle. In Photo. 70, Plate 14,

* An article has since been published. (PEMBERTON, C. C., " Overgrowth of Stumps of Conifers," ' The Canadian Field Naturalist,' May, 1921, pp. 81–87.)

a split has occurred above the two closely approximated roots at the right, while there is none in connection with the wider forking at the left. Frost may also be mainly responsible for the tremendous loss of laterals that a main root shows. We dug out carefully several roots about 20 feet long from a white spruce a foot or so in diameter near the base. In digging these roots, which grew in soft soil, the greatest care was exercised to avoid destroying any laterals. That few, if any, were torn away during the process is shown by the abundance of rootlets remaining attached to the terminal growth, where they have not yet been removed by natural processes. Here, and on the tips of the small laterals, the rootlets come off fairly regularly at very short intervals (Photos. 68 and 69, Plate 14), in many instances less than an eighth of an inch. As Photo. 68 shows, a very great proportion of the laterals is lost early in the life of the root. It is possible that the swaying action of the stem is the chief cause of their detachment. That such action is confined to winter, however, does not seem probable, and one has only to stand on the roots of a tree in a summer gale to realise its extent and probable action at any season.

Injury to roots from the hoofs of passing animals, whether by the tearing away of laterals or by direct wounding, is without doubt an additional factor that plays no small part in the sum total of the traumatic phenomena in the root. The ultimate result is a well-developed system of resin canals, both horizontal and vertical, occurring here as in the stem in response to wounding.

A few illustrations will make the condition in the root clear. Photo. 32 (Plate 10) is from a section through the primary tap root of a black spruce seedling, which, as before stated, came from a peat bog in Muskoka, where there were no domestic animals. Though it is six years old, not a single resin canal was found in the secondary wood of the whole plant. Photo. 30 is from a section of the "secondary" tap root of a seventeen-year-old white spruce at a level where it shows a sudden drop of seven years, and presents a very different condition from the previous one. The secondary wood has no resin canals in the first two years, and then they appear, one in the third year and eight in the fourth, associated with false rings in each case. In another instance we found them appearing earlier, in the second year, where they were associated with an open type wound, and, as the wound was large, in the form of a small tangential series. Such series seem rare in the earlier years of the primary root region. In the later years of this region, however, good tangential series are frequently met with. Photo. 57 (Plate 13), from the nursery plant of the white spruce, illustrates such a series in the fifth year.

Photo. 67 shows the condition in the inner growth rings of a root from an old tree, at a distance of about 15 feet from the stem. There are five canals here in the first year, in addition to the two in the primary wood, and these canals are in scattered arrangement. This is, according to our experience, a rather extreme number of resin canals, even for distal roots of an old tree. A series of sections revealed the cause, which proved to be a severe injury to the root near its tip. This injury, at a distance of

TABLE V.—*Picea Canadensis* (Mill.) B.S.P. (*P. alba* Link) White Spruce.

Resin canal production in the root of an old tree, covering several years' growth in length. Attention is directed to the lack, in 1920, of the year's growth in length, and to the sporadic distribution of the canals, which is as characteristic here as in the stem.

Numbers of resin canals indicated as in former tables. From one to several sections of each year's growth in length are recorded.

Resin Canals produced each Year.							
1923.	1922.	1921.	1920.	1919.	1918.	1917.	1916.
3							
0	2						
2	2						
0	2						
0	6	0					
2	2	5*					
4	2	2					
7	5	2					
14	3	2					
18	11	34	2	2			
2	4	17	0	4			
4	3	17	0	4	0		
5	1	21	0	3	1		
12	11	5	1	5	2		
7	10	8	2	1	5	0	
7	13	5	2	5	3	1	
5	22	19	5	2	4	5	
1	23	0	13	4	3	3	3

6 cm. from the section photographed, produced a considerable disorganisation of the tissues, most of the metaxylem having been replaced by parenchyma. Table V, above, has been constructed from a portion of the same root, including the section photographed, to give a better idea of the variation in the number and distribution of the vertical resin canals. It includes eight years of growth. As in the stem (Table III or IV), a remarkable lack of uniformity of distribution is evident. Though "local" series are not abundant because of the overlapping, yet the presence of the wound areas is as clearly marked as in the stem.

When series of sections of these distal roots of old trees are followed, one finds sudden drops in the number of annual rings like those already referred to in the tap root region. One such drop is shown in Table V, where no growth in length for 1920 is recorded.

* This is the section from which Photo. 67 was made.

Such occurrences are frequent throughout the course of the older roots, and indicate in a most striking manner the severity of the wounding to which the roots are subjected.

Reference has already been made to the great loss of lateral roots. An examination of the exterior of the root shows small lenticel-like areas which indicate the position of the buried vestiges of these structures. The root periderm grows so rapidly that such evidence is soon obliterated. Indeed, even when a fairly large wound of the open type occurs in a root, it is so quickly overgrown that it is soon very difficult to locate. Series of sections in the region of the buried traces disclose slight local increases in the number of canals. We did not find, however, tangential series like those already described as occurring in the case of the buried branches in the stem (*see* certain Photos. of Plate 11). The injuries accompanying the loss of these roots, though slight, recur at such short intervals and result in so much overlapping that the separate responses are merged in a general effect. The importance of such injury, however, can scarcely be overestimated in connection with the occurrence of resin canals in the inner year's growth of old roots. False annual rings apparently do not accompany the loss of these small rootlets, although, when the disturbance of the cambium is more pronounced, they are present in peripheral roots just as in the tap root. When present they resemble the true annual ring of the root type with its narrow, sharply delimited zone of summer wood.

Like the stem, then, the root shows a progressive response to wounding from the seedling to the adult condition, and an accumulation of resin canals in the more distal parts. The false annual ring is often less distinct here than in the stem, the reason for which seems to be connected with the more open character of the wood in distal roots—perhaps also with the more diffuse arrangement of the canals.

A further feature in connection with the loss of the lateral roots might be mentioned here. There are horizontal canals in the secondary wood of the root that originate at the canals in the primary wood and are associated with the vestiges of lateral roots. These continue beyond the buried remains of the laterals into the later formed secondary wood and bast of the main root, and are so similar to the ordinary horizontal ones of the medullary rays as to be readily mistaken for them. The fact that they occur often in pairs, and at a very slight tangential distance apart, is helpful in establishing their identity. On being traced inwards the pairs are often found to join just before the primary canal of the main root is reached.

8. Conclusions.

1. Anastomosis of the different systems of resin canals is far from the rule in Picea :—

(*a*) No single instance of anastomosis of the primary cortical resin canals with those of the adjacent bast in the *stem* has been found, even where wounding has produced an excessive number of resin canals. In the *root*, primary cortical resin canals are wanting.

(*b*) In the case of the stem we found no evidence of anastomosis between the vertical and horizontal systems or between the canals of the wood and bast. The same is true of the seedling root, though in the distal roots of mature trees a certain amount of anastomosis does occur.

2. With the exception of those in the primary cortex of the stem, and possibly in the root wood of mature trees, the resin canals in Picea are composed of series of cysts separated by parenchyma.

3. The bast has only one type of canal, the horizontal, occupying secondary medullary rays and characterised by series of bulbous expansions, which might easily be mistaken for vertical canals such as occur in the wood, if single sections only are studied.

4. The horizontal canals are confined to the secondary medullary rays and are never found in the primary. They originate in association with vertical canals in the wood.

5. The canals in the primary cortex of the stem, and those in the secondary bast of both root and stem continue growth, adding considerably to their original size and the thickness of their walls by "cambial" activity. This is not true of the canals in the wood.

6. That increased food supply or great vigour of growth is the prime cause of resin canal production is disproved by the lack of correlation between these factors and the distribution of resin canals in Picea.

7. In the secondary tissues of young spruce growing in protected situations resin canals are often lacking from the first few years of growth. They are present earlier and in greater abundance where the plants are more exposed to injury. In the latter instance dwarfing is a usual concomitant feature. When the canals are present in secondary tissues, we have never failed to find connected with them either direct evidence of injury, or a false annual ring, or both.

8. Our experimental work has shown that the false annual ring may be caused by a variety of conditions that injure or irritate the cambium, but need not be of such a nature as to destroy the cells and produce a typical overgrown wound, and that such conditions also produce resin canals. It is therefore concluded that all resin canals in the secondary tissues of Picea are caused by injury to, or irritation of, the cambium.

9. In proximity to the wound, the resultant canals are arranged in a more or less close tangential series. At a short distance from the wound centre they scatter both tangentially and radially, the arrangement being more diffuse as the distance from the wound increases. Thus the accepted practice of restricting the term *traumatic* to such canals as occur in close tangential series overlooks the major portion of the response. Not only so, but it gives a fallacious and misleading idea of the origin of the scattered type of resin canal.

10. In young spruce with few wounds the resin canals are in isolated groups associated with the individual wounds, while in old trees which have undergone many injuries the delimitation is not complete, because of overlapping among the responses. There is also an appearance of increased sensitiveness with age. In any case the effects of the

numerous wounds accumulate and overlap to such an extent that the resin canals are much more abundant and much more uniformly distributed than in the young plant. The mature spruce, however, never attains the abundance and the degree of regularity found in the pine.

11. The condition in the secondary wood of the root, except for the more open character of the canals, is similar to that in the stem. A great amount of injury is sustained by the root, and results in a well-developed system of resin canals.

12. Canals are not present in the primary wood of the root in the early tissues of the seedling. When they do appear they are preceded by solid parenchyma, which recurs at intervals, close at first, and later more distant, until the mature and more open condition of the canal is attained. In the distal roots of old trees the canals do not appear for a considerable distance from the growing point, and are preceded by solid parenchyma. These features indicate that the presence of an open canal is not the primitive condition. This conclusion is in keeping with the absence of resin canals from the primary wood of the root of primitive forms of living and fossil conifers.

13. The results of this study of Picea have a distinct bearing on at least two general aspects of the resin canal problem in the conifers. In the first place, we have, in the accumulation of wound stimuli, an œcological explanation of the sporadic occurrence of resin canals in the outermost branches of mature trees of species from which they are otherwise absent; and, in the second, the whole body of evidence from the study of Picea favours the hypothesis of a phylogenetic increase of sensitiveness to wound stimuli among the conifers.

9. Acknowledgments.

From the Ontario Forestry Nursery at St. Williams we received our supply of cultivated material, while Messrs. Alfred Kay and A. Simpson have given much appreciated assistance in connection with the securing of material from the wild. To Miss Myrtle McCullough, M.A., formerly Technical Assistant here, now of the Seed Branch, Ottawa, and to Miss Myrtle B. Givens, B.A., the present Technical Assistant, we are indebted for most valuable help with the work.

10. Description of Plates.

Plate 8.

Photo. 1.—*Picea canadensis*. Transverse of old stem wood. × 15. Distribution of resin canals.

Photo. 2.—*Pinus Strobus*. Transverse of old stem wood. × 15. Distribution of resin canals.

Photo. 3.—*Picea canadensis*. Transverse of stem. × 35. Resin canals of bast and primary cortex.

Photo. 4.—*P. canadensis*. Radial of cortex of stem. × 240. Secondary growth in the wall of a resin bulb in the bast (right of photograph), and of a vertical canal in the primary cortex.

PHOTO. 5.—*P. canadensis*. Radial through bast of stem. × 95. Horizontal resin canal enlarged into a series of bulbs. There were two more such bulbs beyond the region of the photograph.

PHOTO. 6.—*P. canadensis*. Radial through bast of stem. × 240. Lining cells of resin bulb in face view.

PHOTO. 7.—*P. canadensis*. Radial through bast of stem. × 95. Meristematic growth in thickness of the walls of resin bulbs. The older bulb (left) has more layers in its wall than the younger.

PHOTO. 8.—*P. canadensis*. Radial through cortex of stem. × 45. Canal of the primary cortex (left) with resin bulb of the bast near by, but not anastomosing with it.

PHOTO. 9.—*P. canadensis*. Radial through bast of stem. × 95. Bast parenchyma cells near the cambium (right), and those farther out in the region of the large bulb.

PHOTO. 10.—*P. canadensis*. Tangential through wood of stem near cambium. × 240. Lumen of horizontal canal still small.

PHOTO. 11.—*P. canadensis*. Tangential through cambium of stem. × 225. Multiseriate ray in bast (above) and in wood (below).

PHOTO. 12.—*P. canadensis*. Tangential through old bast of stem. × 95. Resin bulb and bast parenchyma below it.

PHOTO. 13.—*P. canadensis*. Tangential of bast of stem. × 45. Resin bulbs with remains of multiseriate rays. Appearance of bast parenchyma nearer the cambium than Photo. 12.

PHOTO. 14.—*P. canadensis*. Tangential through bast of stem. × 95.

PLATE 9.

PHOTO. 15.—*Picea canadensis*. Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 16.—*P. canadensis*. Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 17.—*P. canadensis*. Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 18.—*P. canadensis*. Radial of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 19.—*P. canadensis*. Tangential of stem. × 35. Resin canals and medullary rays.

PHOTO. 20.—*P. canadensis*. Transverse of stem. × 240. Resin canals and medullary ray.

PHOTO. 21.—*P. canadensis*. Tangential of stem. × 95. Resin canals and medullary rays.

PHOTO. 22.—*P. canadensis*. Tangential of stem. × 95. Resin canals and medullary rays.

PHOTO. 23.—*P. canadensis.* Transverse of stem. × 95. Tangential series of resin canals.

PHOTO. 24.—*Abies balsamea.* Transverse of stem. × 95. Tangential series of resin canals.

PHOTO. 25.—*Picea canadensis.* Transverse of stem. × 240. Structure of resin canals.

PHOTO. 26.—*Abies balsamea.* Transverse of stem. × 240. Structure of resin canals.

PLATE 10.

PHOTO. 27.—*Pinus Strobus.* Transverse of stem. × 240. Structure of resin canals.

PHOTO. 28.—*Picea mariana* seedling six years old. Transverse of cotyledonary region. × 90. (First annual ring indistinct.)

PHOTO. 29.—*P. canadensis.* Transverse of stem. × 240. False annual ring.

PHOTO. 30.—*P. canadensis.* Transverse of tap root. × 15.

PHOTO. 31.—*P. canadensis.* Transverse of stem. × 35. Resin canals associated with false annual rings.

PHOTO. 32.—*P. mariana.* Same seedling as Photo. 28. Transverse of primary root just below hypocotyl. × 90. (First annual ring indistinct here also.)

PHOTO. 33.—*P. Omorica.* Transverse of branch. × 25. False annual ring and extra resin canals resulting from continued pressure by clothes-peg.

PHOTO. 34.—*P. Omorica.* Transverse of root. × 240. Resin canals resulting from continued pressure by clothes-peg.

PHOTO. 35.—*P. pungens.* Transverse of leader. × 35. Resin canals resulting from slight crushing with pliers.

PLATE 11.

PHOTOS. 36, 37, 38, 39, 42, 43 and 45.—*Picea canadensis.* Transverse sections from one plant. × 15. Connection between resin canals and wounds.

PHOTOS. 40 and 41.—*P. canadensis.* Portions of Photo. 39. × 35.

PHOTO. 44.—*P. canadensis.* Part of Photo. 43. × 95.

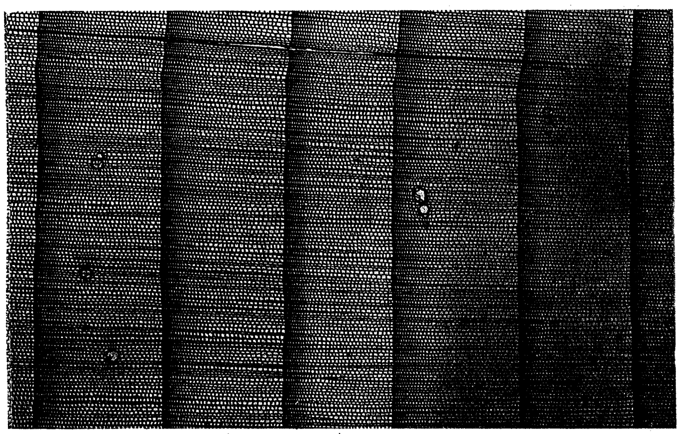
PLATE 12.

PHOTOS. 46, 47, 48, 49, 50, 51, 52 and 56.—*Picea canadensis.* Transverse sections from same plant as those of Plate 4. × 15.

PHOTOS. 53, 54 and 55.—*P. canadensis.* Transverse from same plant. × 35. Illustration of loss of a resin canal at a leaf trace. Photo. 53 above, Photo. 54 at level of, and Photo. 55 below leaf trace at which the resin canal is lost.

PLATE 13.

PHOTO. 57.—*Picea canadensis.* Transverse of tap root of same plant as those of Plate 5. × 15. Wound and tangential series of resin canals.



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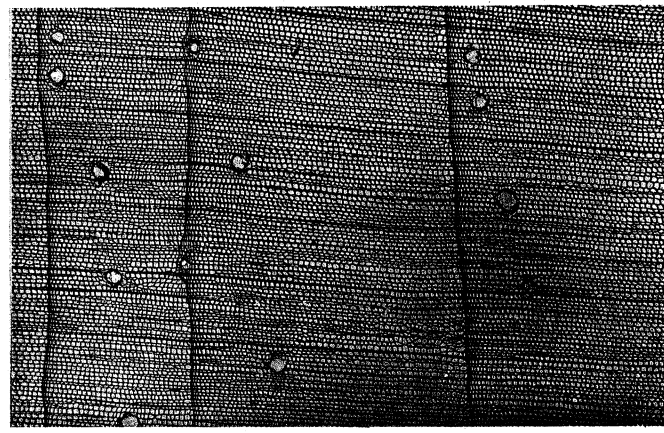

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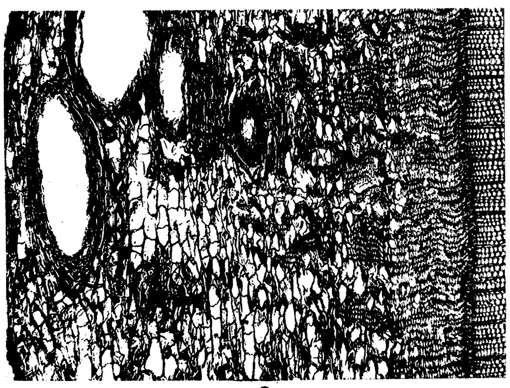

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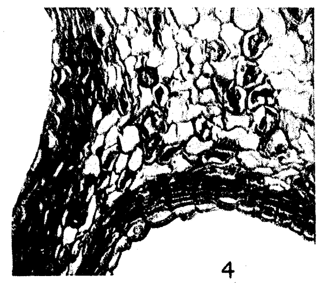

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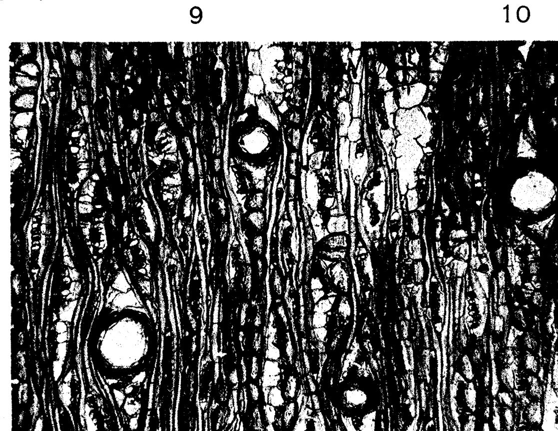

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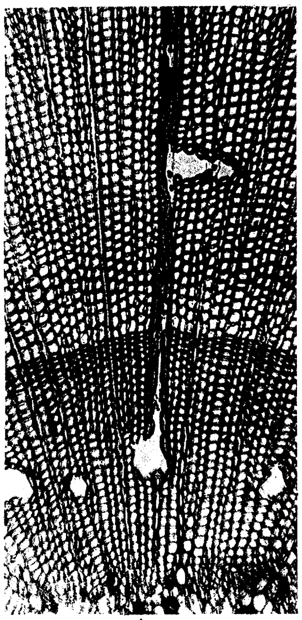

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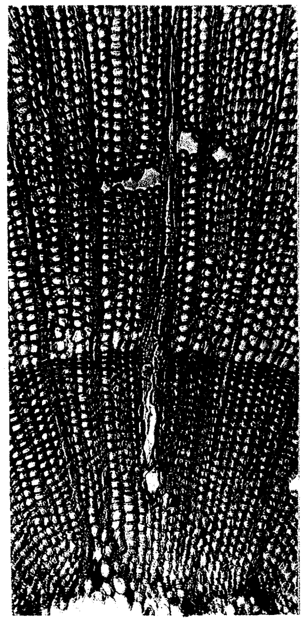

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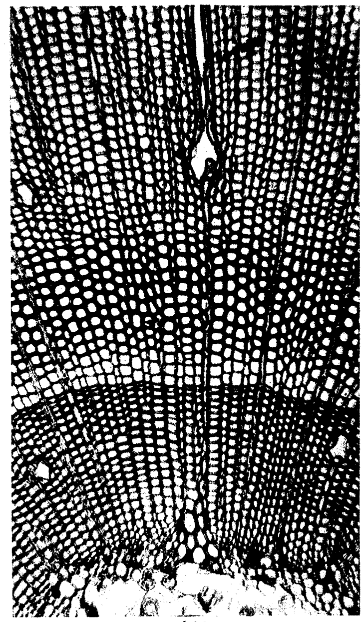

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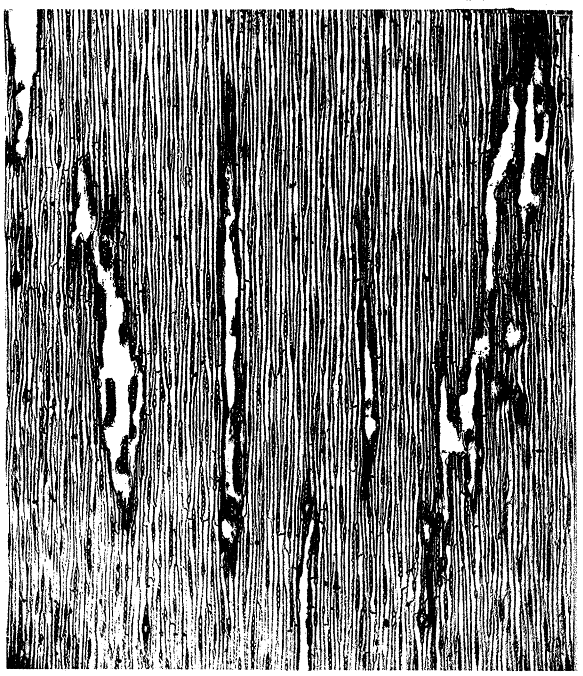

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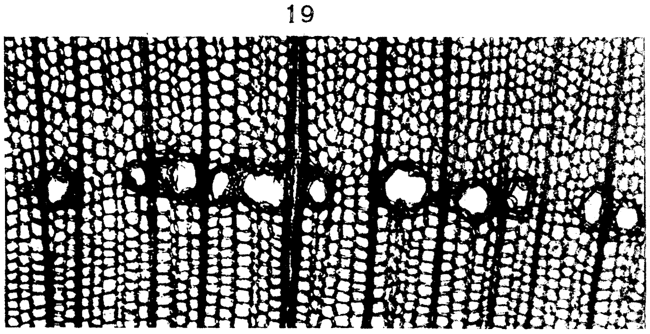

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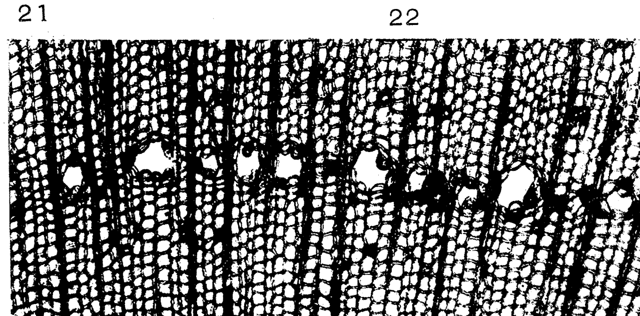

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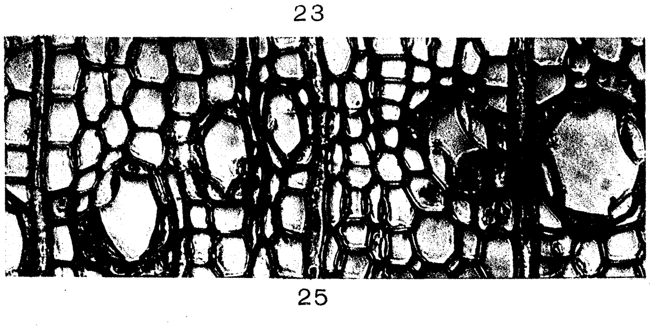

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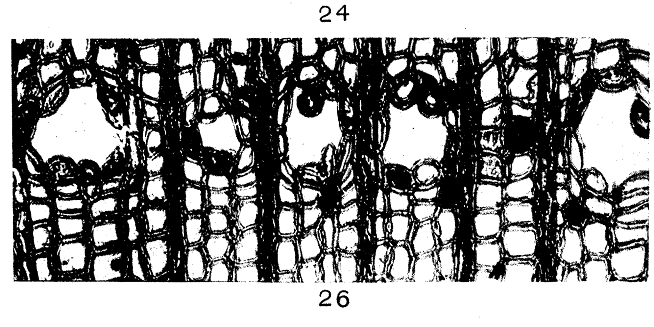

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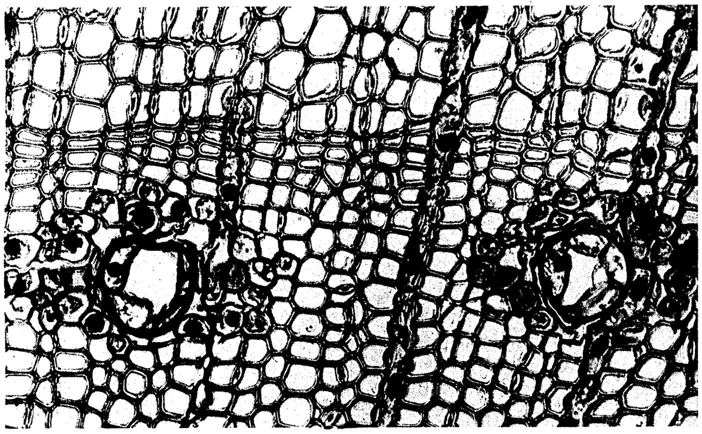

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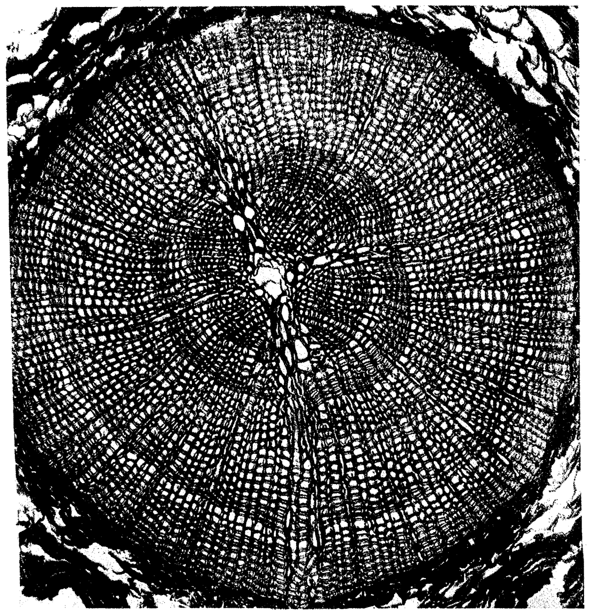

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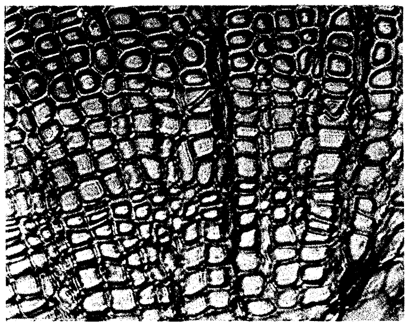

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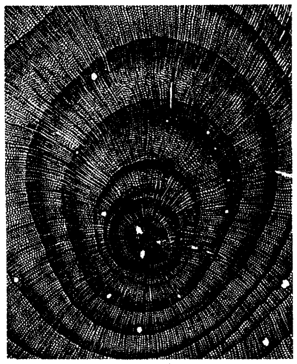

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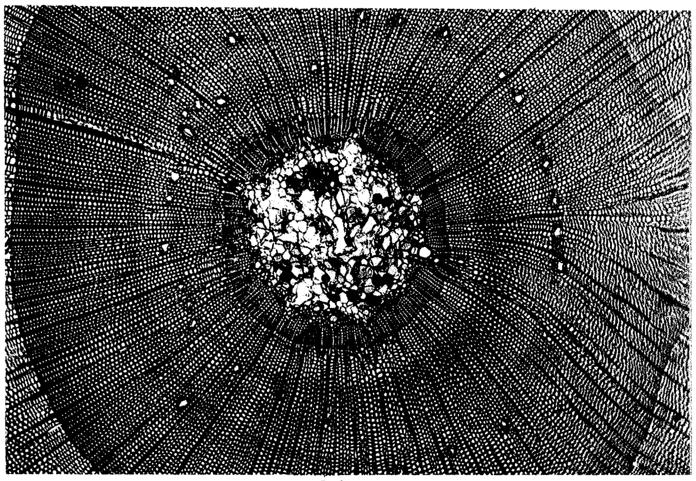

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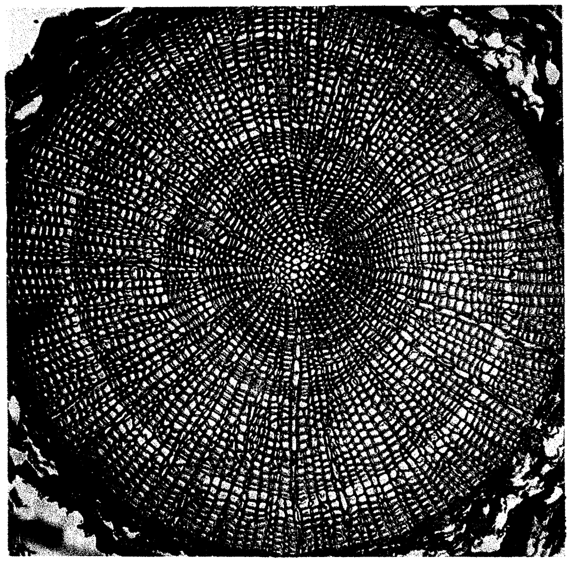

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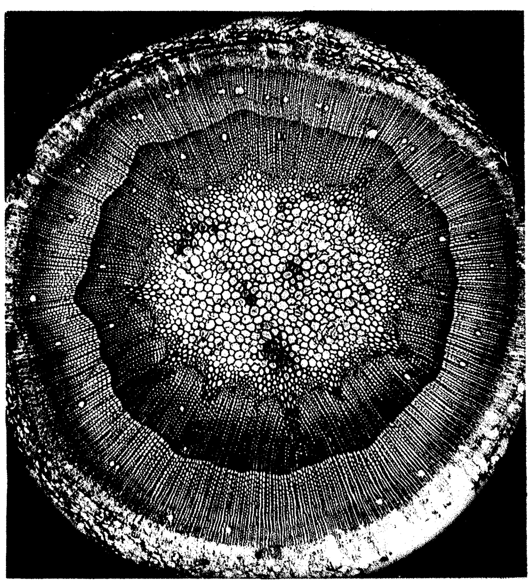

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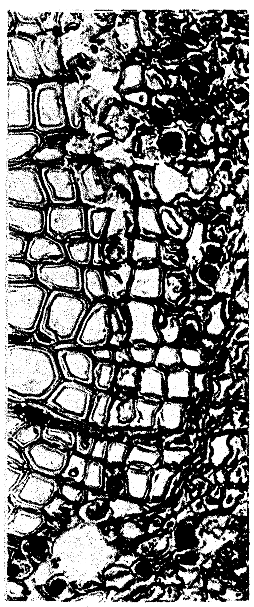

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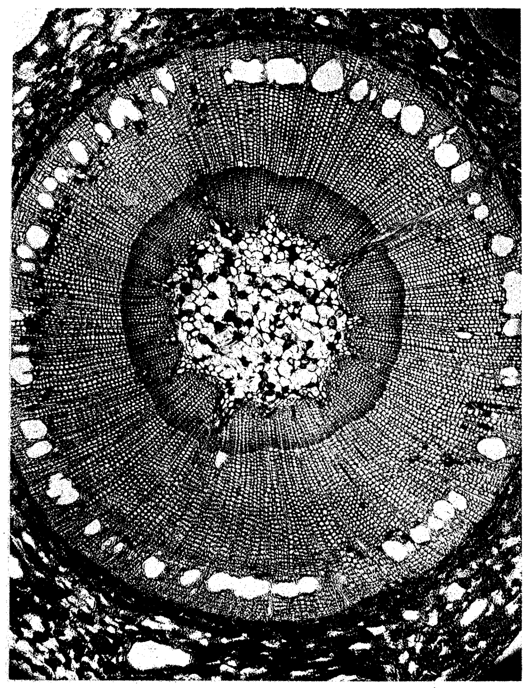

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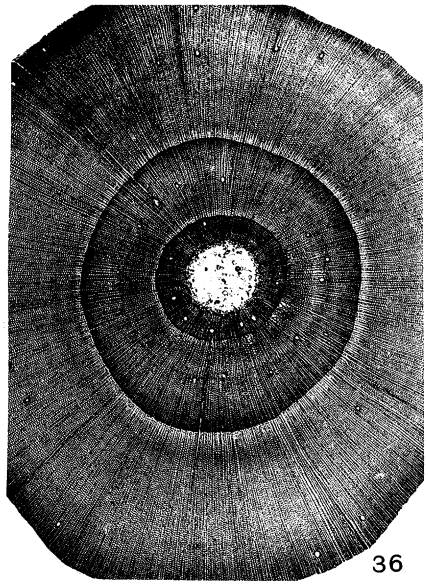

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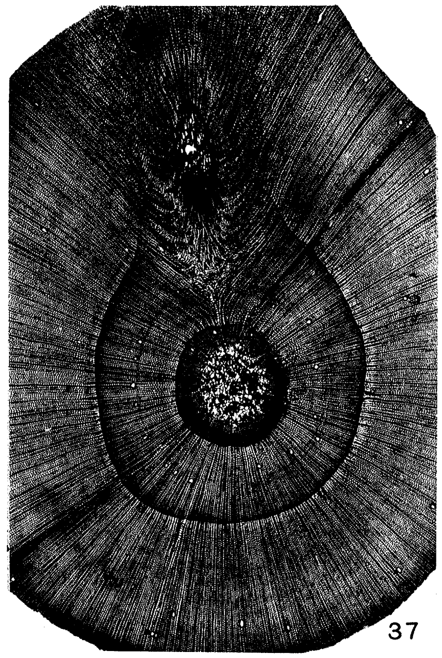

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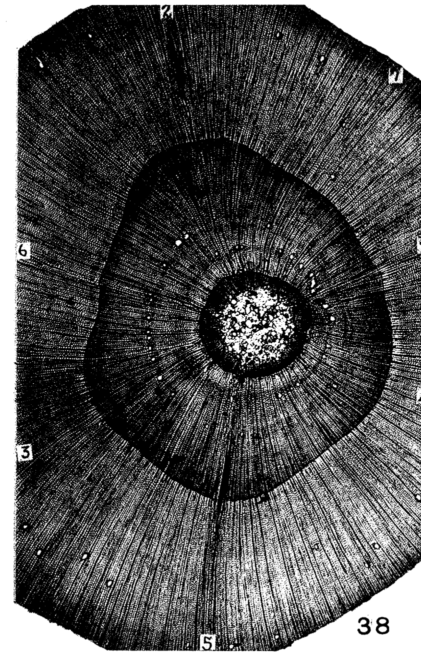

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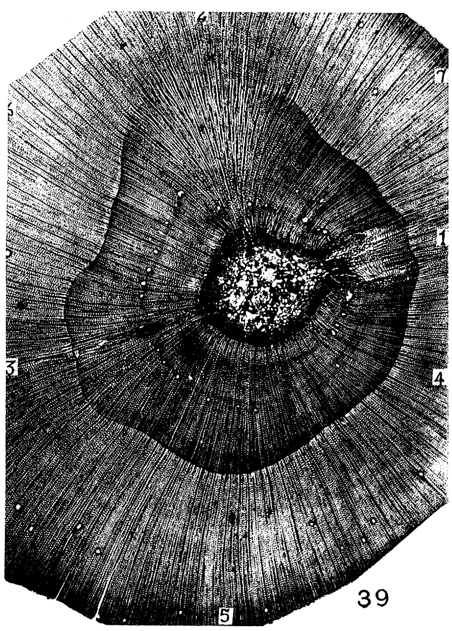

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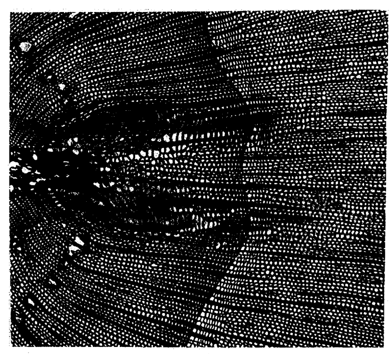

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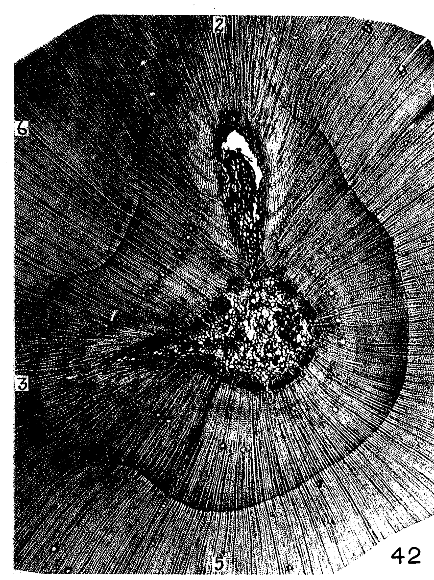

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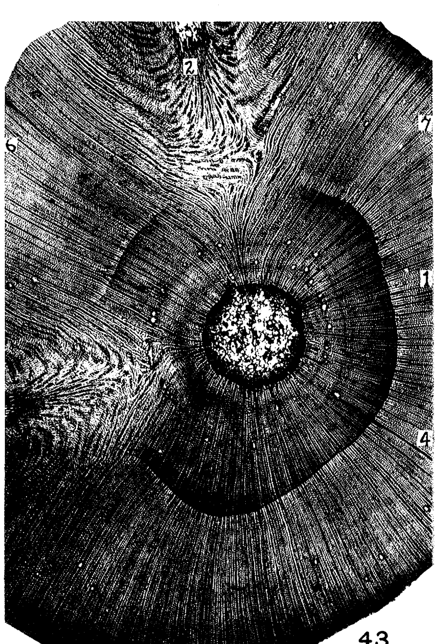

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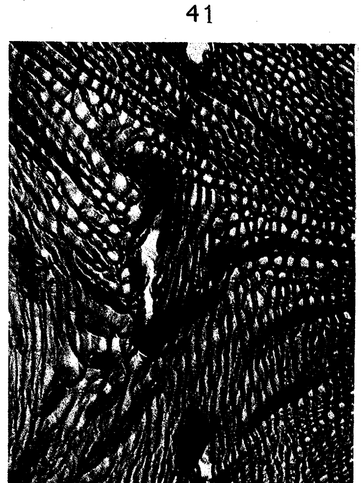

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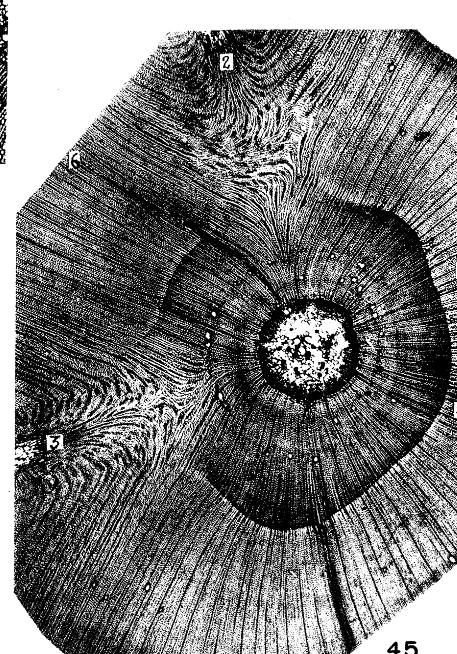

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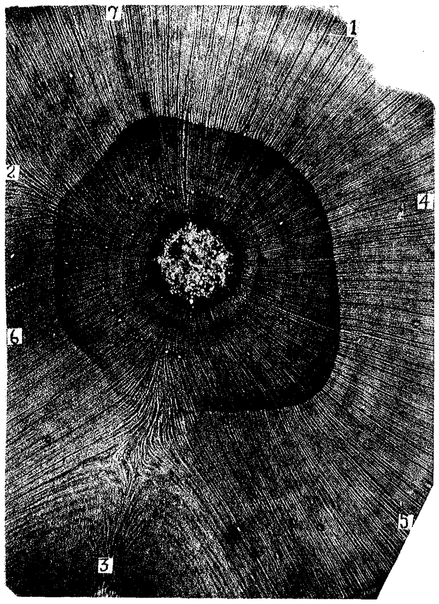
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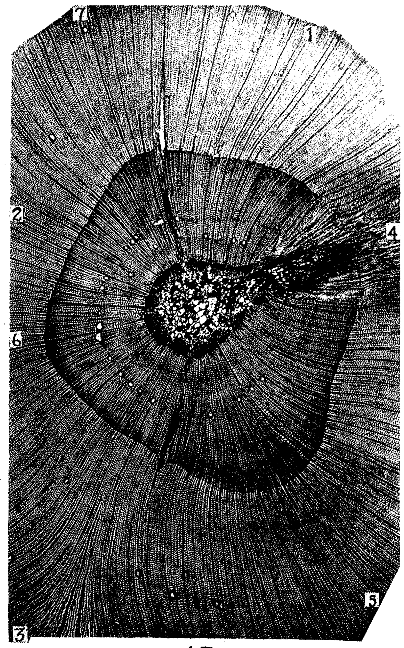
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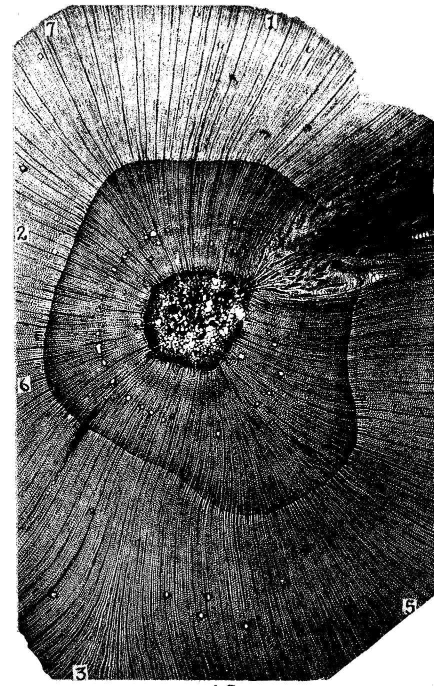
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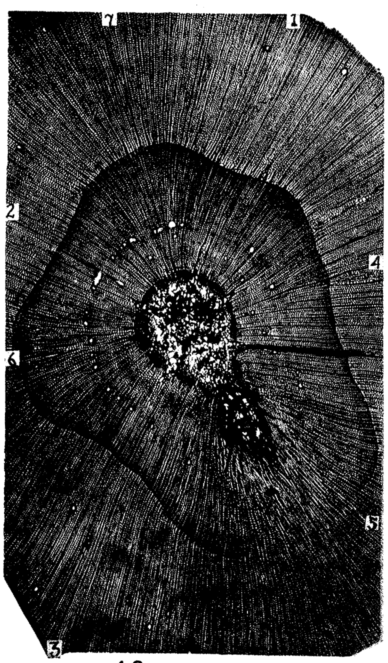
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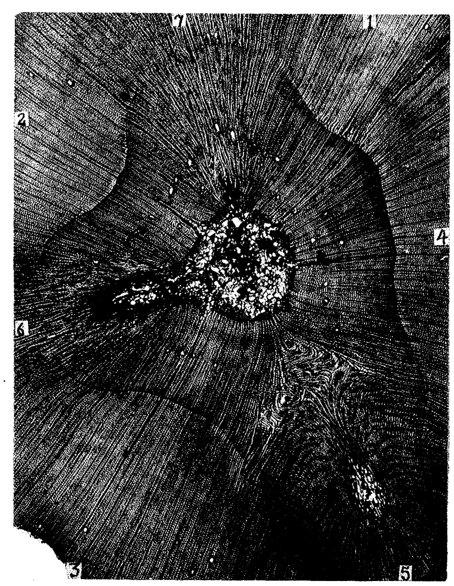
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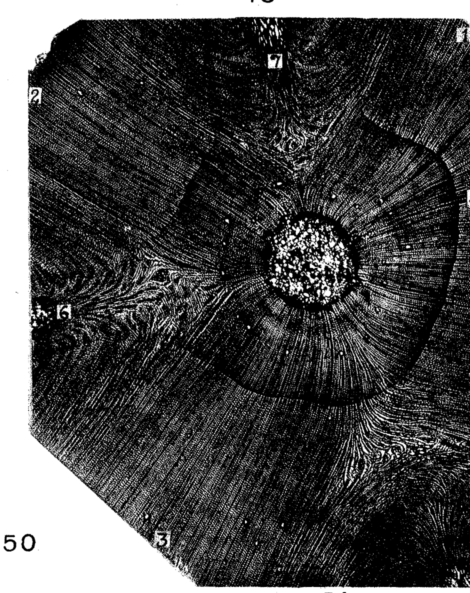
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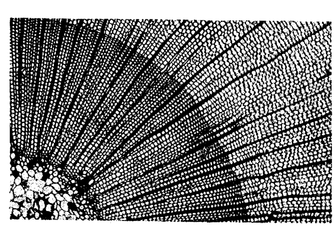
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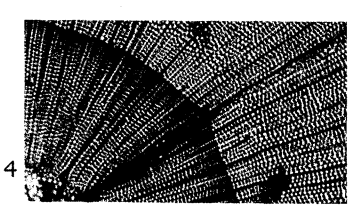
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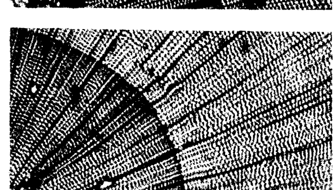
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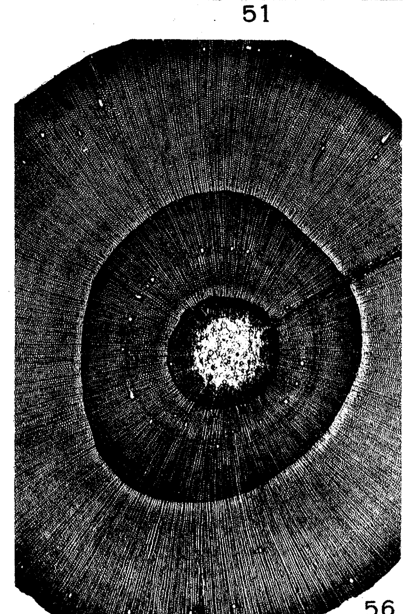
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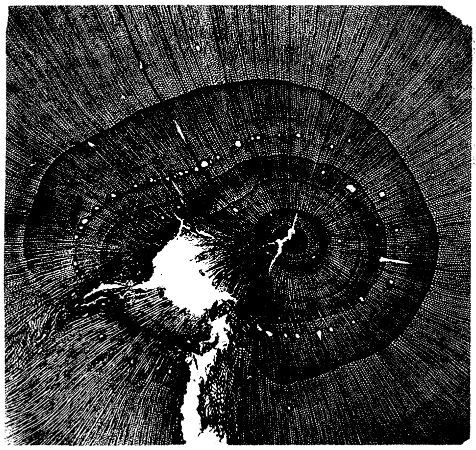
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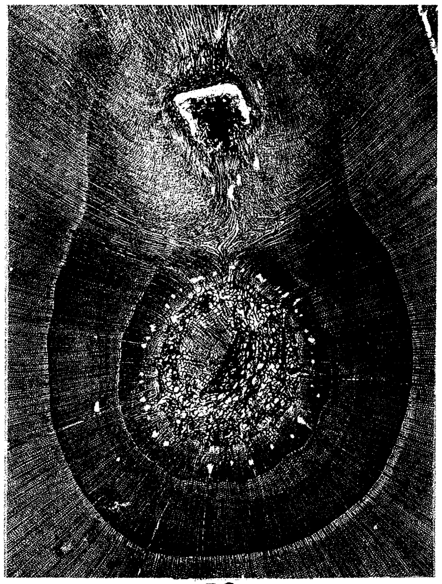
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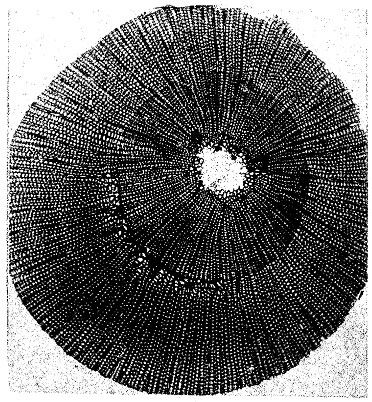
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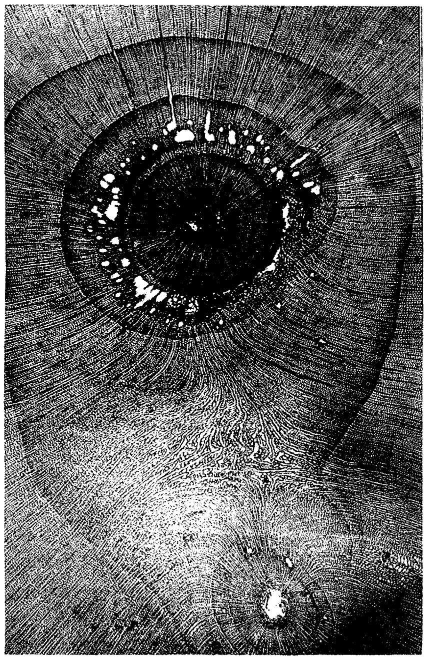
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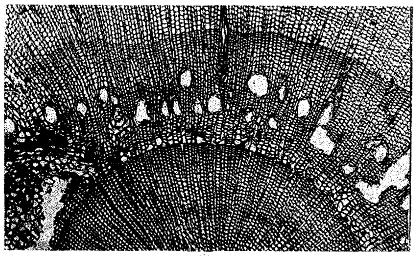
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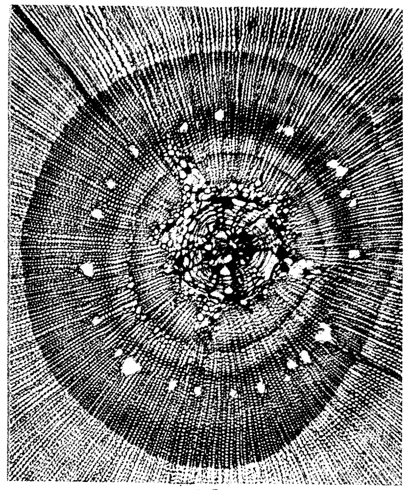
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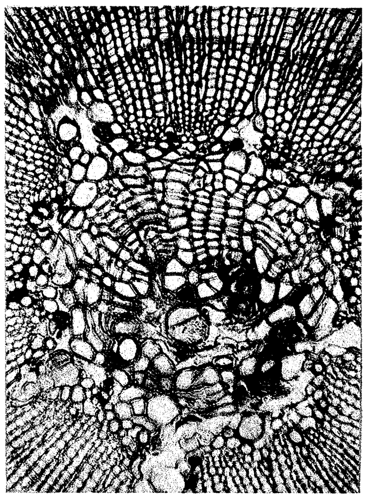
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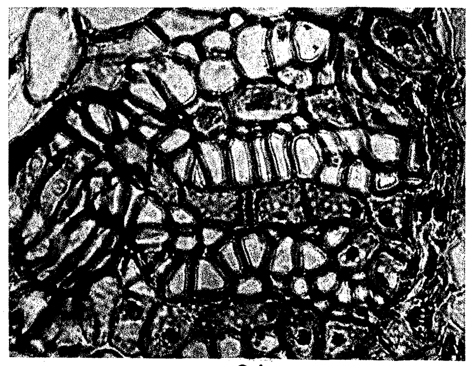
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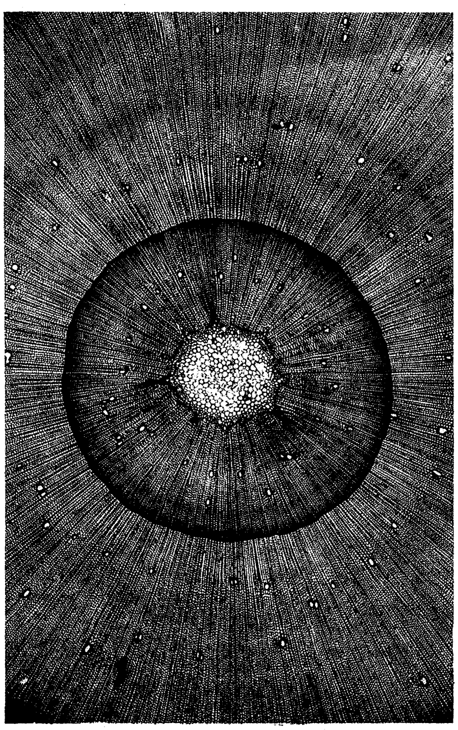
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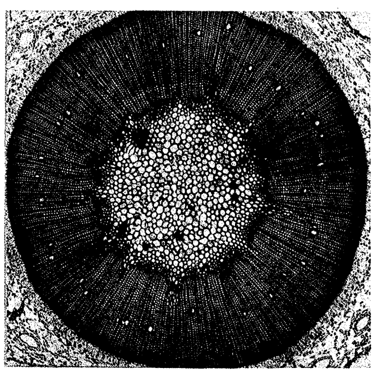
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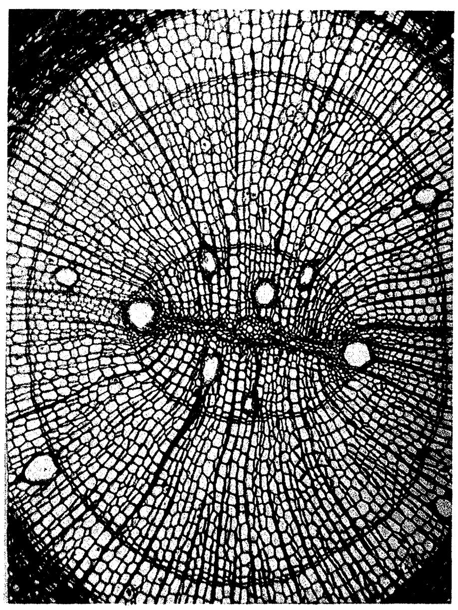
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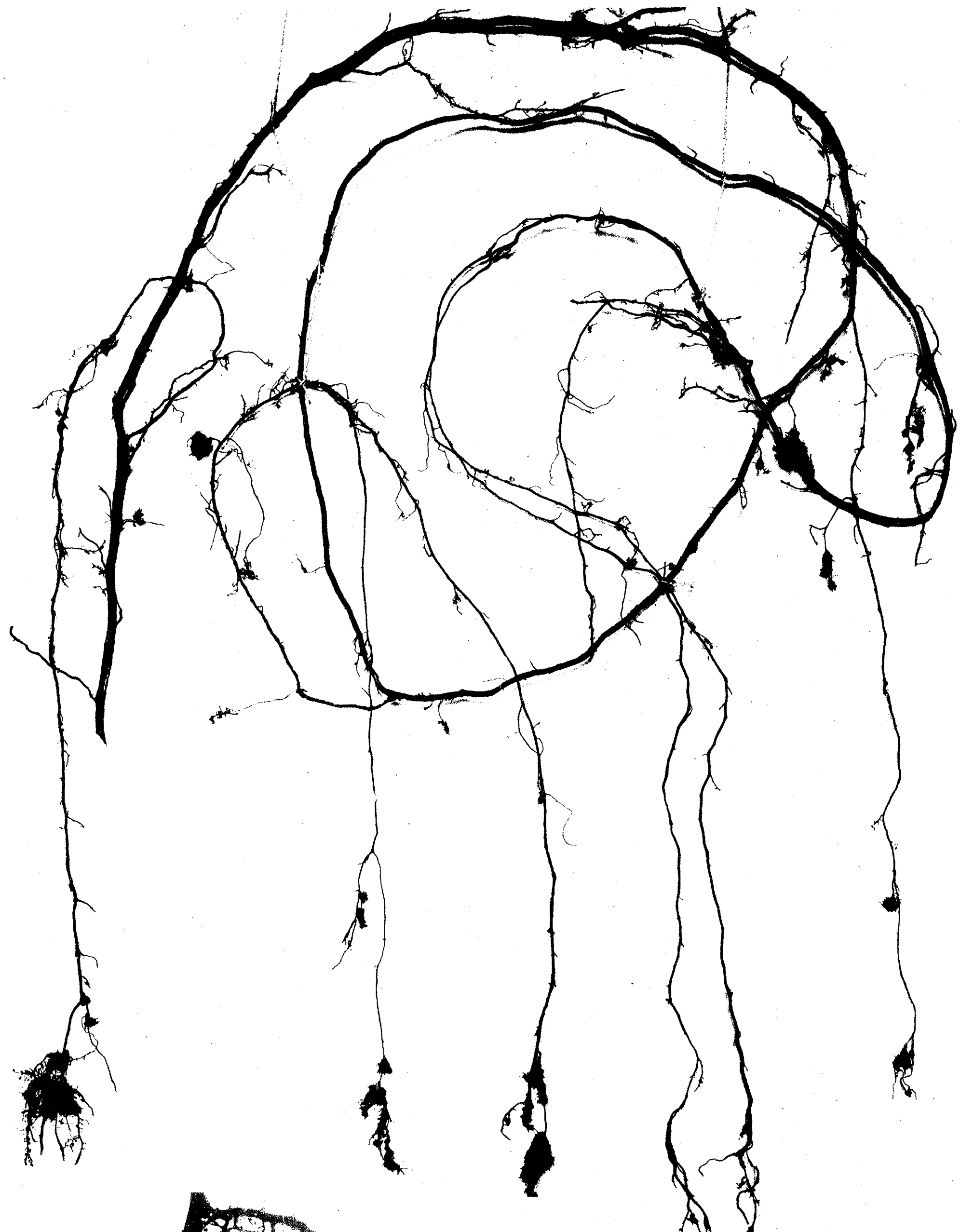

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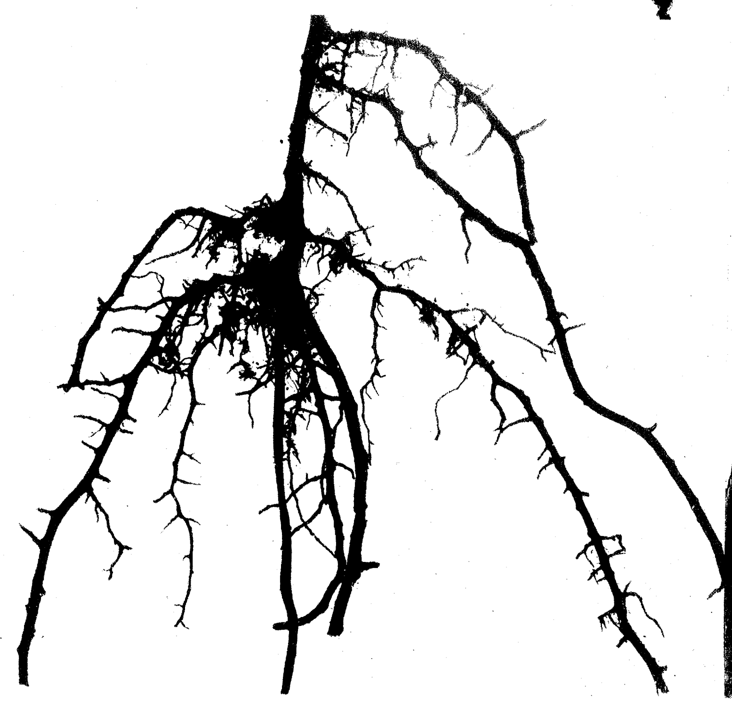

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PHOTO. 58.—*P. canadensis*. Transverse of stem of same plant. × 15. Injury to branch connected with resin canals in fourth year's growth of stem (as illustrated in fig. 4, Nos. 7 and 8).

PHOTO. 59.—*P. canadensis*. Unwounded branch from same node as Photo. 58. × 35.

PHOTO. 60.—*P. canadensis*. Transverse of stem of same plant. × 15. Wound at lower right of the ring with many resin canals. Secondary wood in pith.

PHOTO. 61.—*P. canadensis*. Transverse showing same wound as that in Photo. 60, but at a different level. × 35.

PHOTO. 62.—*P. canadensis*. Transverse lower down in same node as Photo. 60. × 35. Secondary wood forms a circle in pith.

PHOTO. 63.—*P. canadensis*. Another region of secondary growth in pith. × 95.

PHOTO. 64.—*P. canadensis*. Secondary growth in pith showing cambium at right. × 250.

PHOTOS. 65 and 66.—*P. canadensis*. Transverse of leader of a plant 27 years old. × 15. Scattered resin canals and false annual rings.

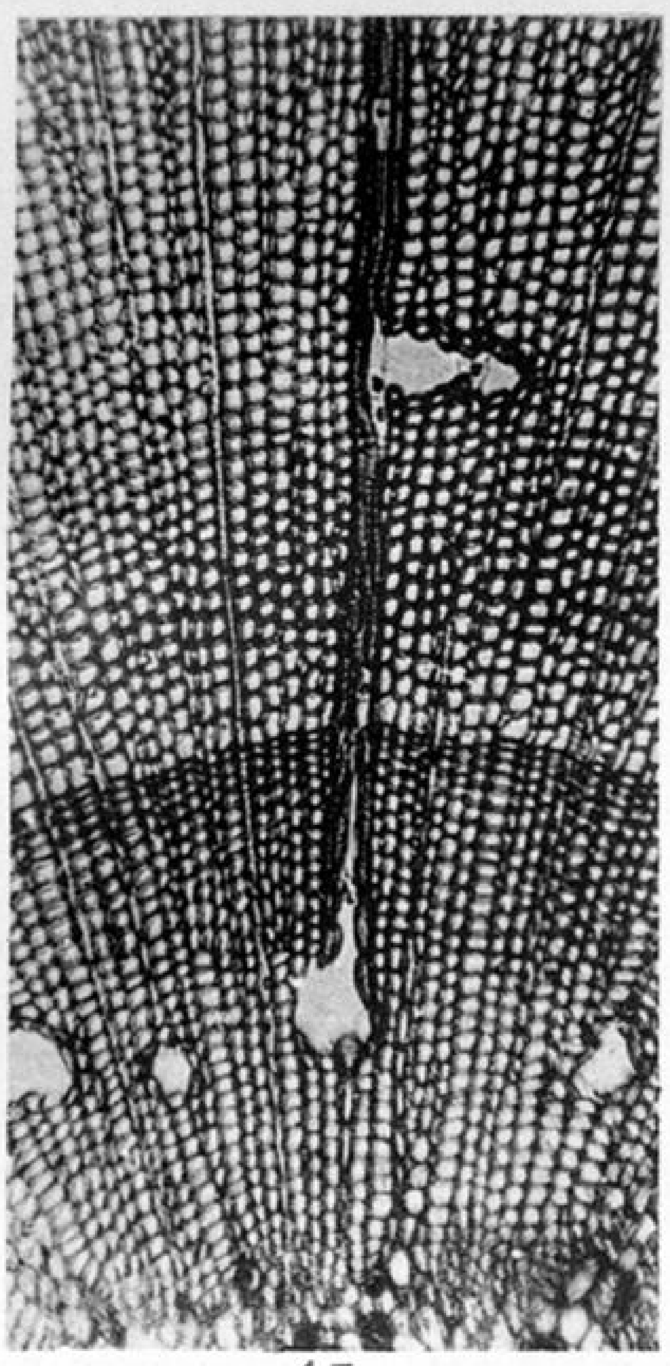
PHOTO. 67.—*P. canadensis*. Transverse of a side root of an old tree at a considerable distance from the trunk. × 35. Five resin canals in secondary wood of the inner year's growth.

PLATE 14.

PHOTO. 68.—*Picea canadensis*. Long lateral root from an old tree, much reduced, showing numerous rootlets at tips of branches. Most of the rootlets have been lost from the older parts.

PHOTO. 69.—*P. canadensis*. One of the tip clusters from the root shown in Photo. 68—about natural size.

PHOTO. 70.—*P. canadensis*. Roots, natural size. Splitting has occurred between the two parallel branches.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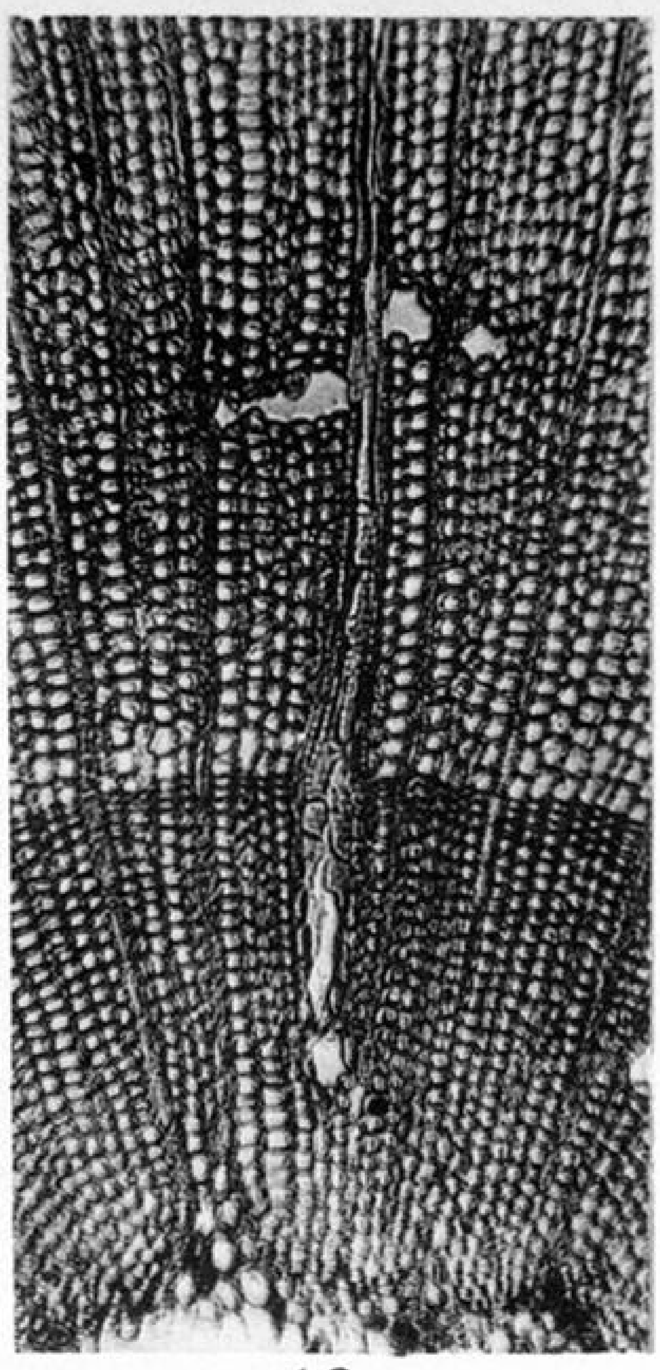
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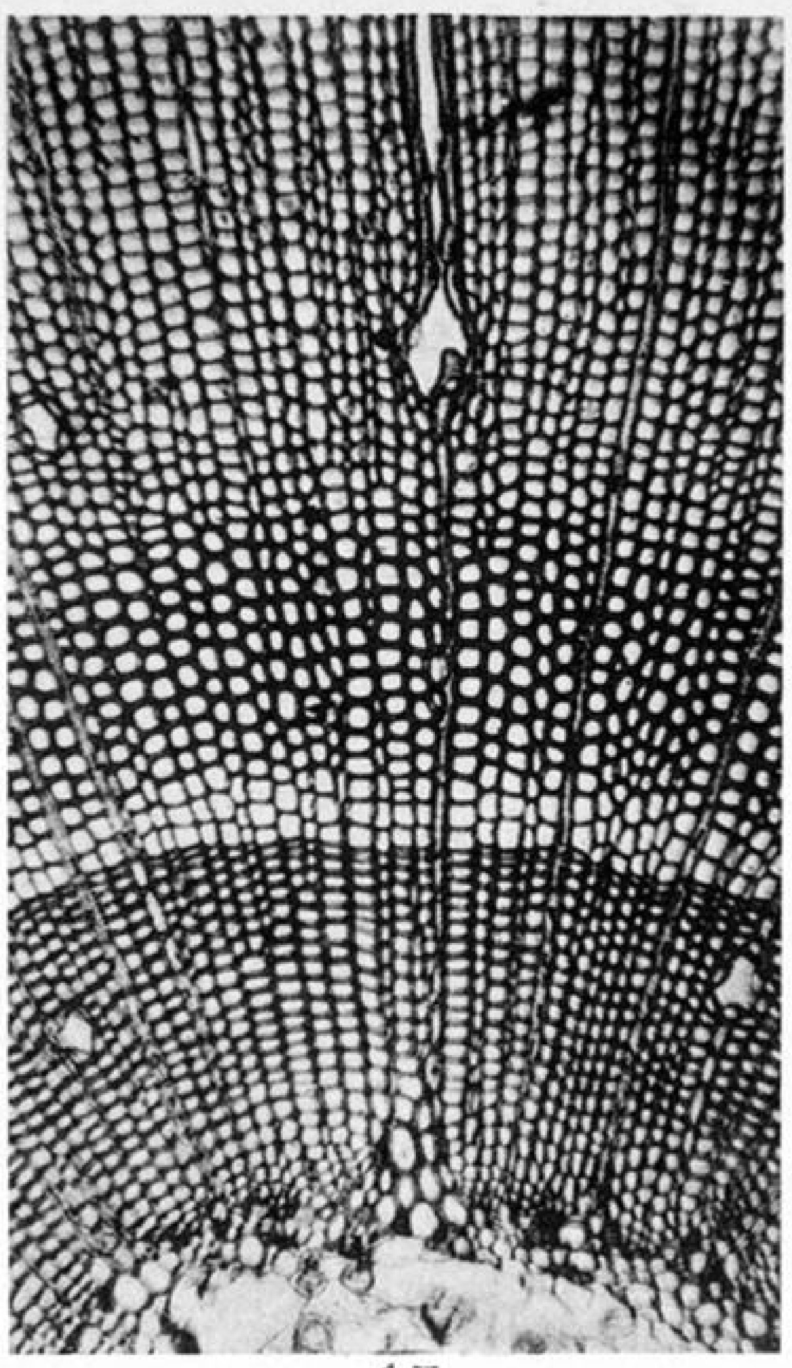
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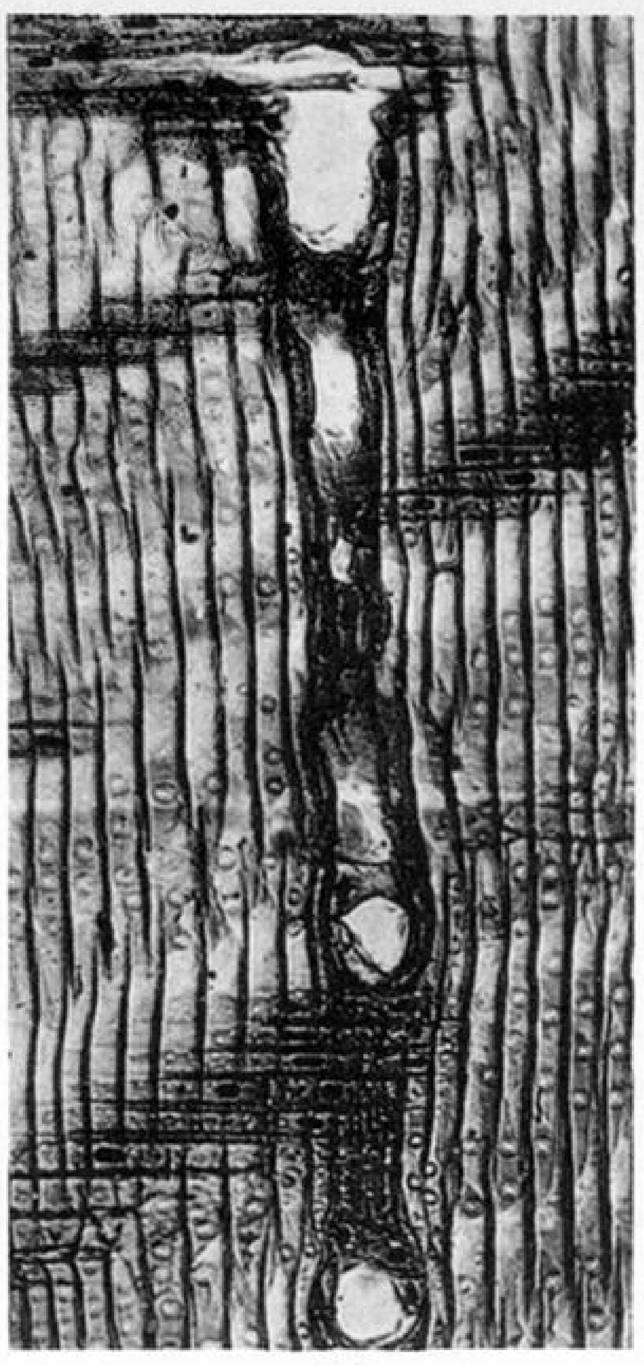
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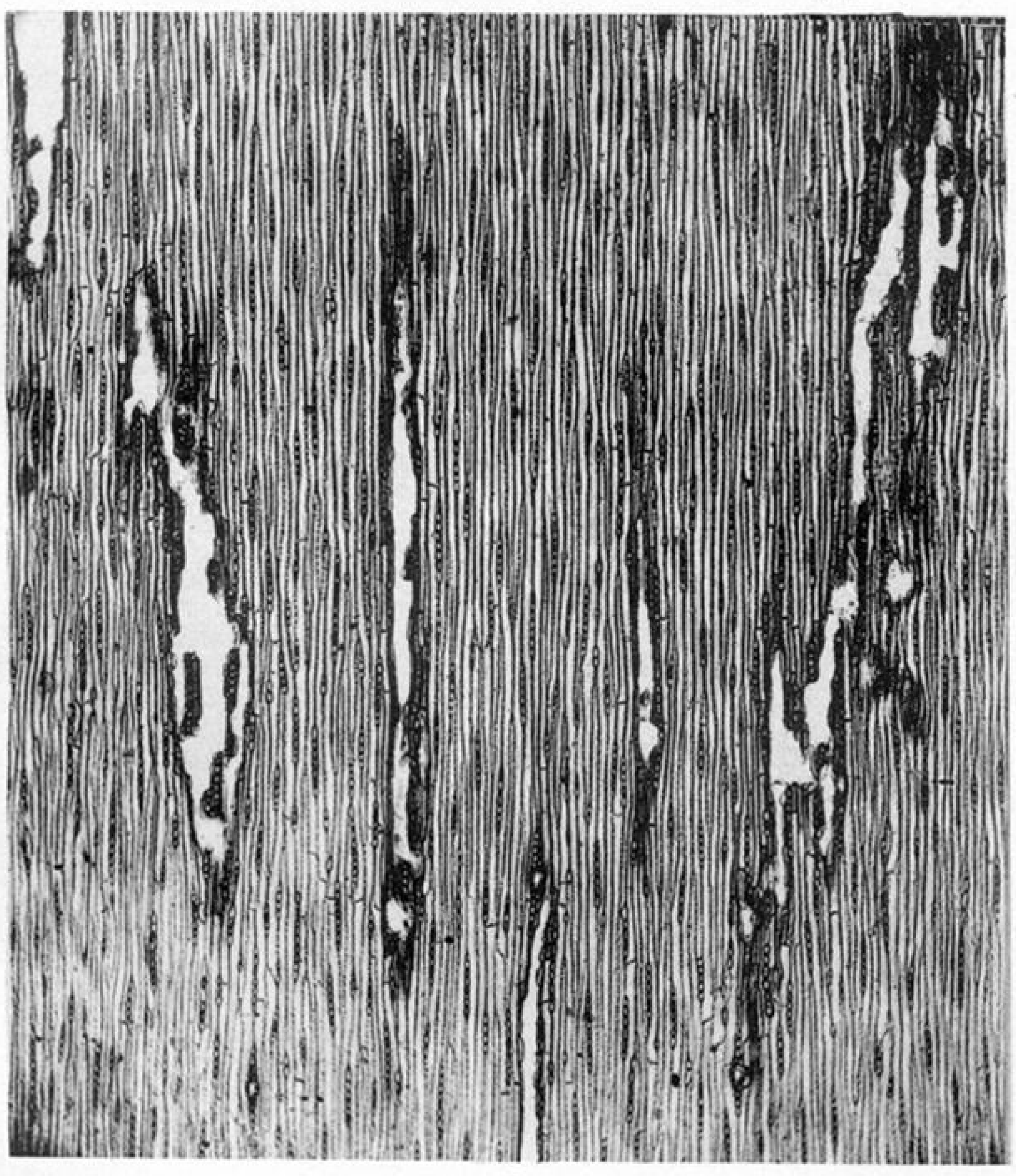
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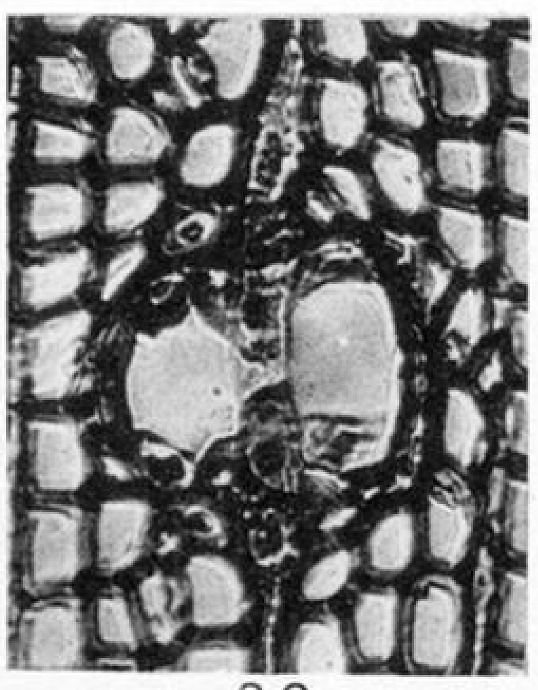
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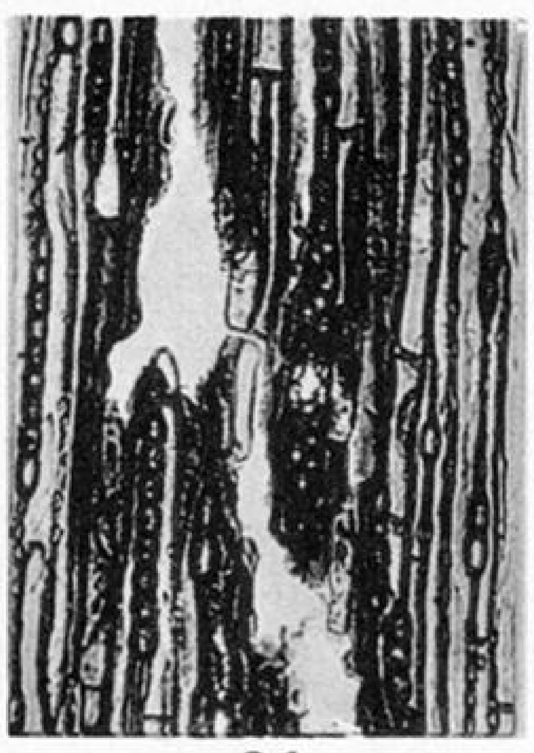
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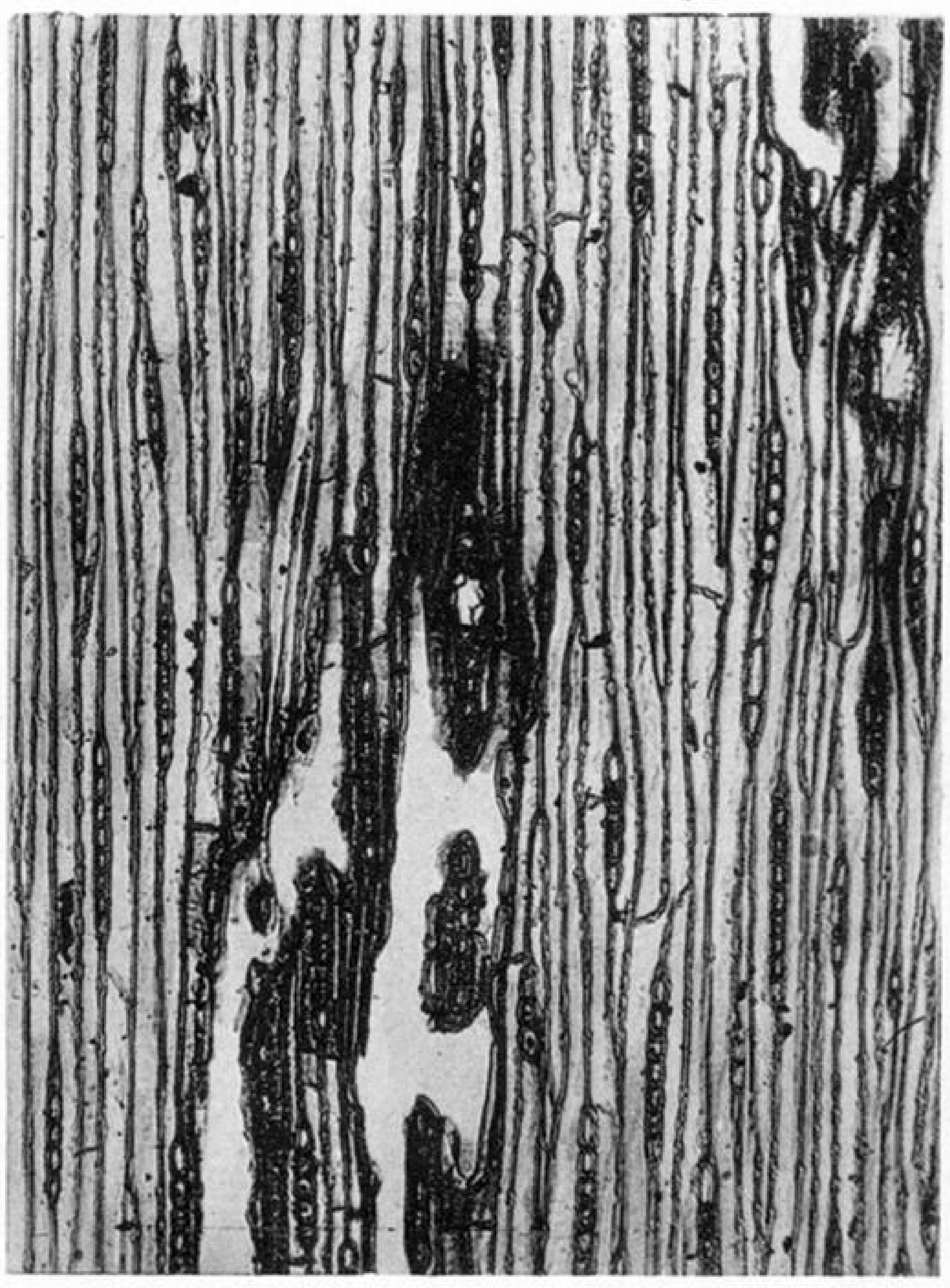
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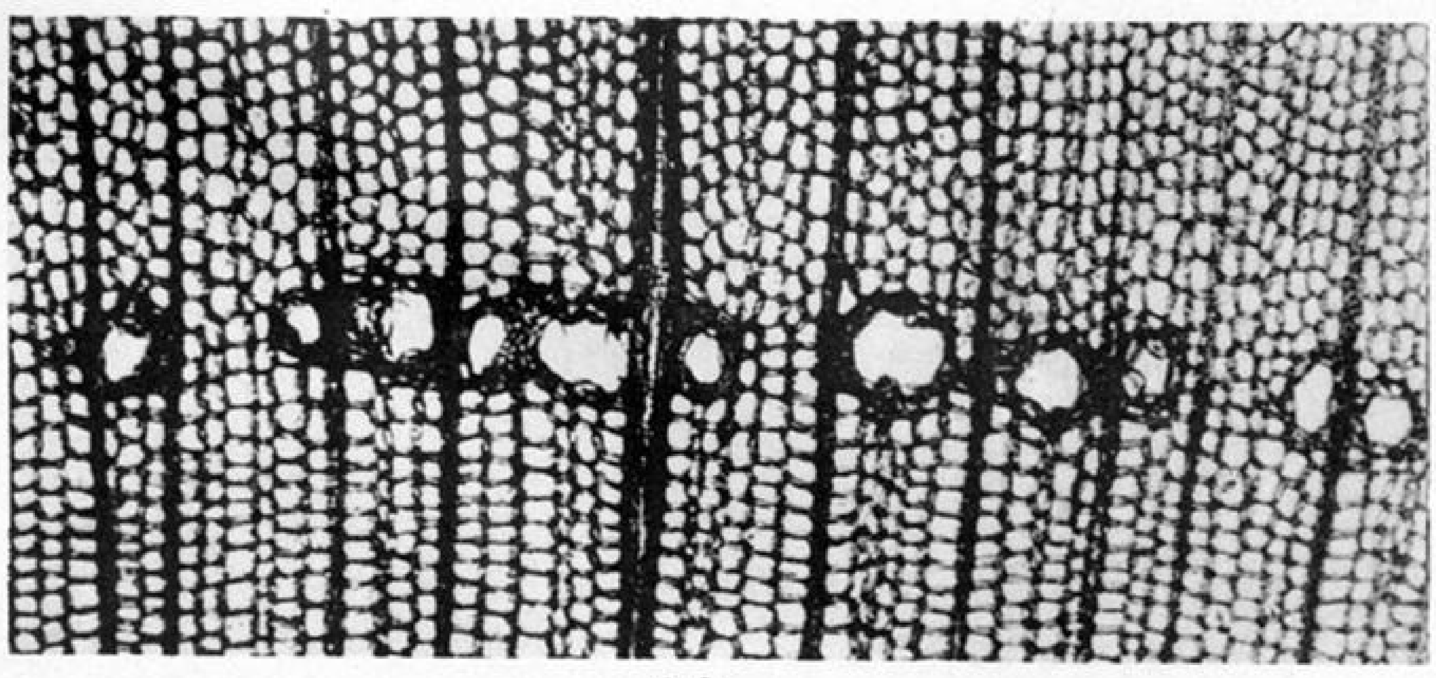
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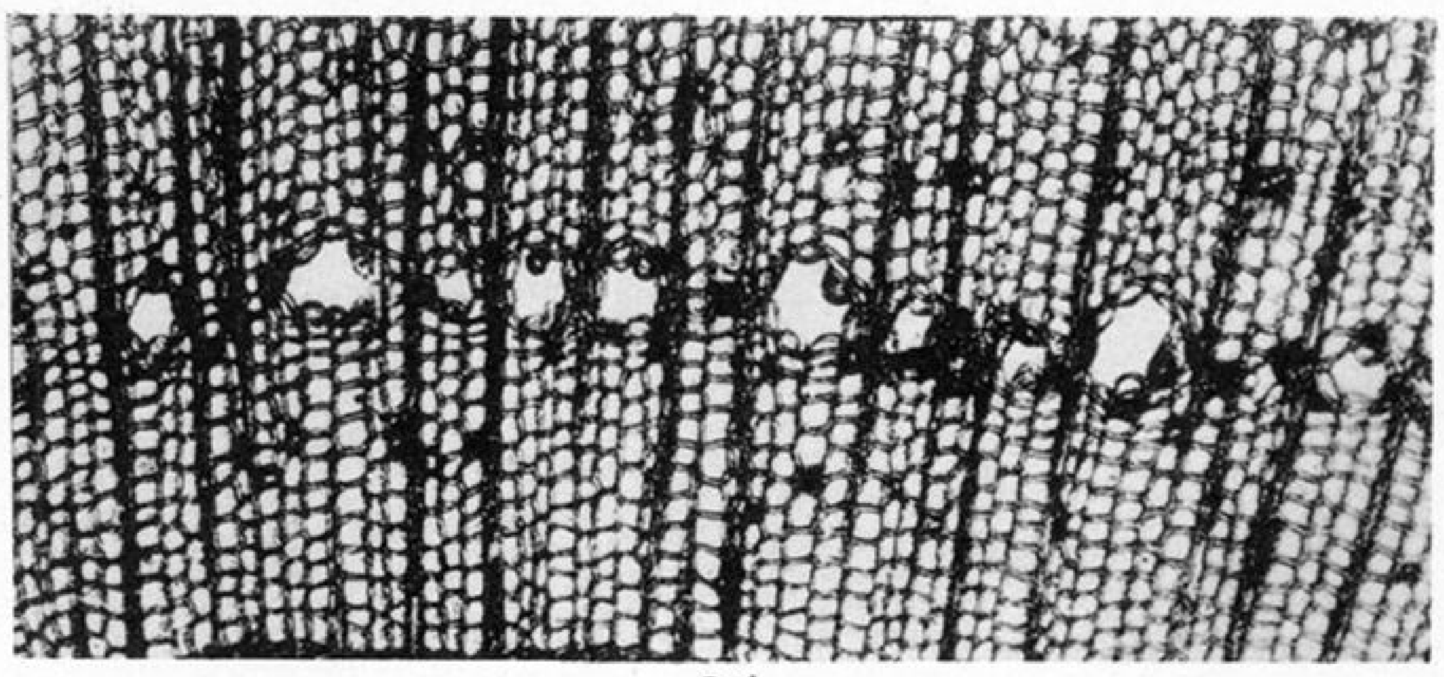
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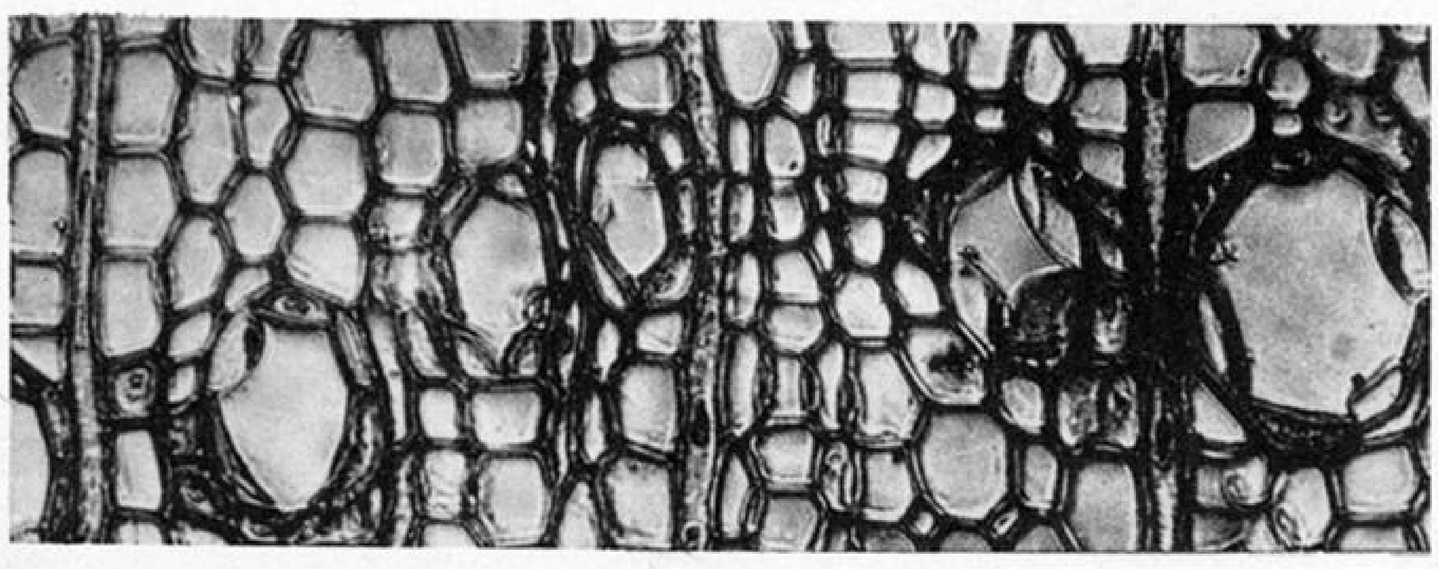
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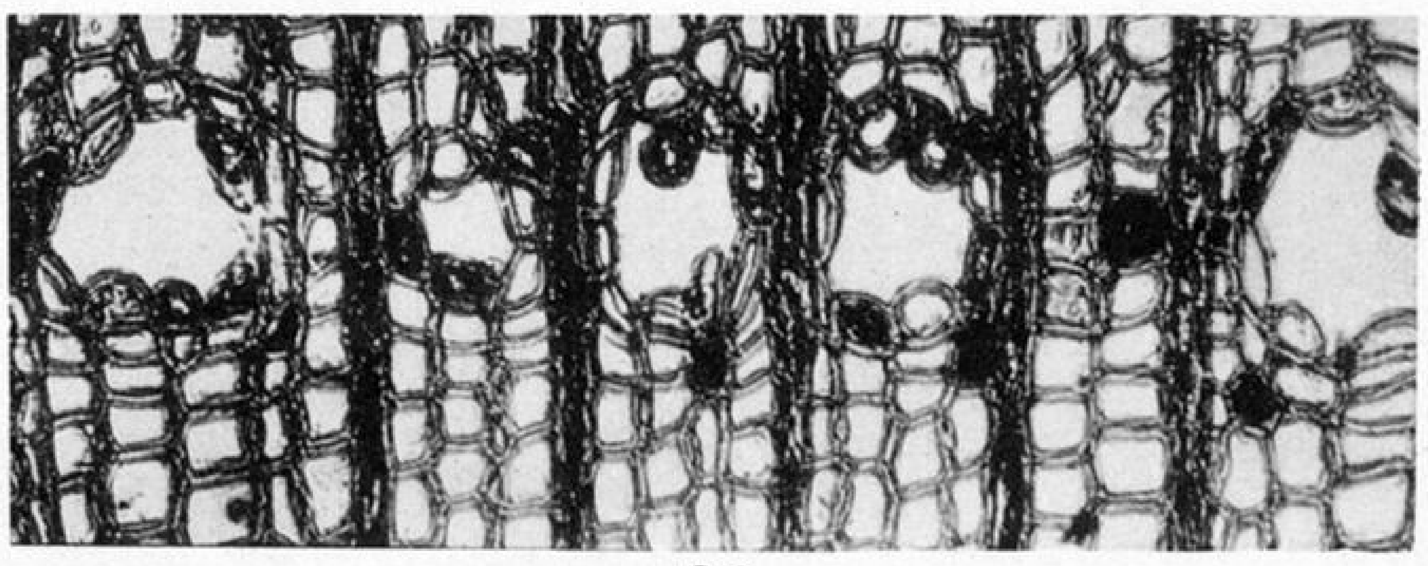
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PLATE 9.

PHOTO. 15.—*Picea canadensis.* Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 16.—*P. canadensis.* Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 17.—*P. canadensis.* Transverse of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 18.—*P. canadensis.* Radial of stem. × 95. Vertical and horizontal resin canals.

PHOTO. 19.—*P. canadensis.* Tangential of stem. × 35. Resin canals and medullary rays.

PHOTO. 20.—*P. canadensis.* Transverse of stem. × 240. Resin canals and medullary ray.

PHOTO. 21.—*P. canadensis.* Tangential of stem. × 95. Resin canals and medullary rays.

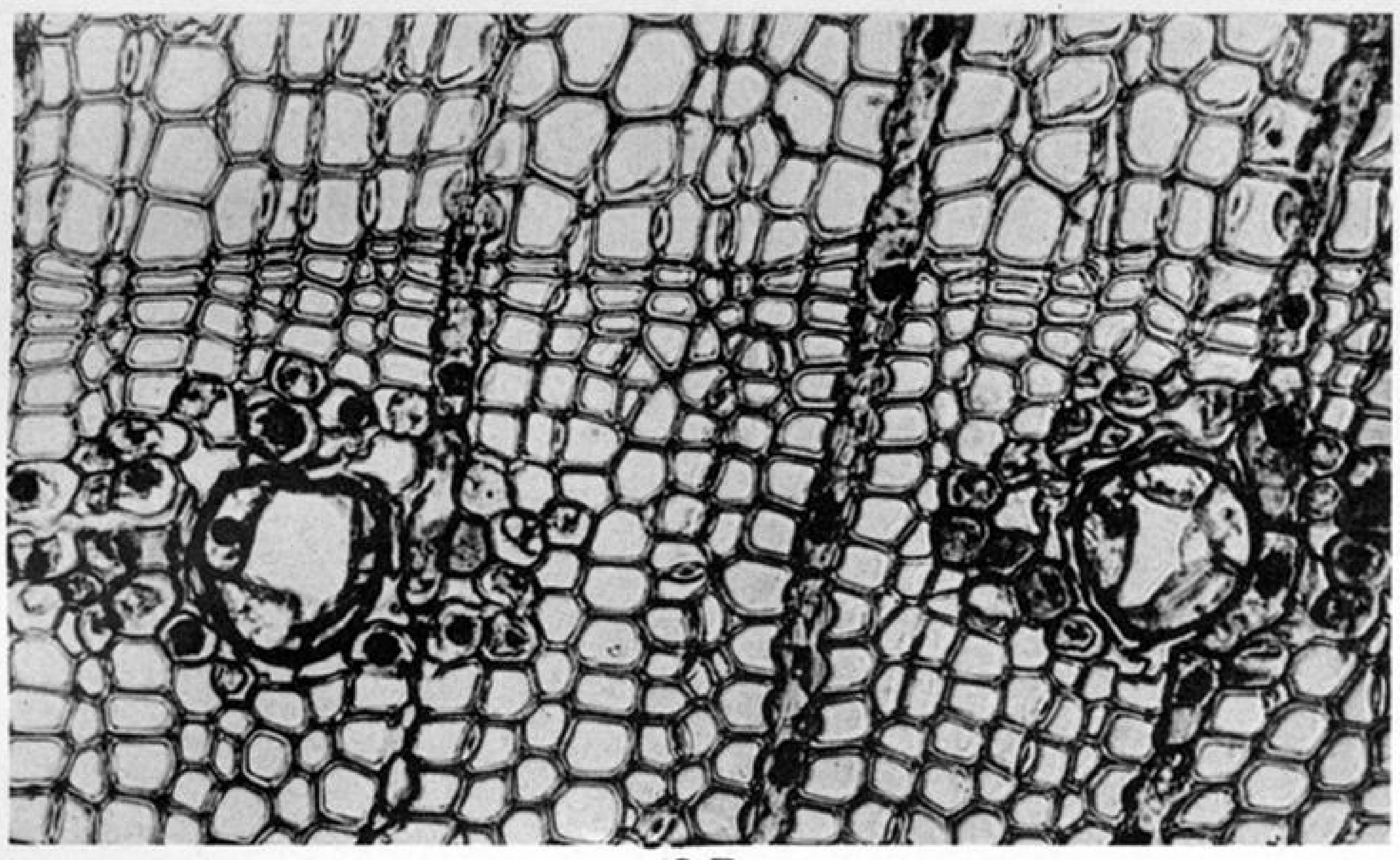
PHOTO. 22.—*P. canadensis.* Tangential of stem. × 95. Resin canals and medullary rays.

PHOTO. 23.—*P. canadensis.* Transverse of stem. × 95. Tangential series of resin canals.

PHOTO. 24.—*Abies balsamea.* Transverse of stem. × 95. Tangential series of resin canals.

PHOTO. 25.—*Picea canadensis.* Transverse of stem. × 240. Structure of resin canals.

PHOTO. 26.—*Abies balsamea.* Transverse of stem. × 240. Structure of resin canals.



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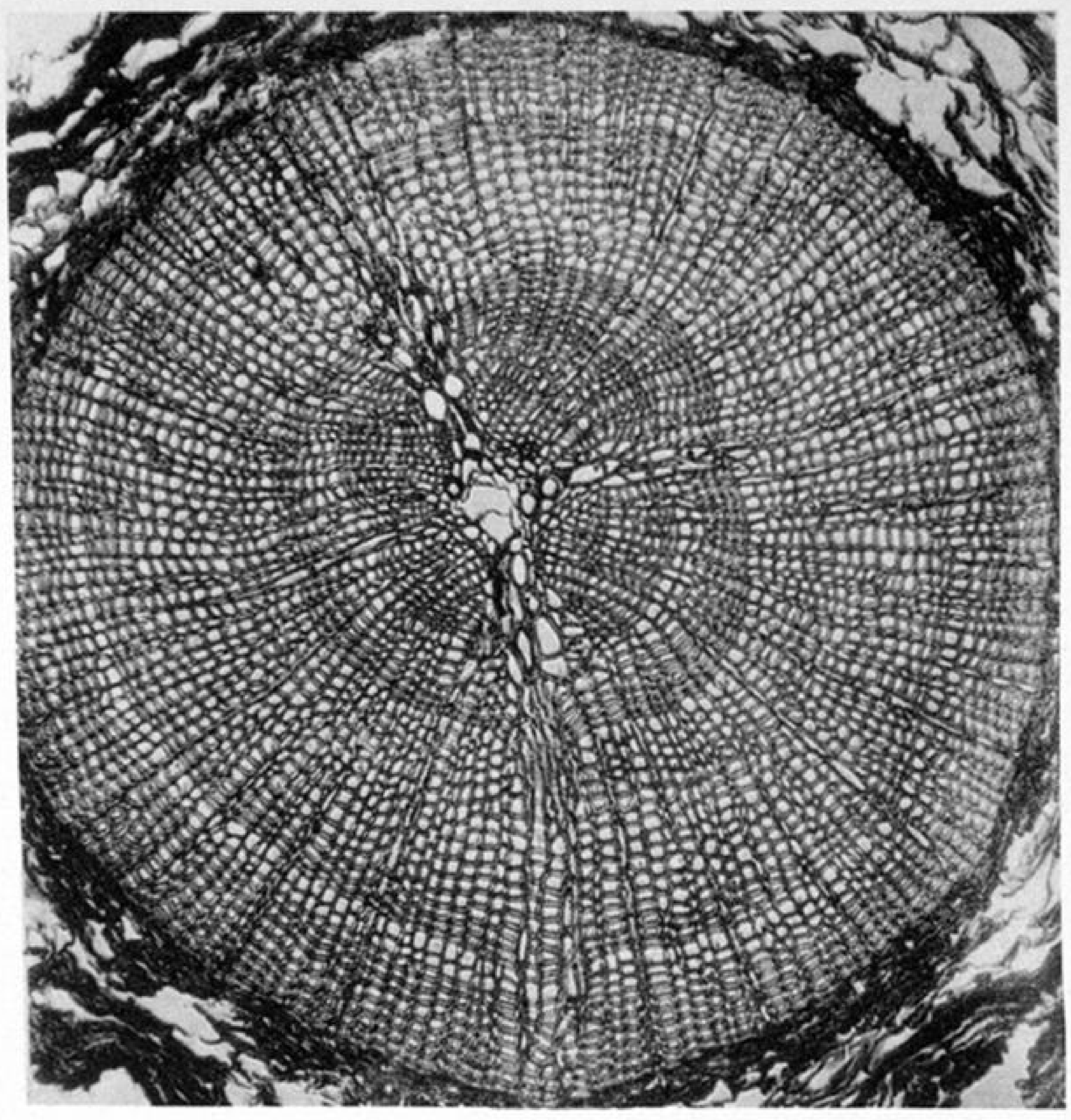

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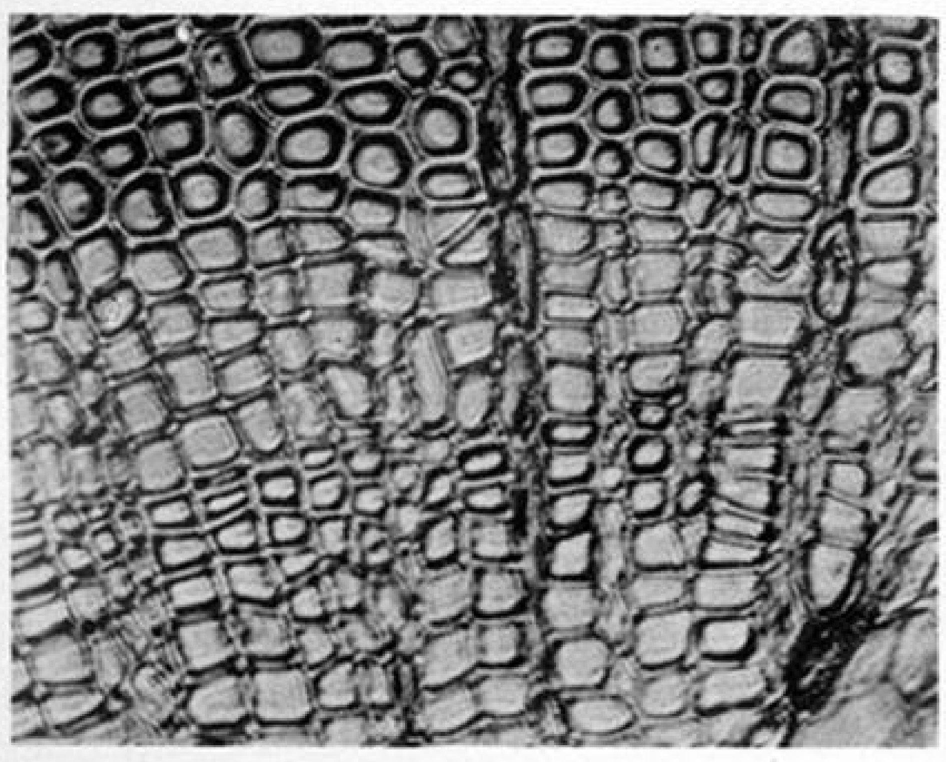

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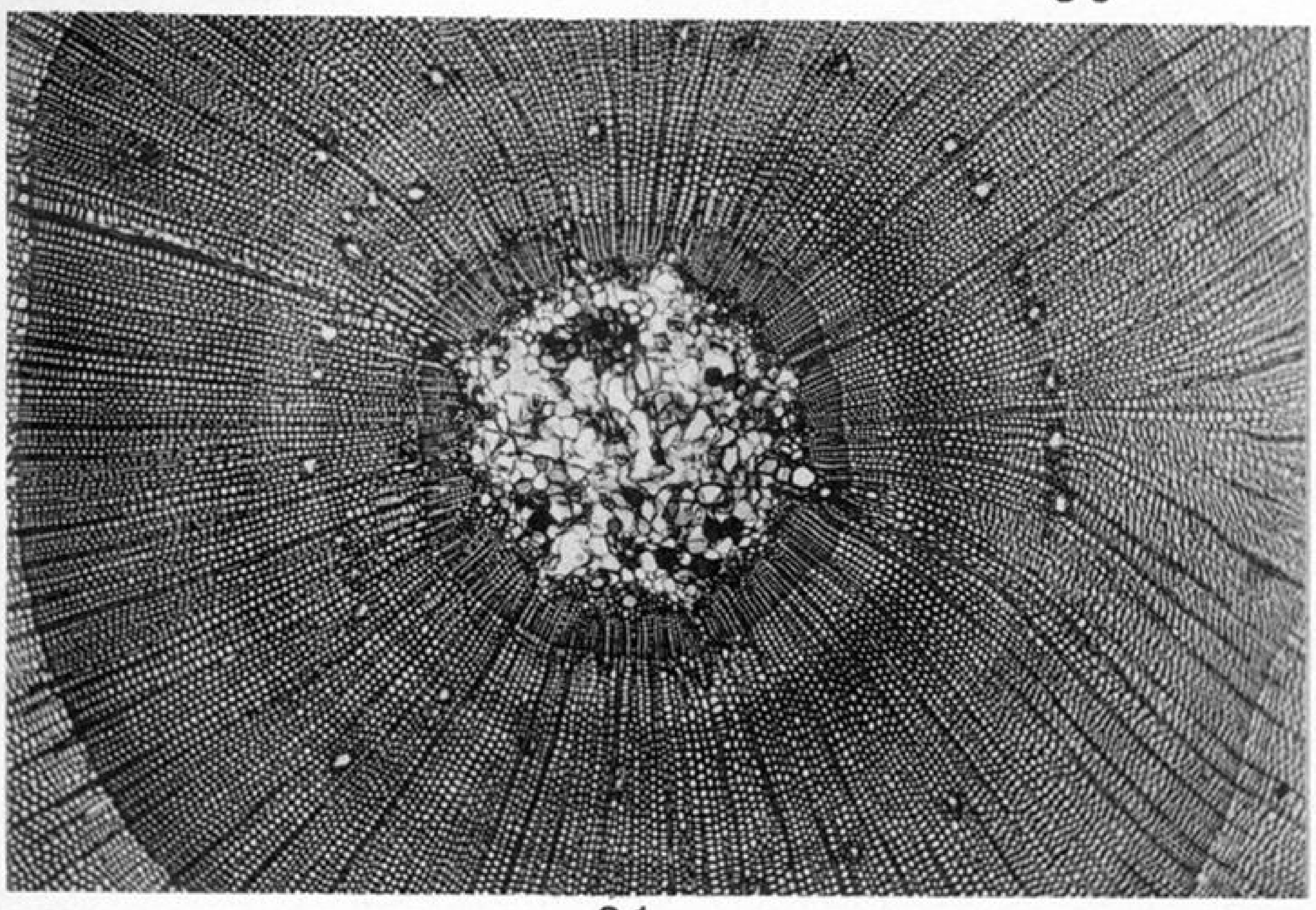

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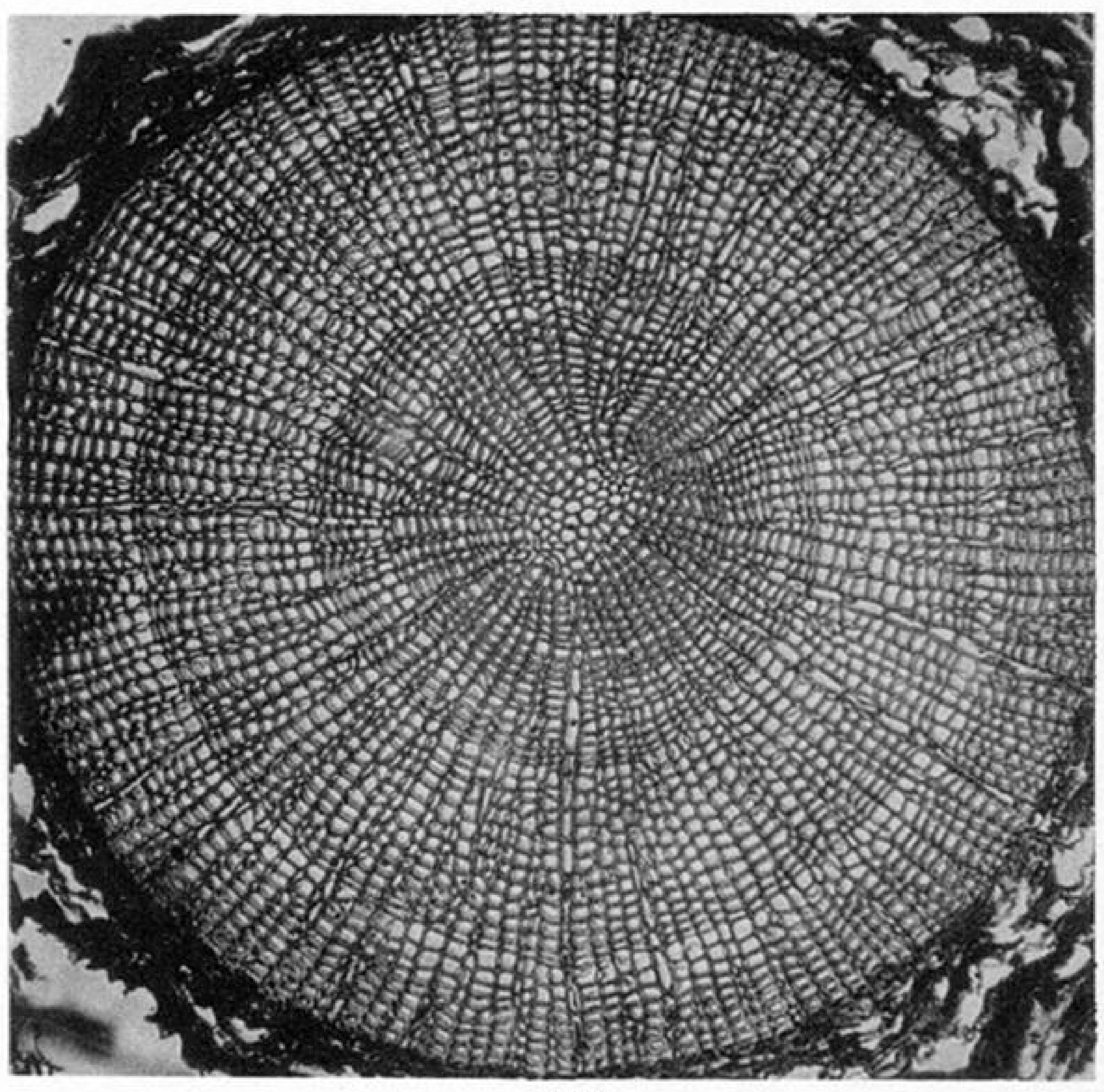

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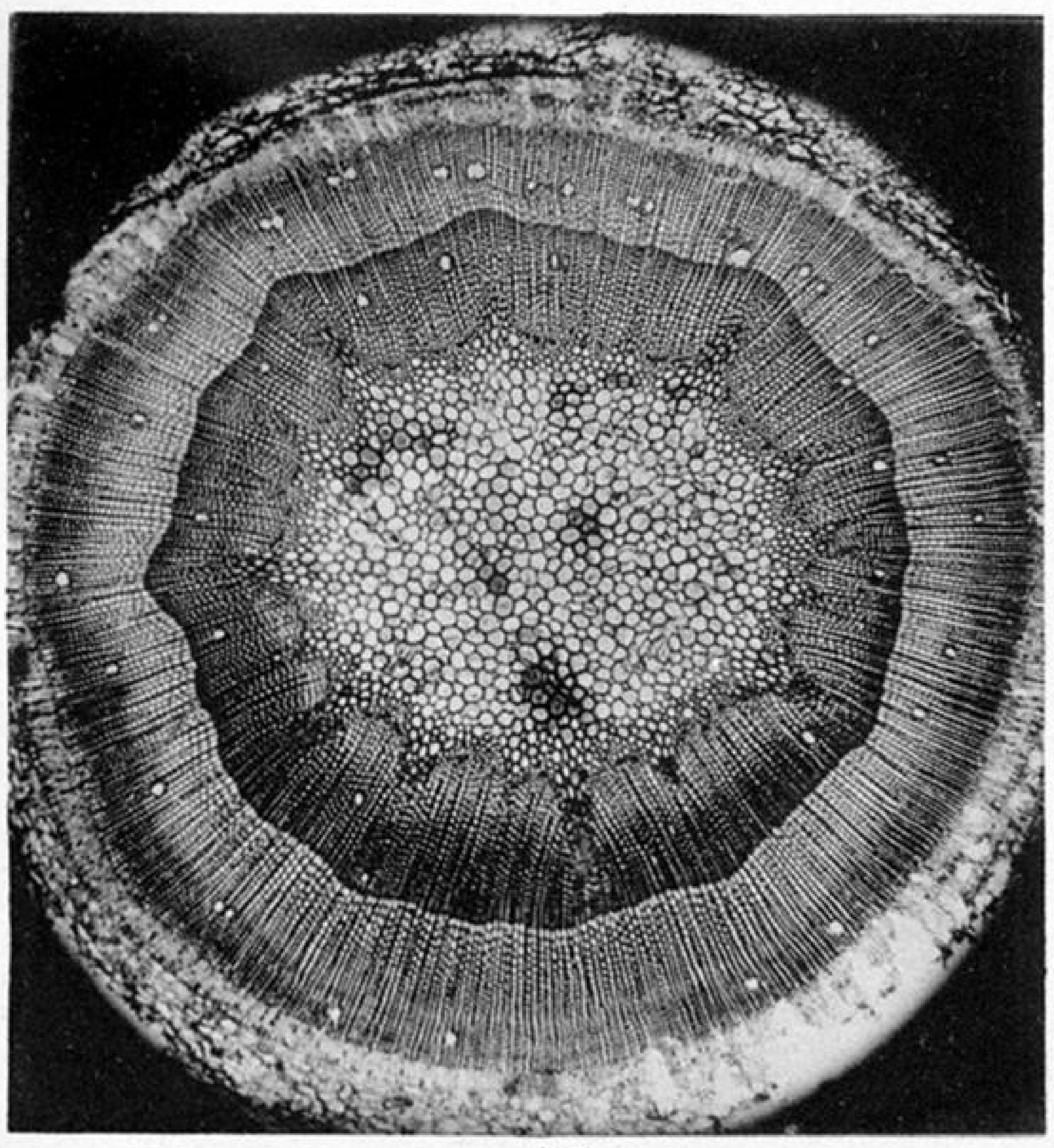

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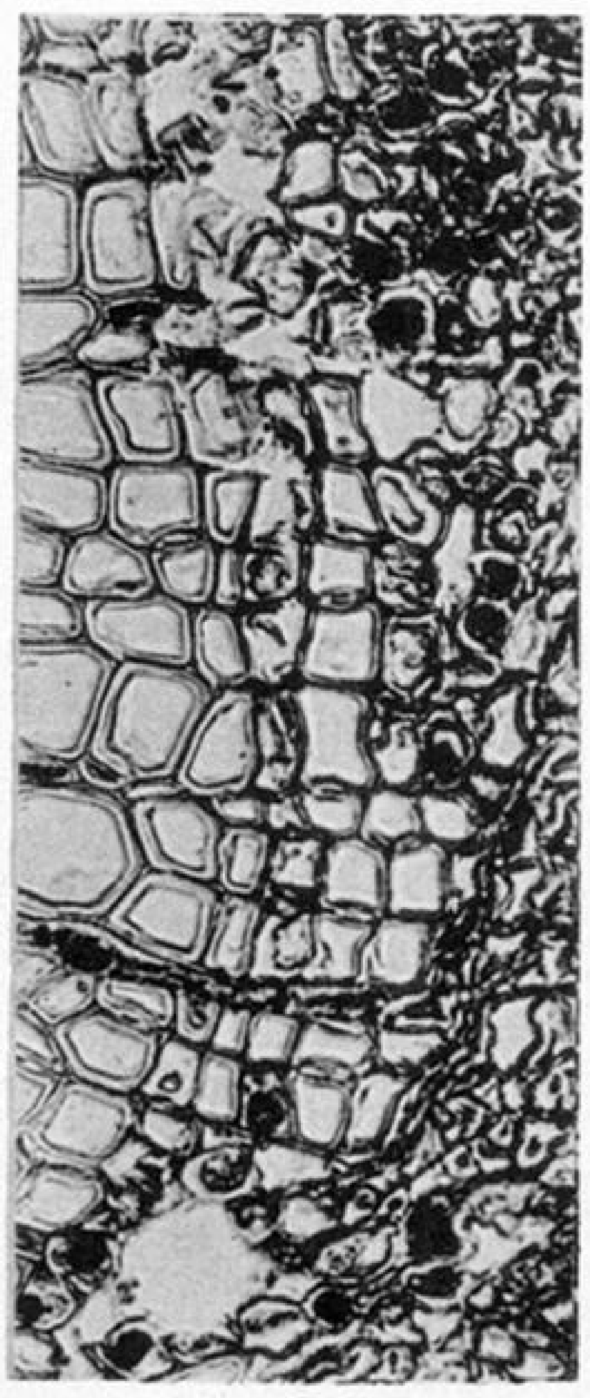

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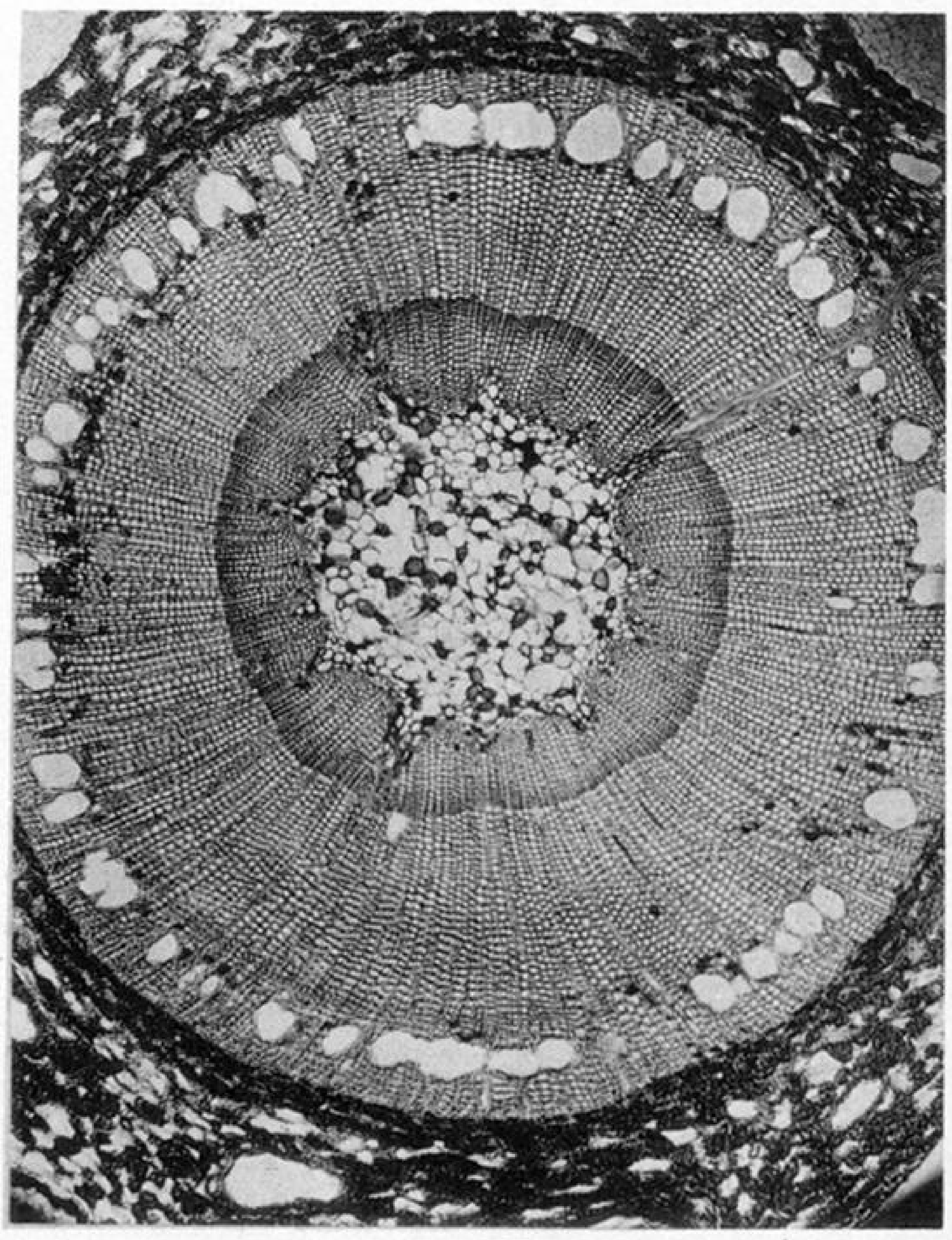

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PLATE 10.

PHOTO. 27.—*Pinus Strobus*. Transverse of stem. × 240. Structure of resin canals.

PHOTO. 28.—*Picea mariana* seedling six years old. Transverse of cotyledonary region. × 90. (First annual ring indistinct.)

PHOTO. 29.—*P. canadensis*. Transverse of stem. × 240. False annual ring.

PHOTO. 30.—*P. canadensis*. Transverse of tap root. × 15.

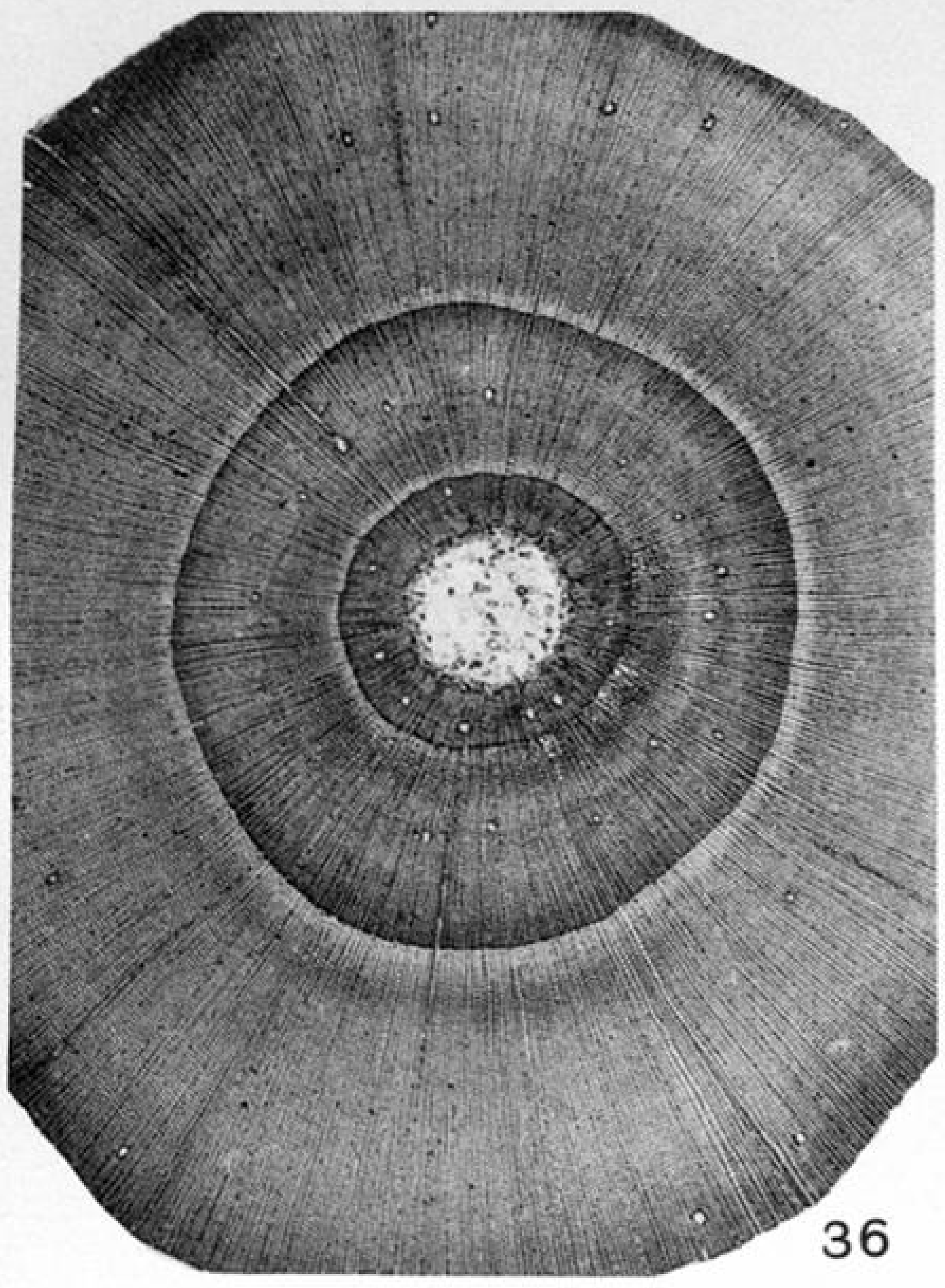
PHOTO. 31.—*P. canadensis*. Transverse of stem. × 35. Resin canals associated with false annual rings.

PHOTO. 32.—*P. mariana*. Same seedling as Photo. 28. Transverse of primary root just below hypocotyl. × 90. (First annual ring indistinct here also.)

PHOTO. 33.—*P. Omorica*. Transverse of branch. × 25. False annual ring and extra resin canals resulting from continued pressure by clothes-peg.

PHOTO. 34.—*P. Omorica*. Transverse of root. × 240. Resin canals resulting from continued pressure by clothes-peg.

PHOTO. 35.—*P. pungens*. Transverse of leader. × 35. Resin canals resulting from slight crushing with pliers.



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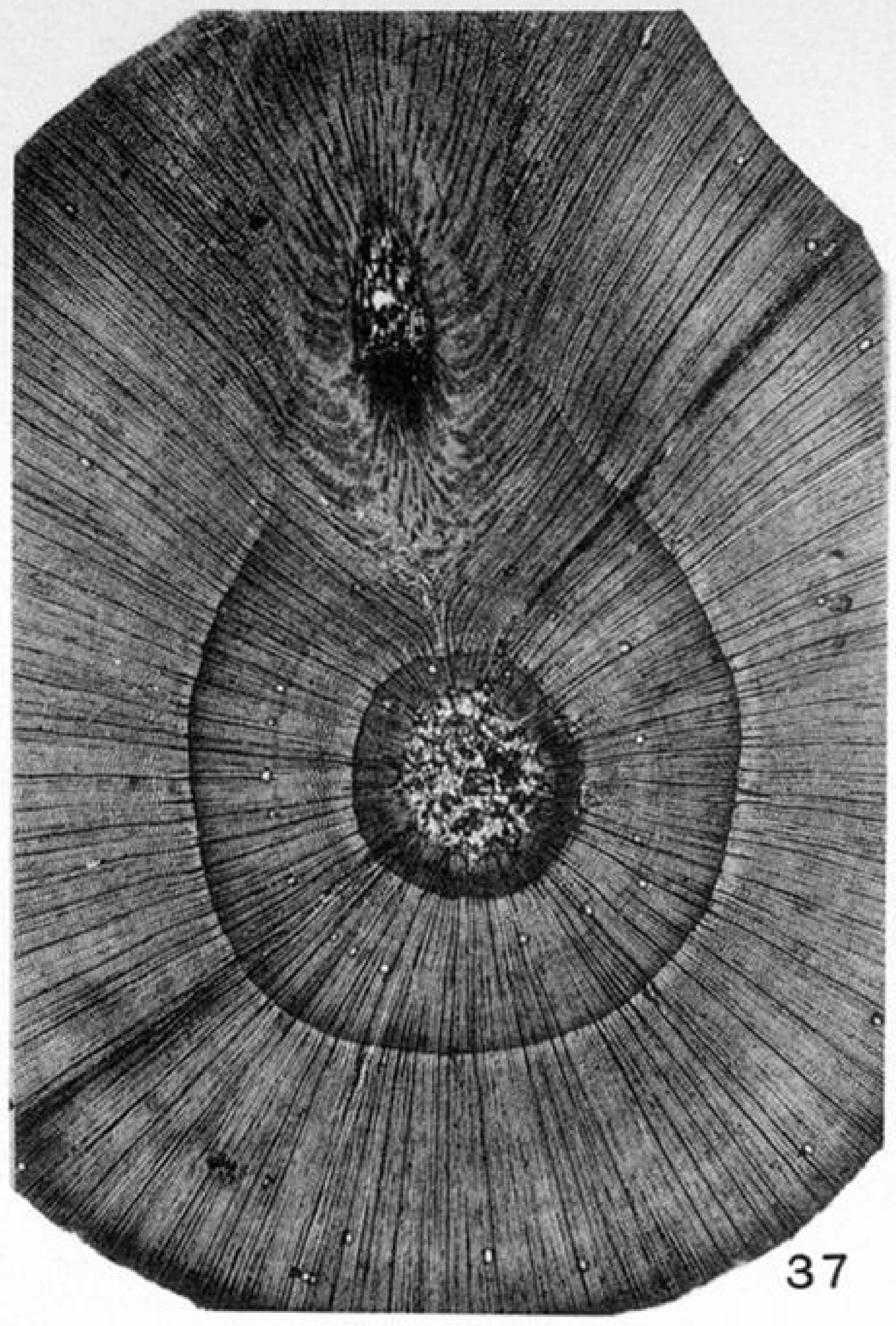

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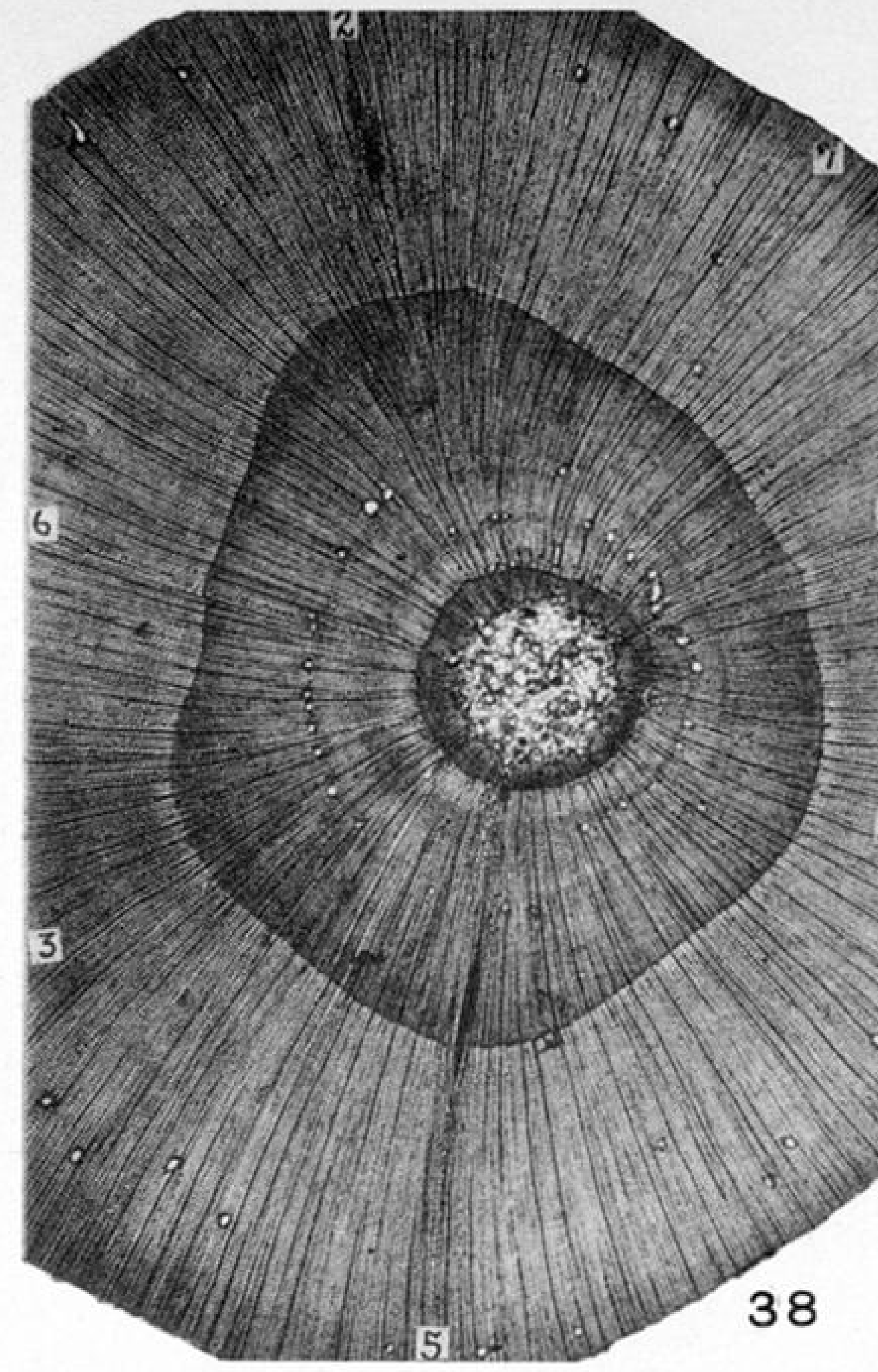

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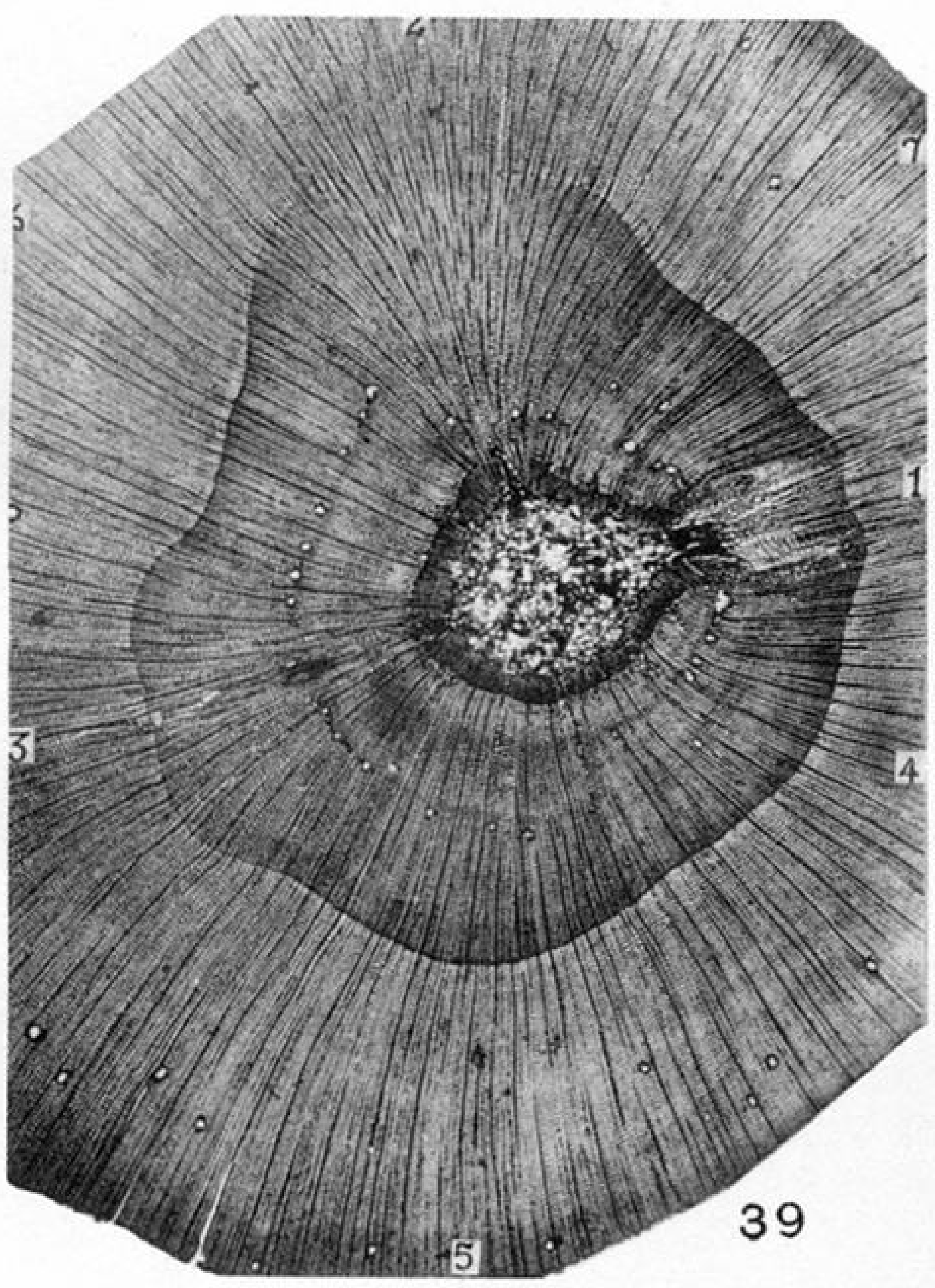

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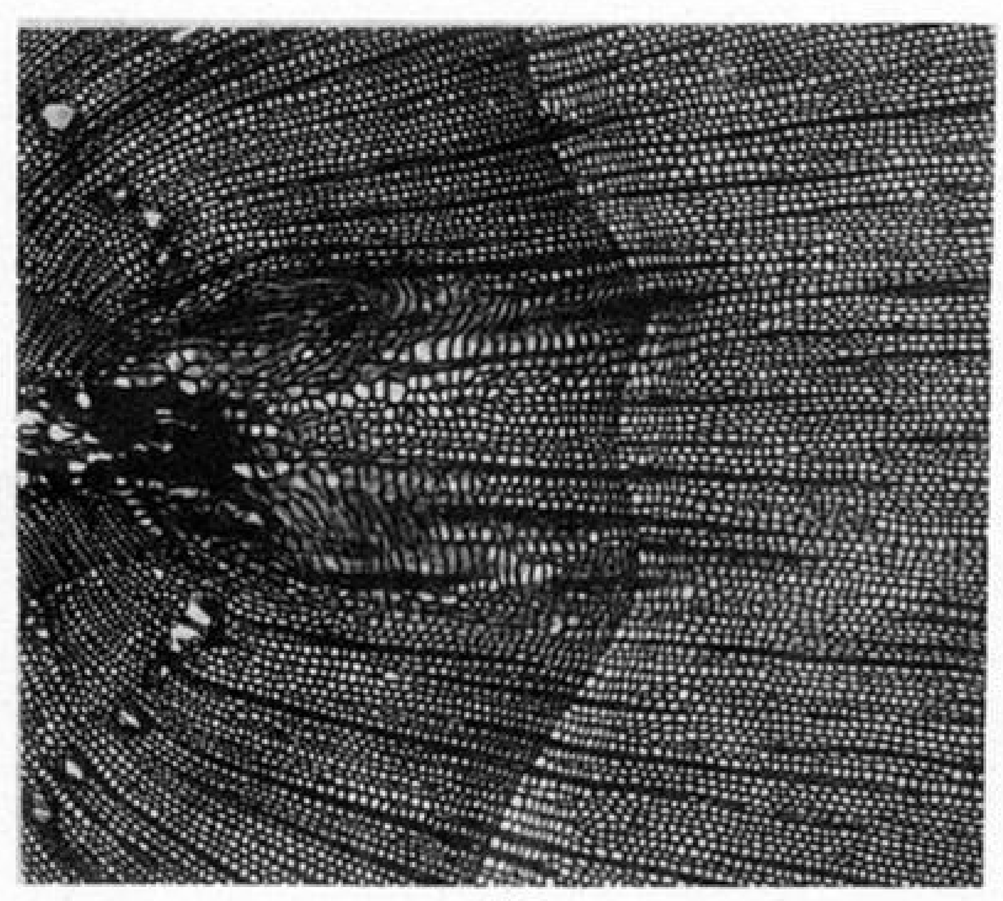

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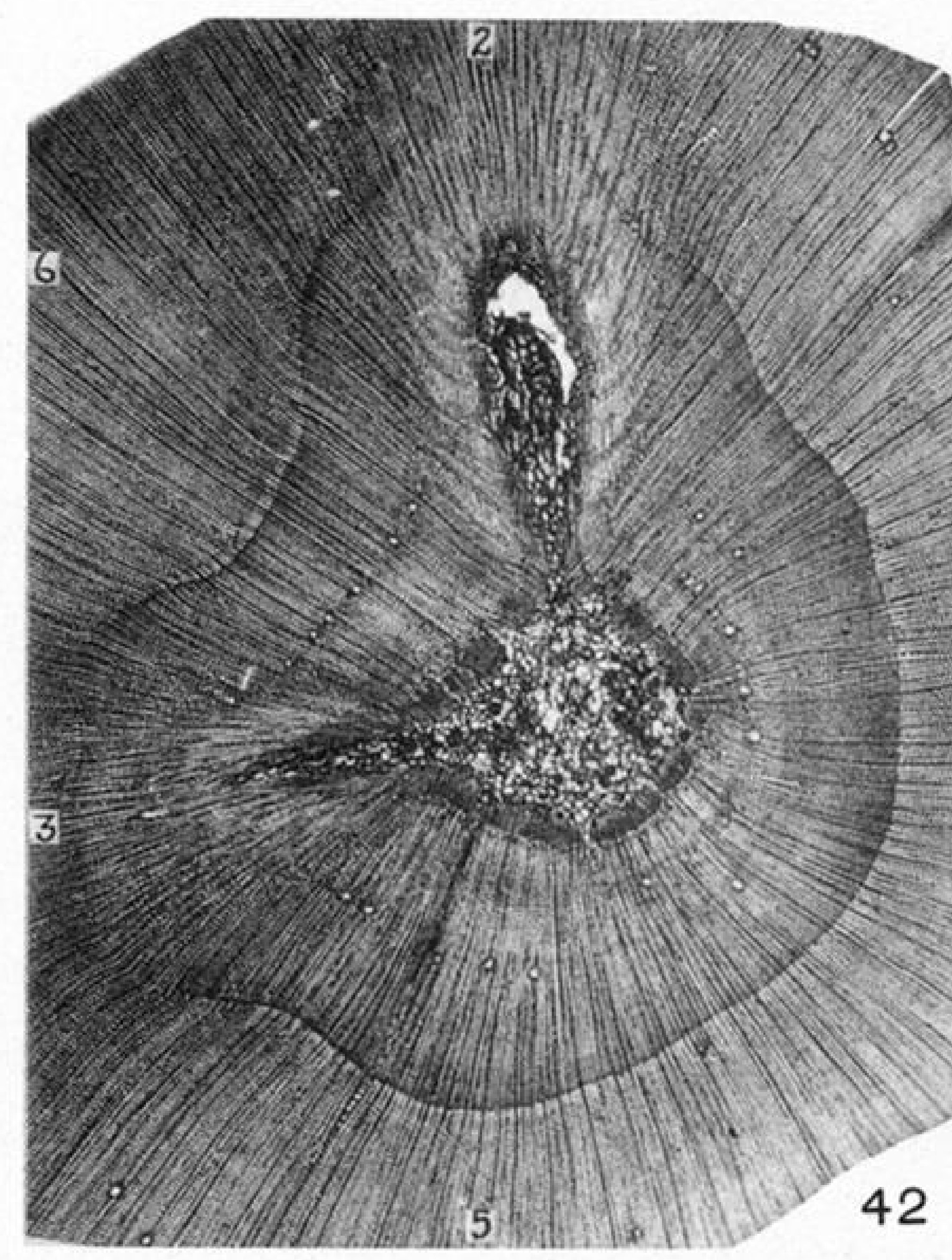

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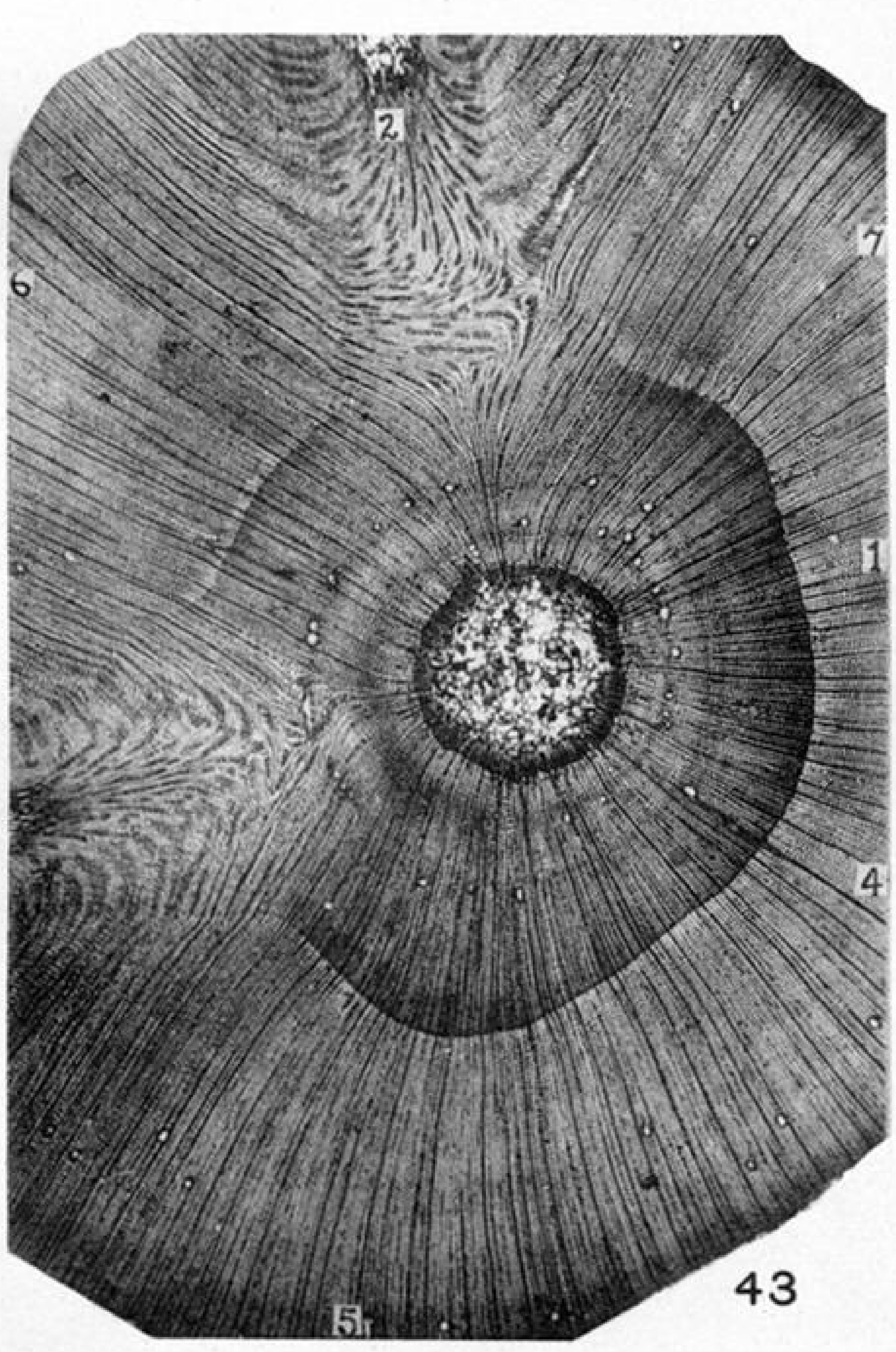

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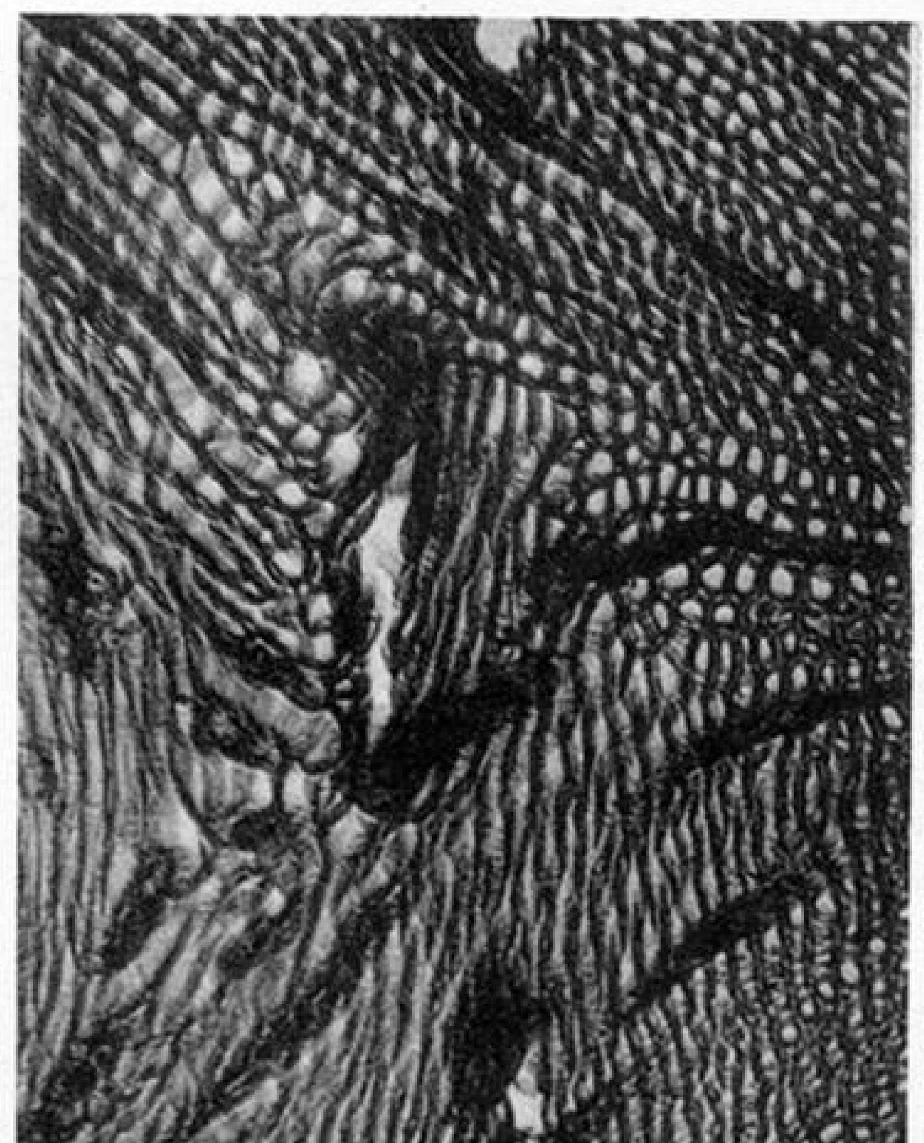

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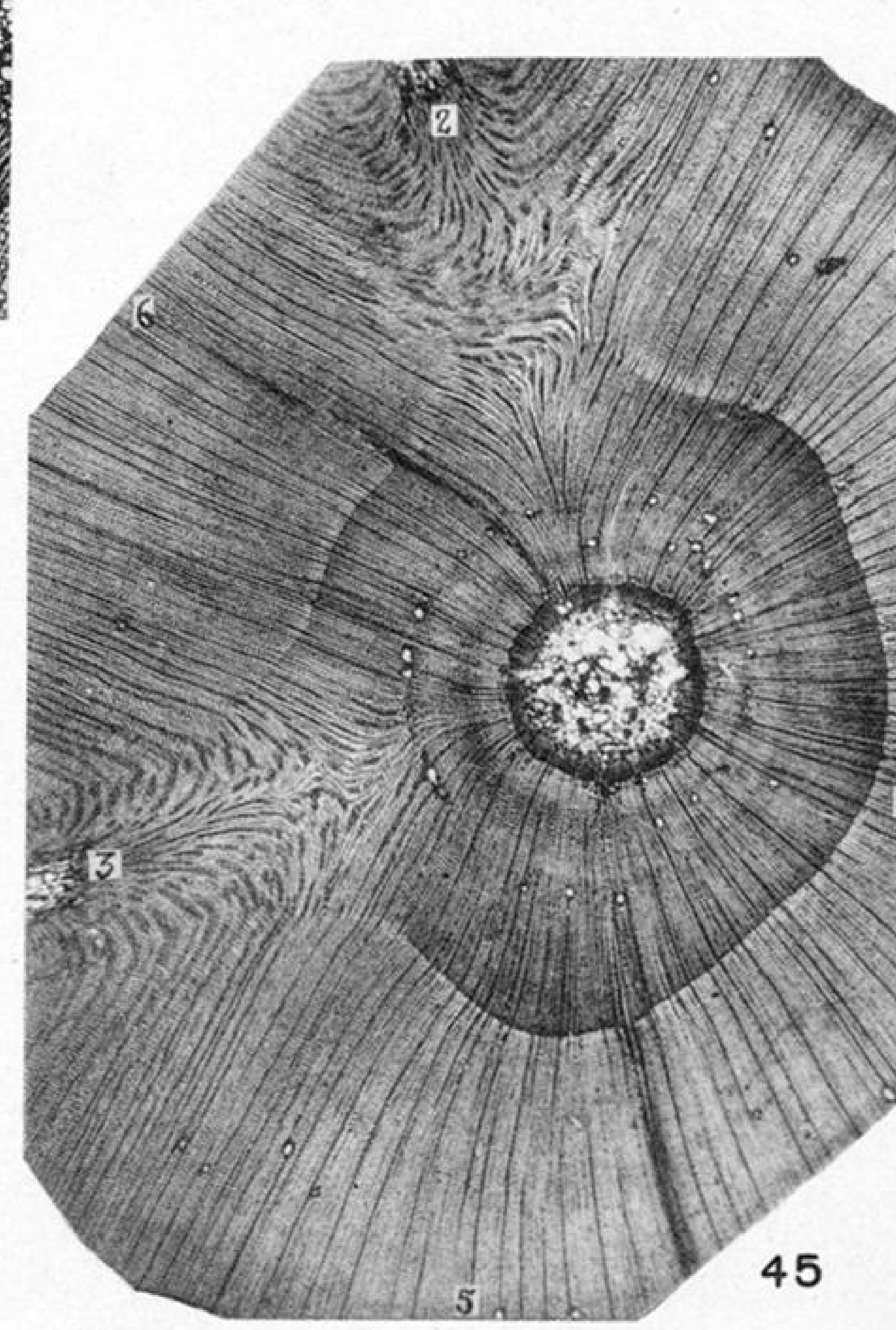

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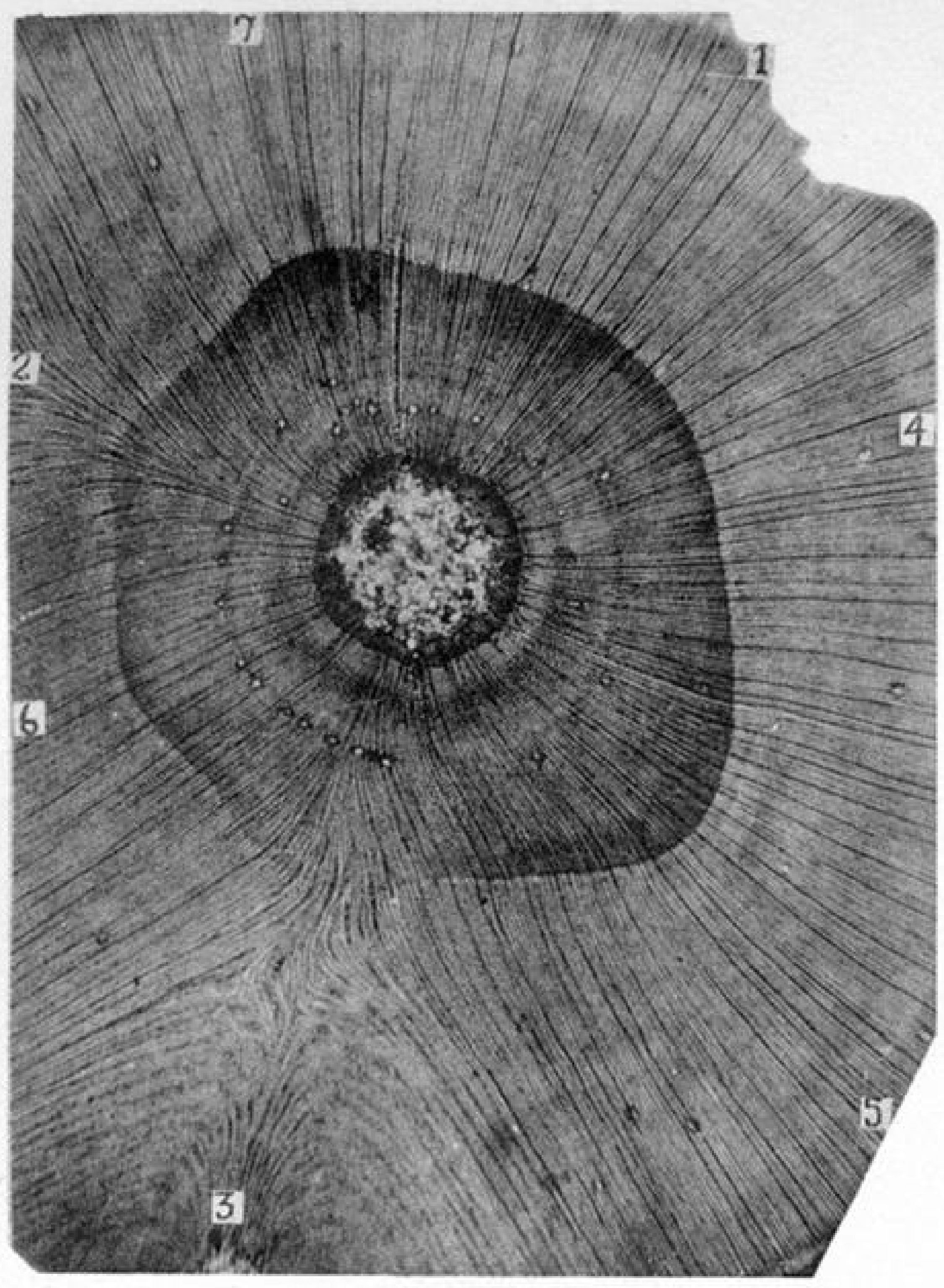
PLATE 11.

PHOTOS. 36, 37, 38, 39, 42, 43 and 45.—*Picea canadensis*. Transverse sections from one plant. × 15. Connection between resin canals and wounds.

PHOTOS. 40 and 41.—*P. canadensis*. Portions of Photo. 39. × 35.

PHOTO. 44.—*P. canadensis*. Part of Photo. 43. × 95.



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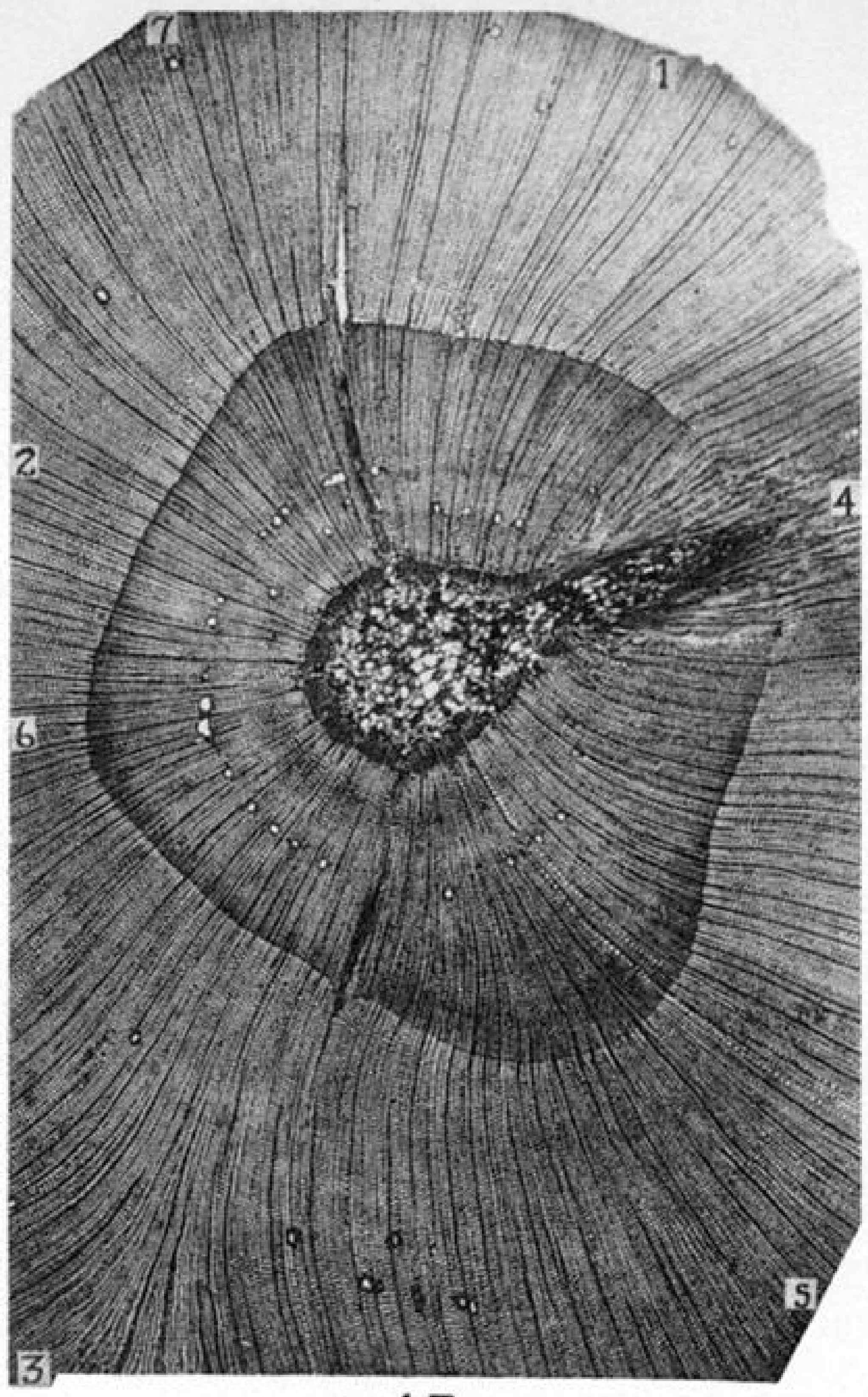

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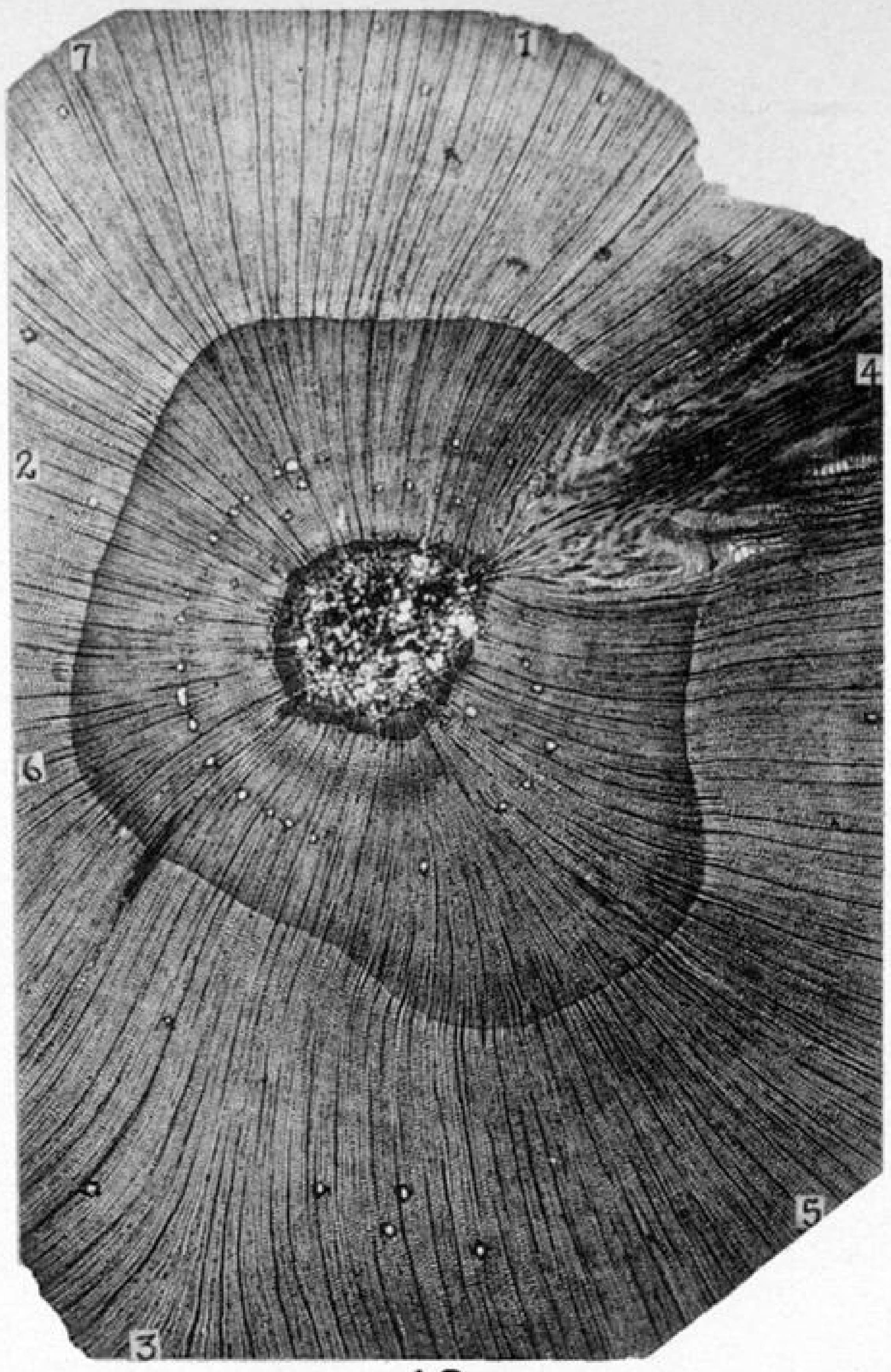

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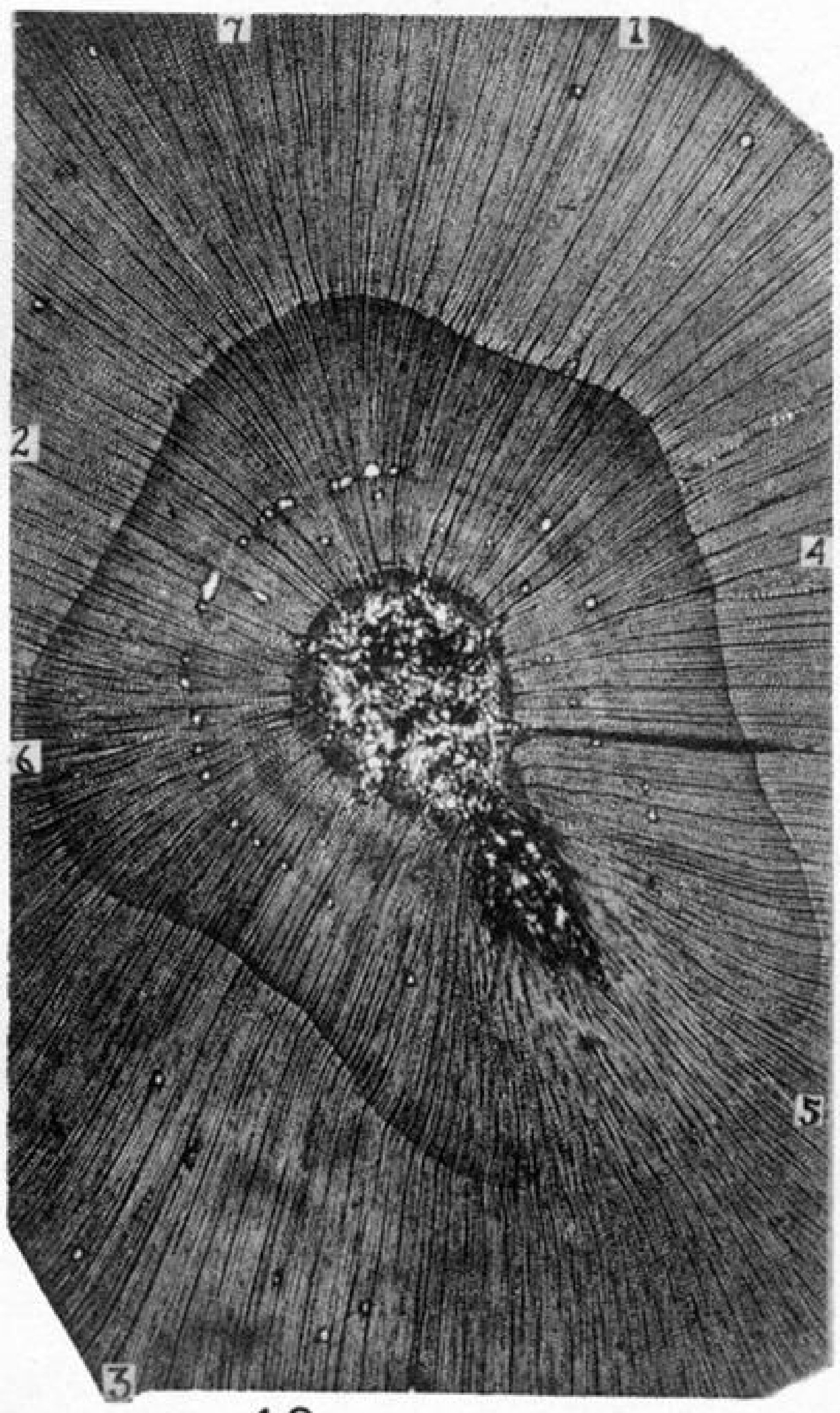

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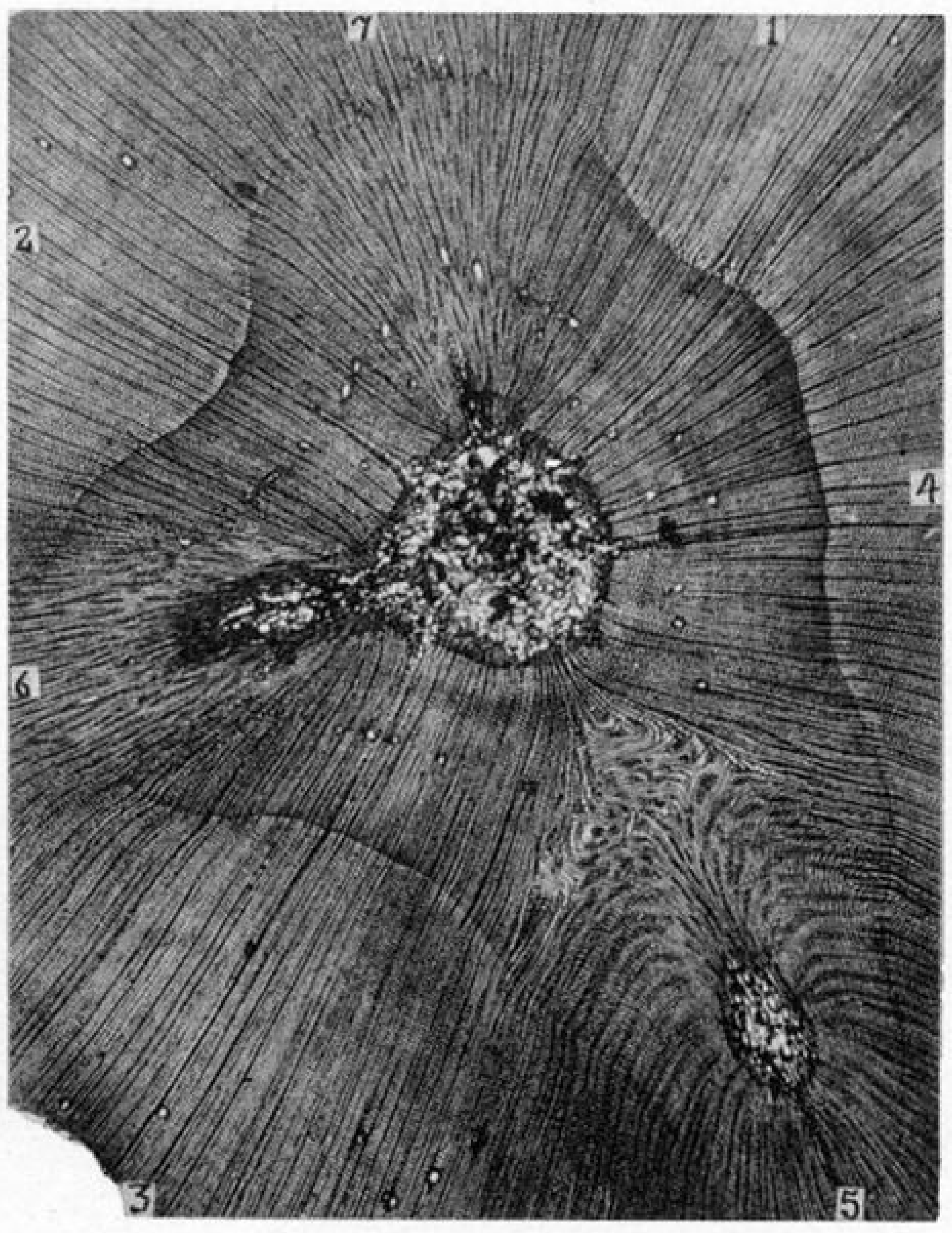

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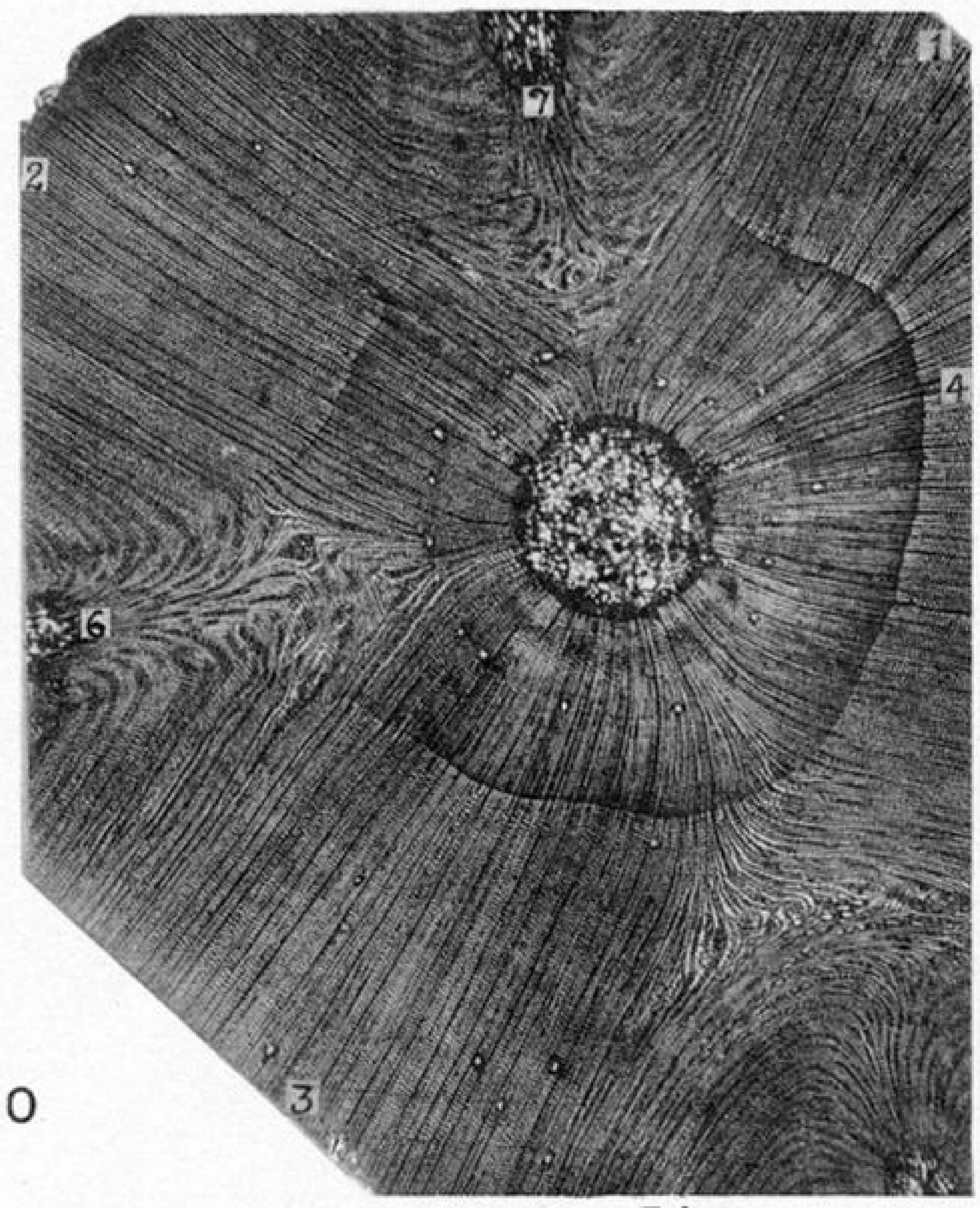

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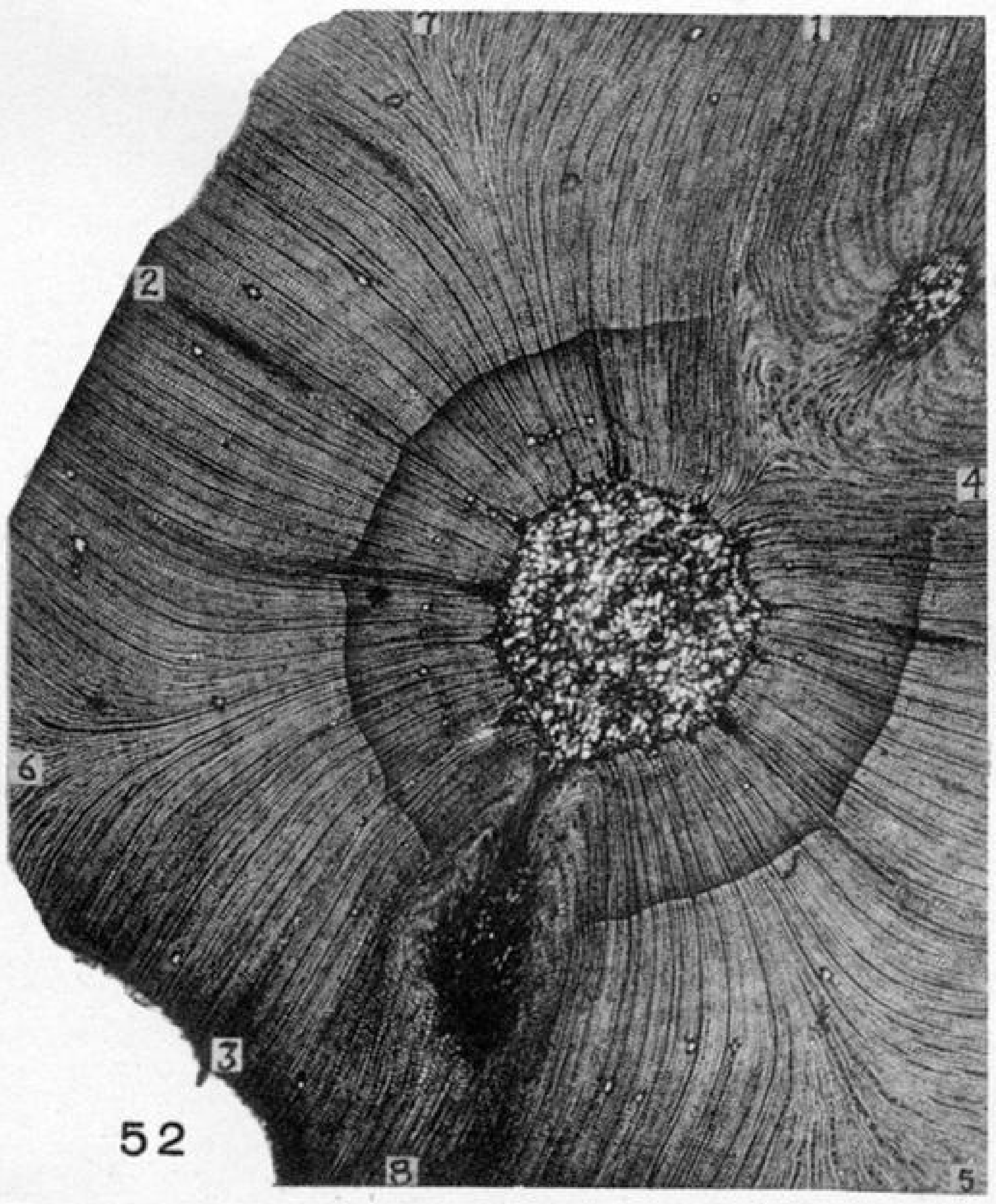

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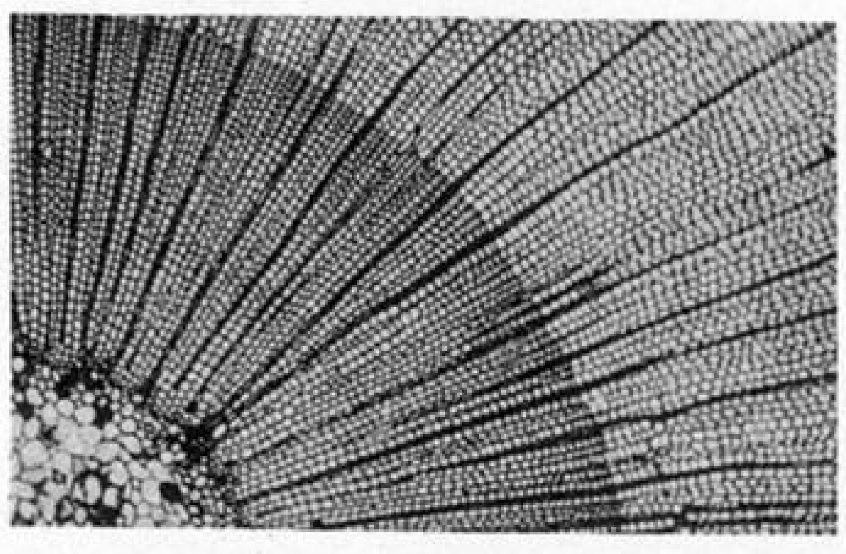

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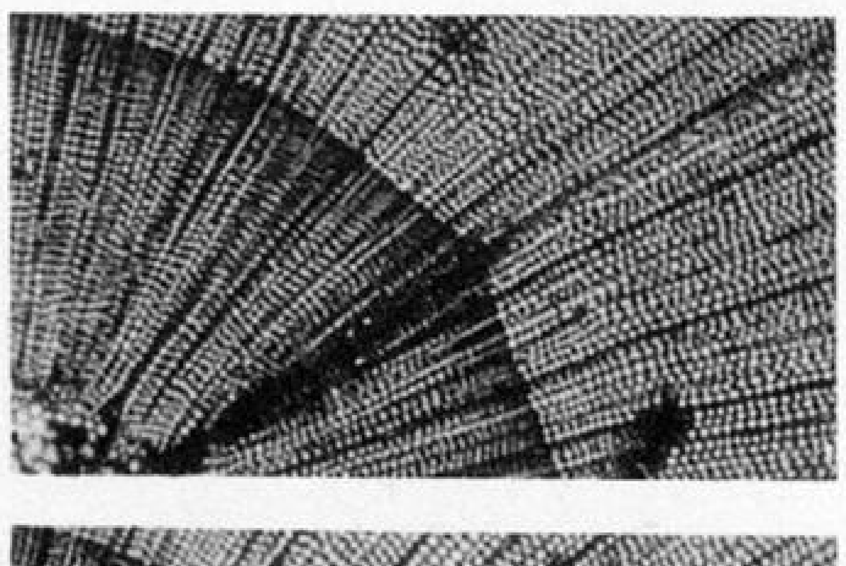

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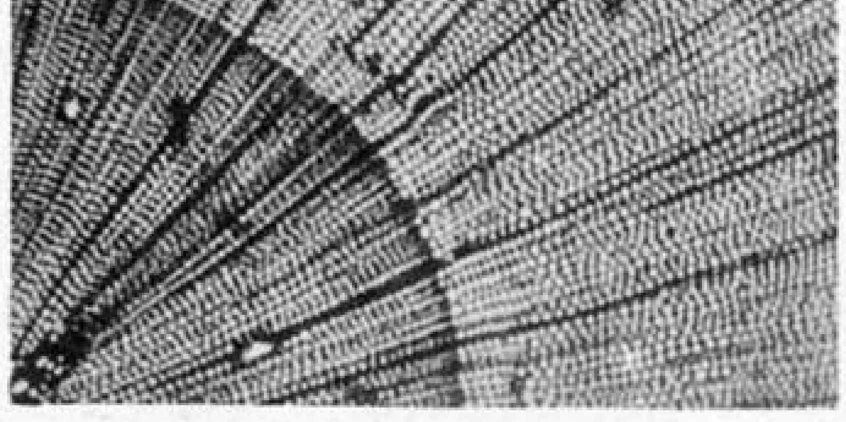

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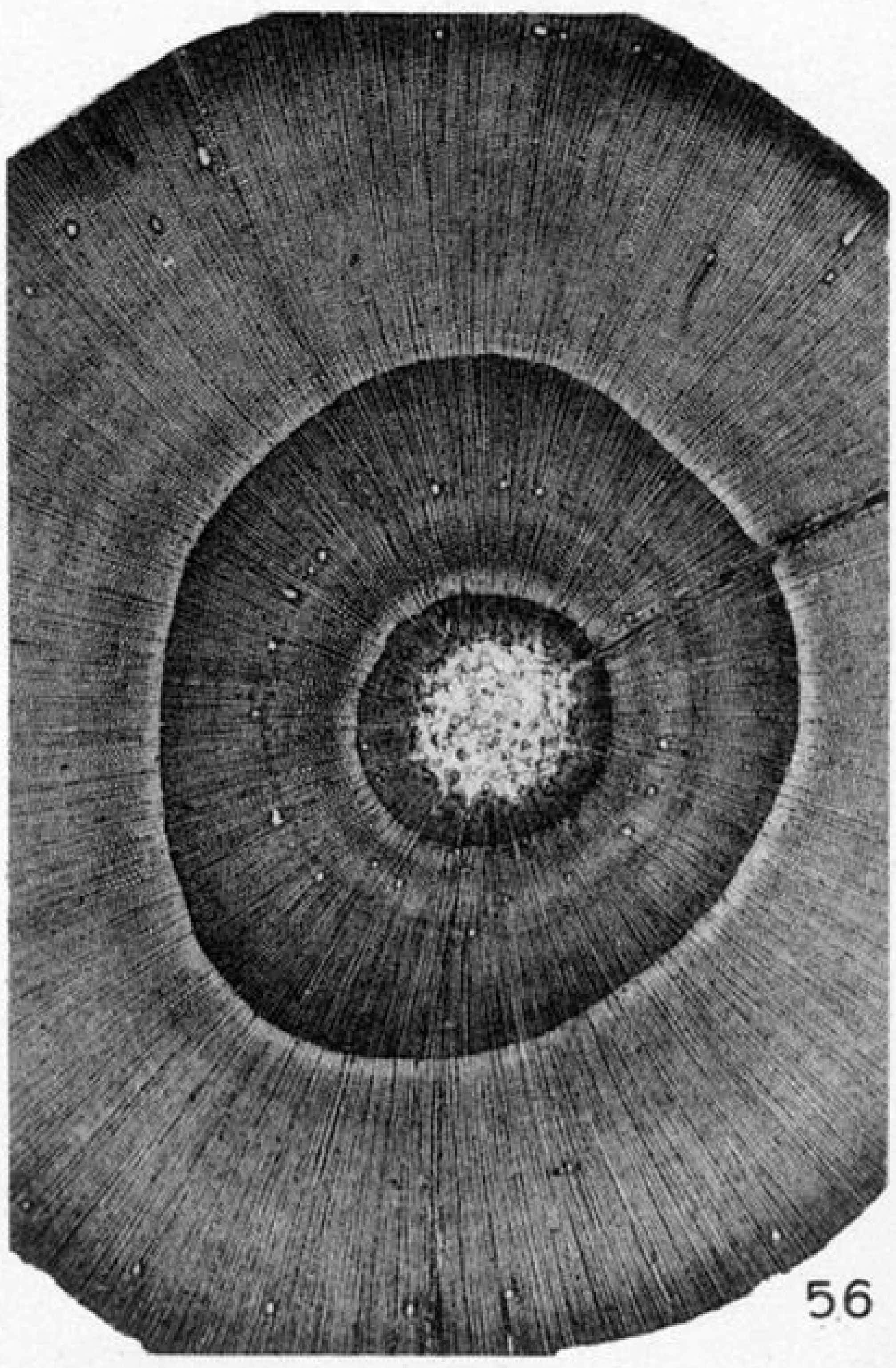

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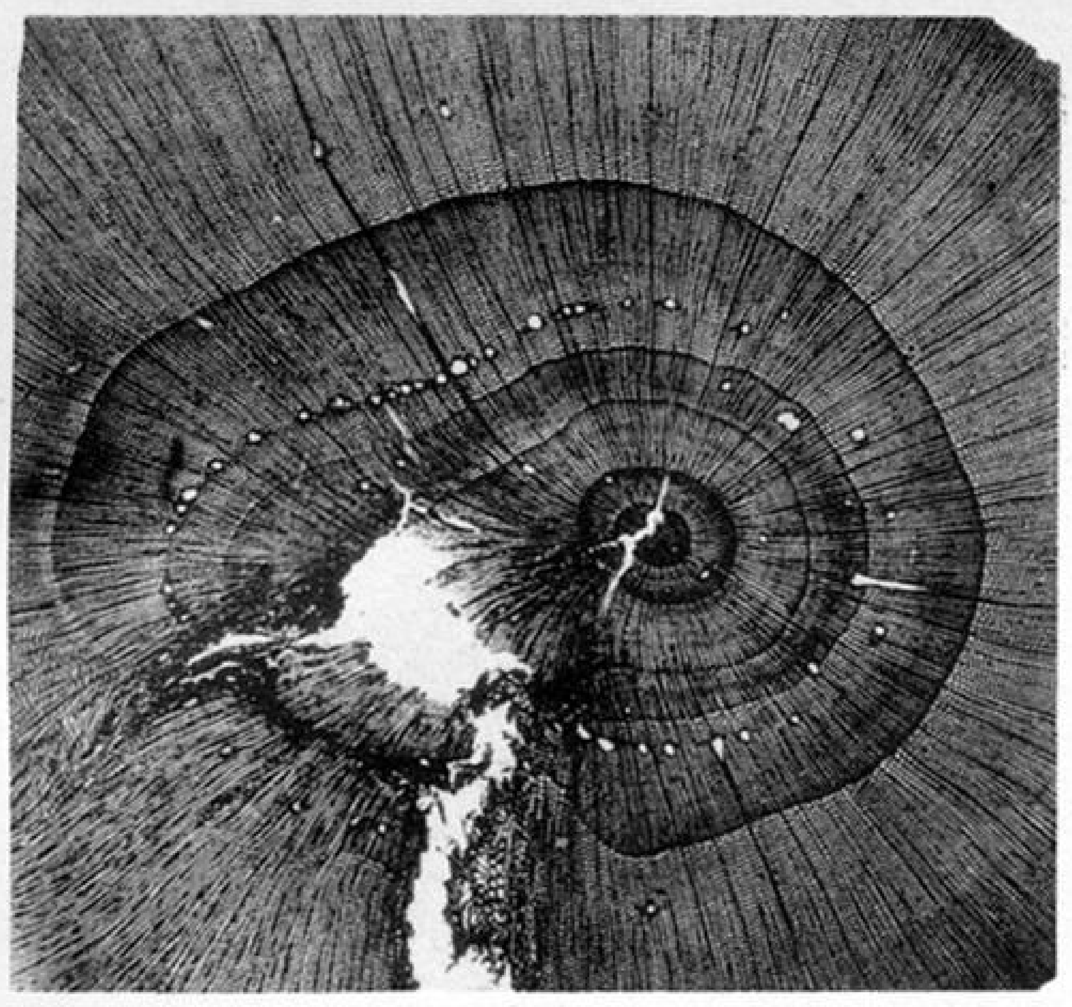
PLATE 12.

PHOTOS. 46, 47, 48, 49, 50, 51, 52 and 56.—*Picea canadensis*. Transverse sections from same plant as those of Plate 4. × 15.

PHOTOS. 53, 54 and 55.—*P. canadensis*. Transverse from same plant. × 35. Illustration of loss of a resin canal at a leaf trace. Photo. 53 above, Photo. 54 at level of, and Photo. 55 below leaf trace at which the resin canal is lost.



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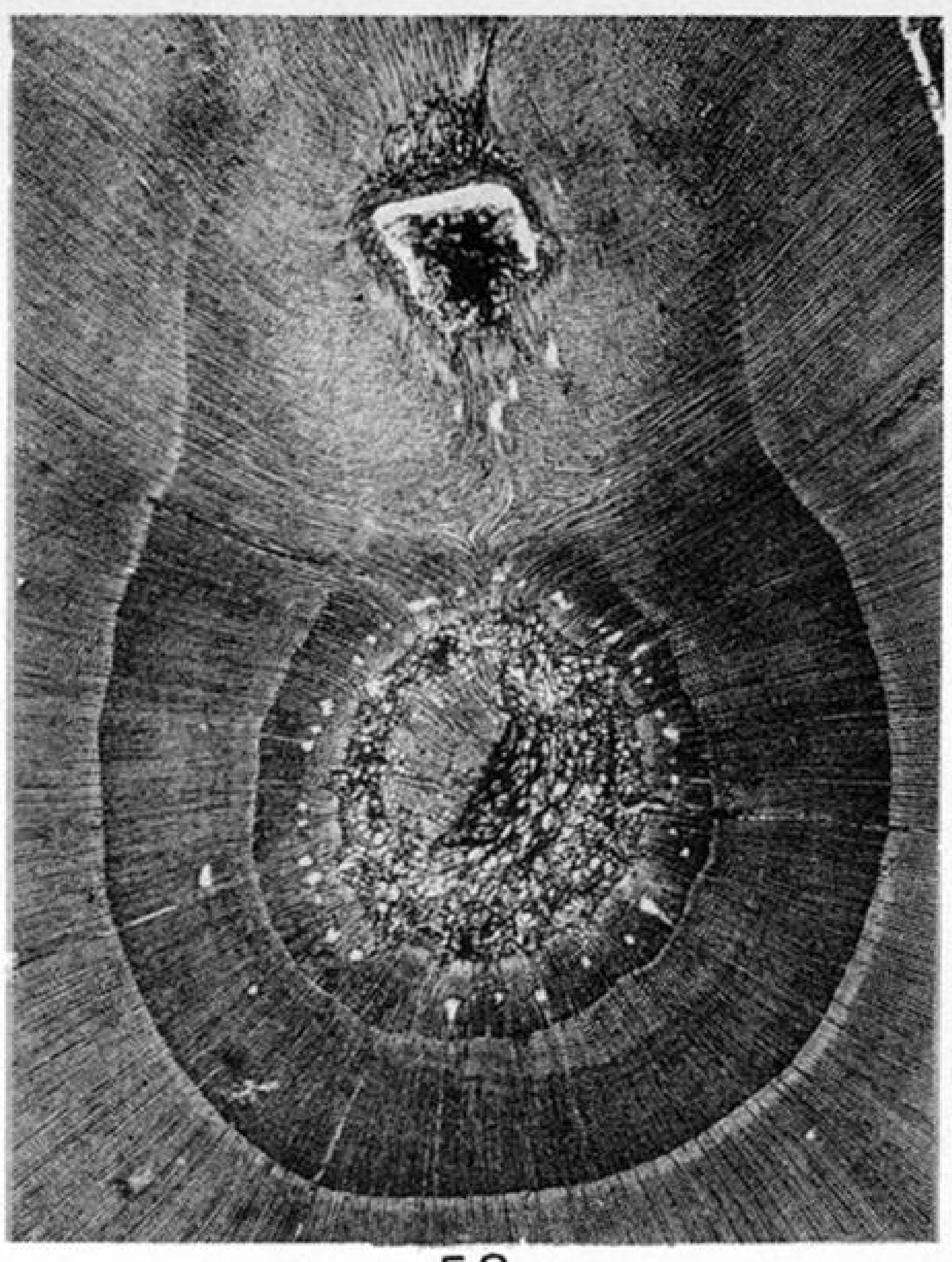

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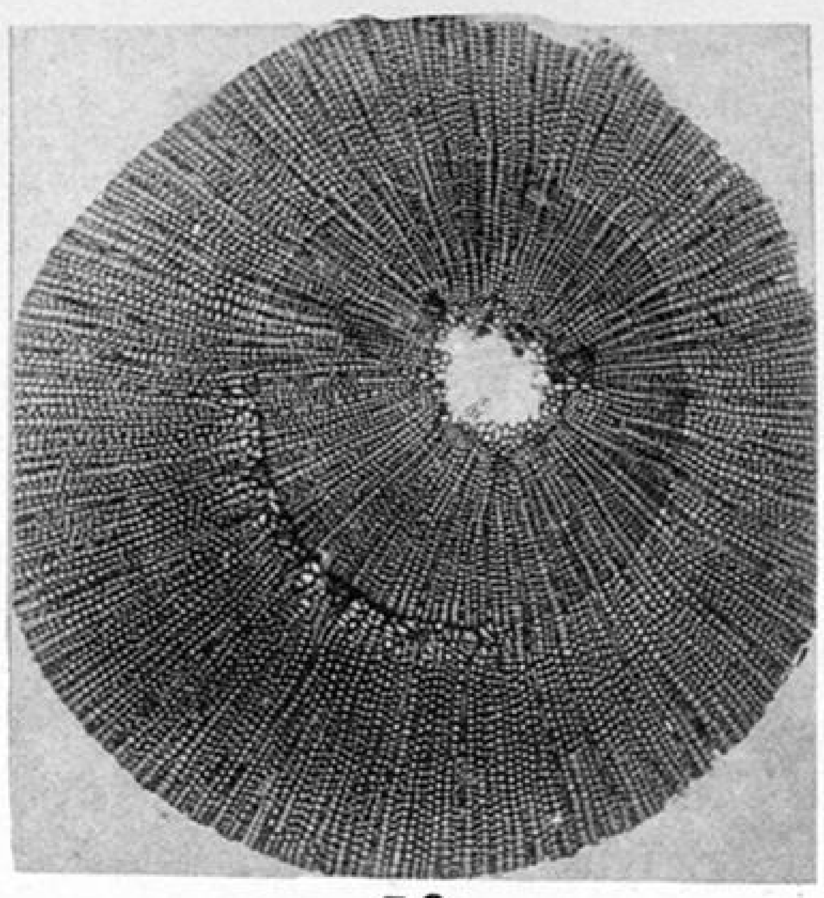

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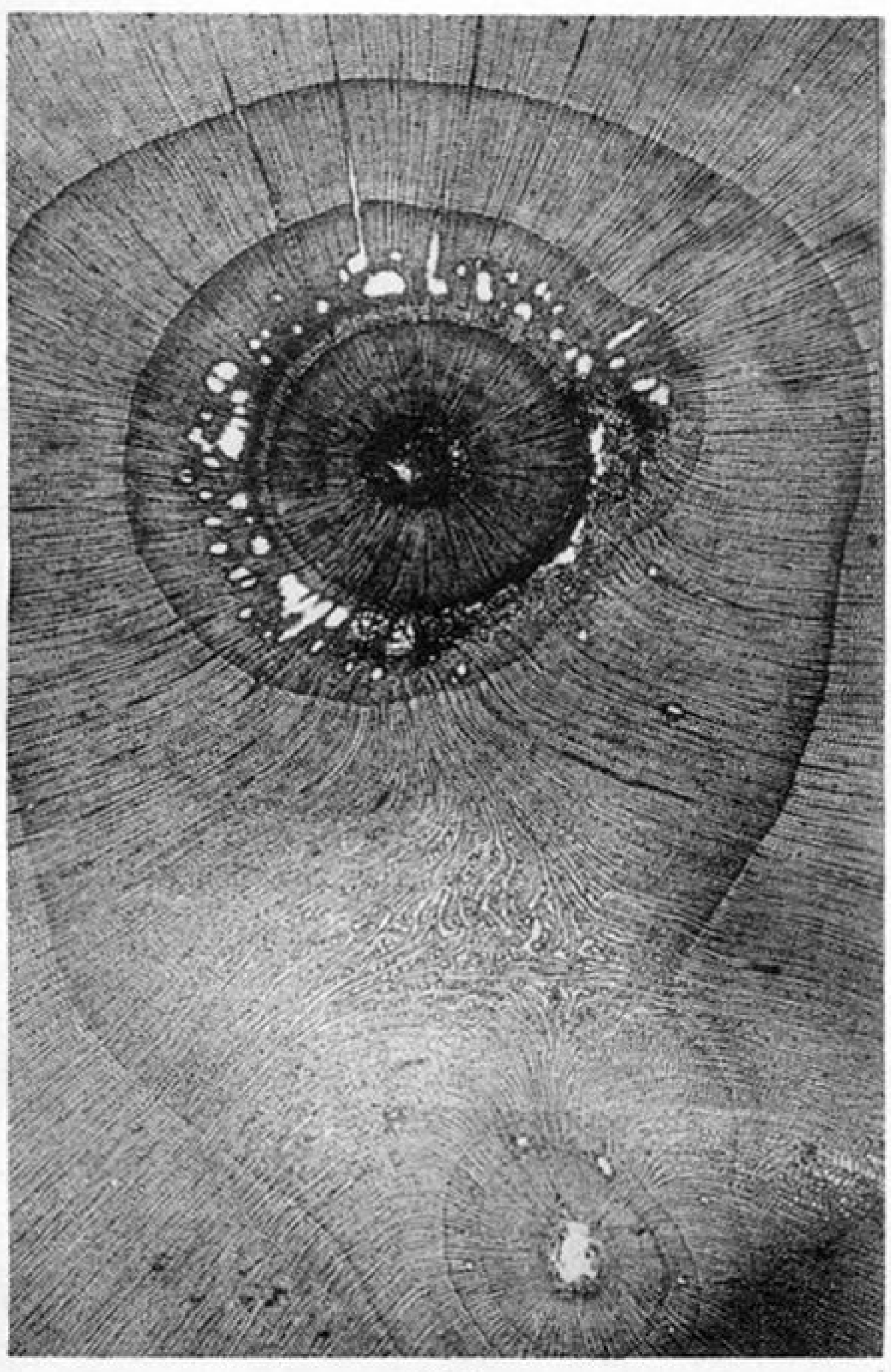

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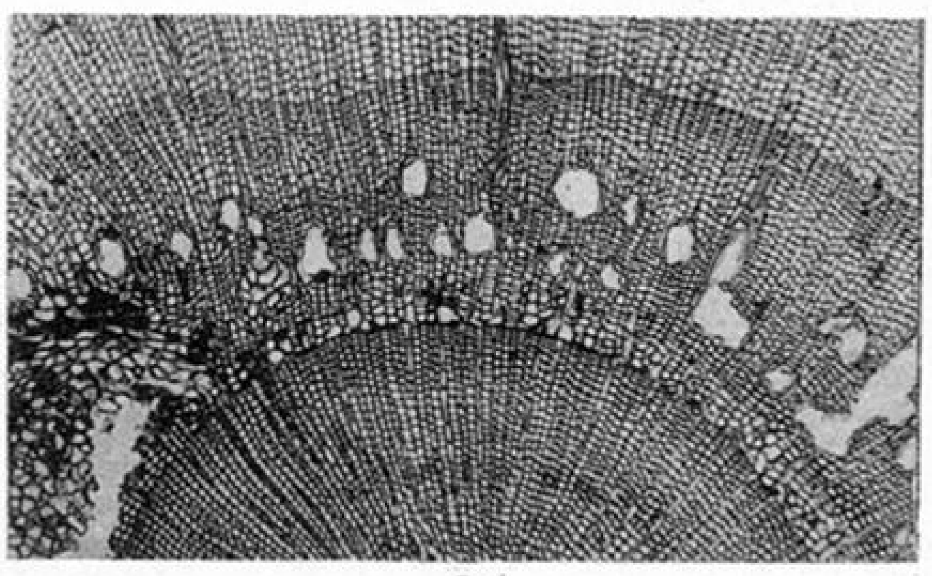

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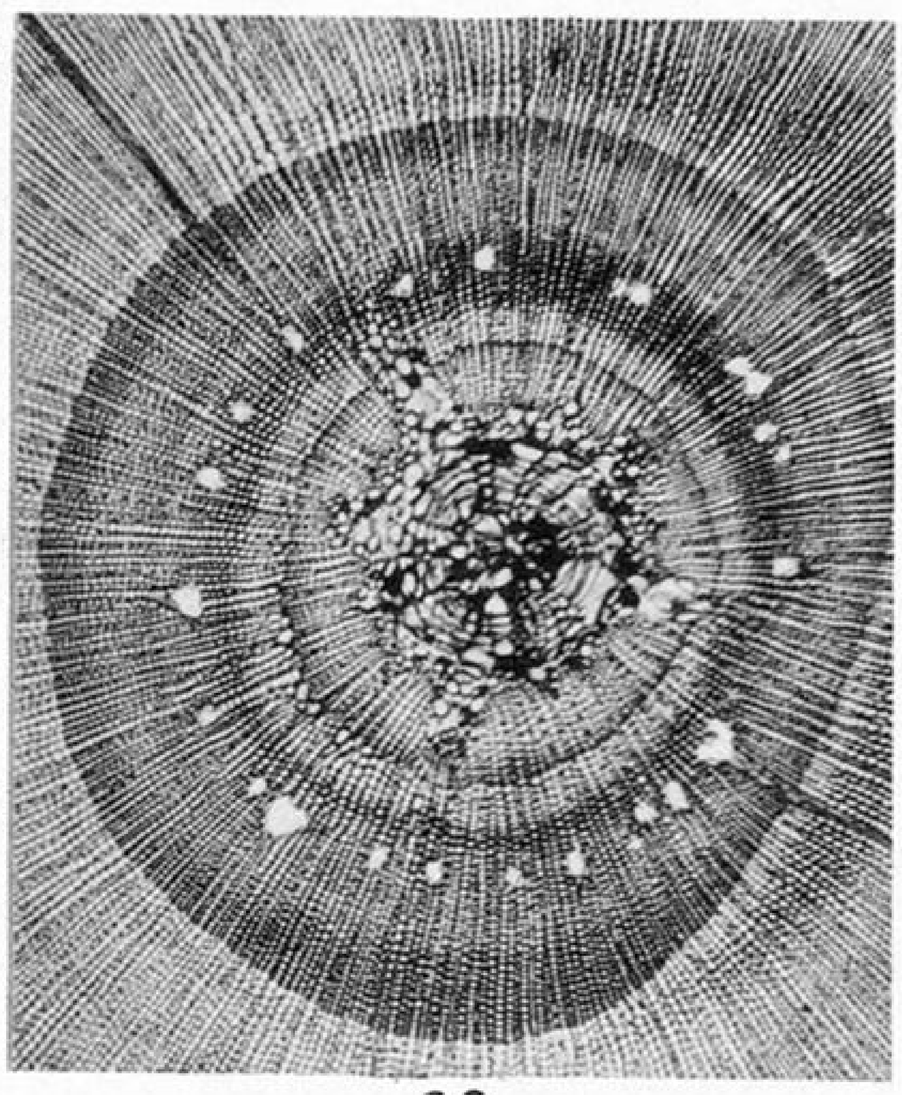

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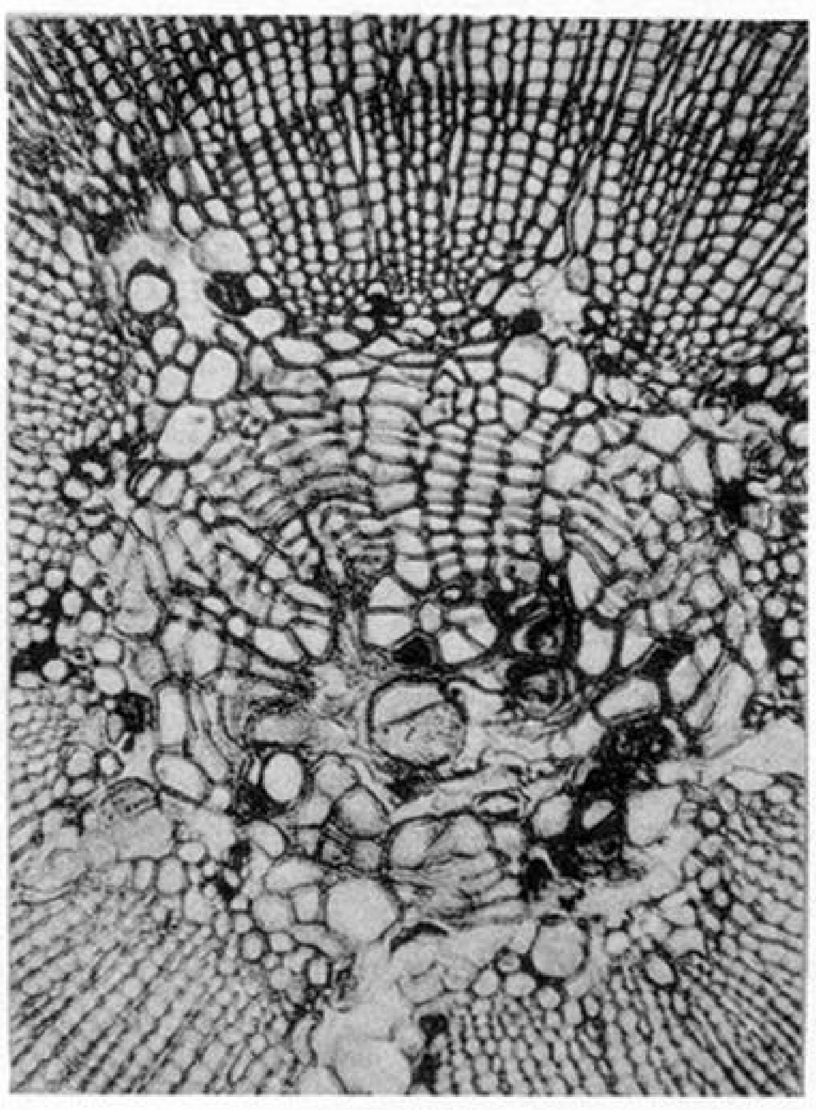

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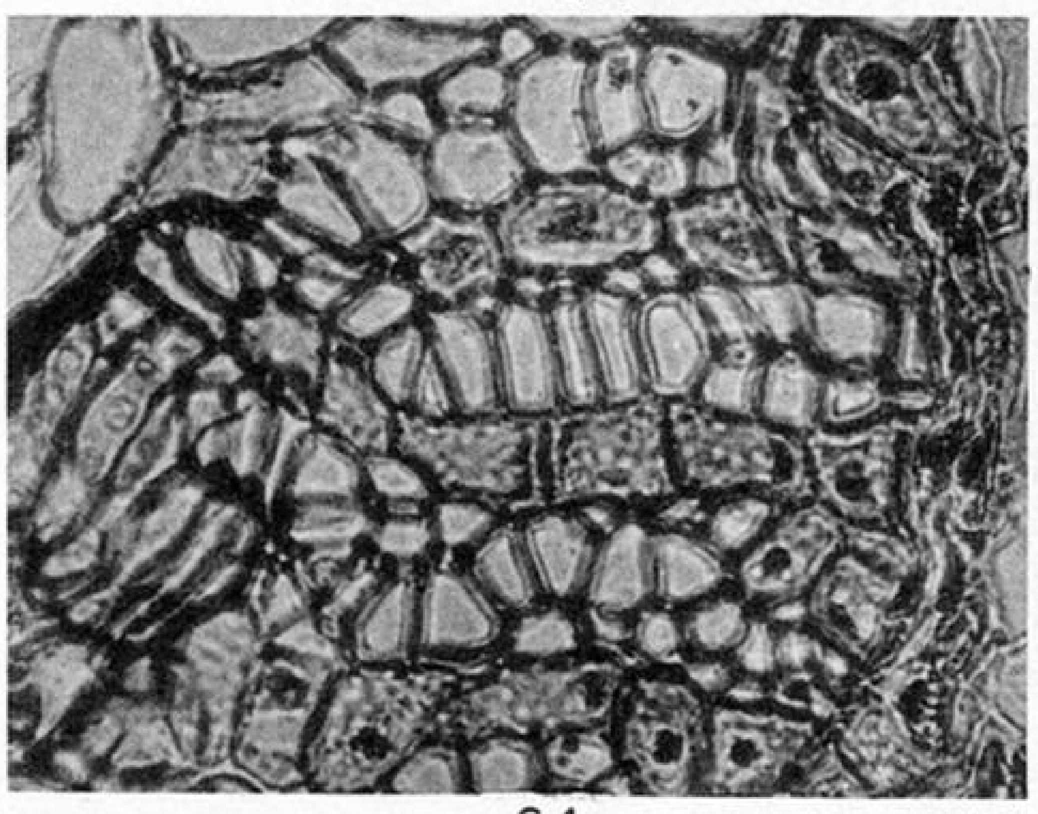

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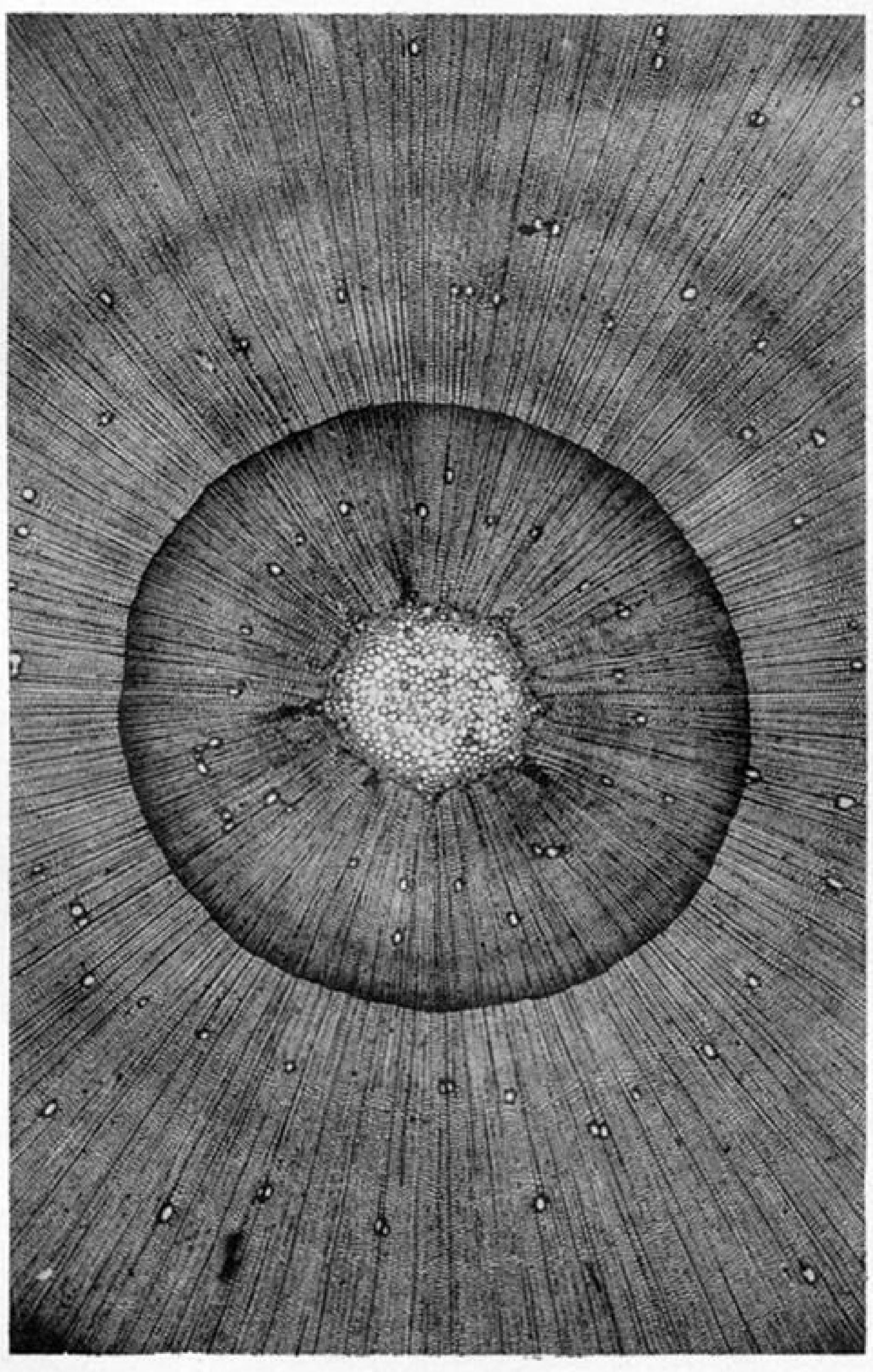

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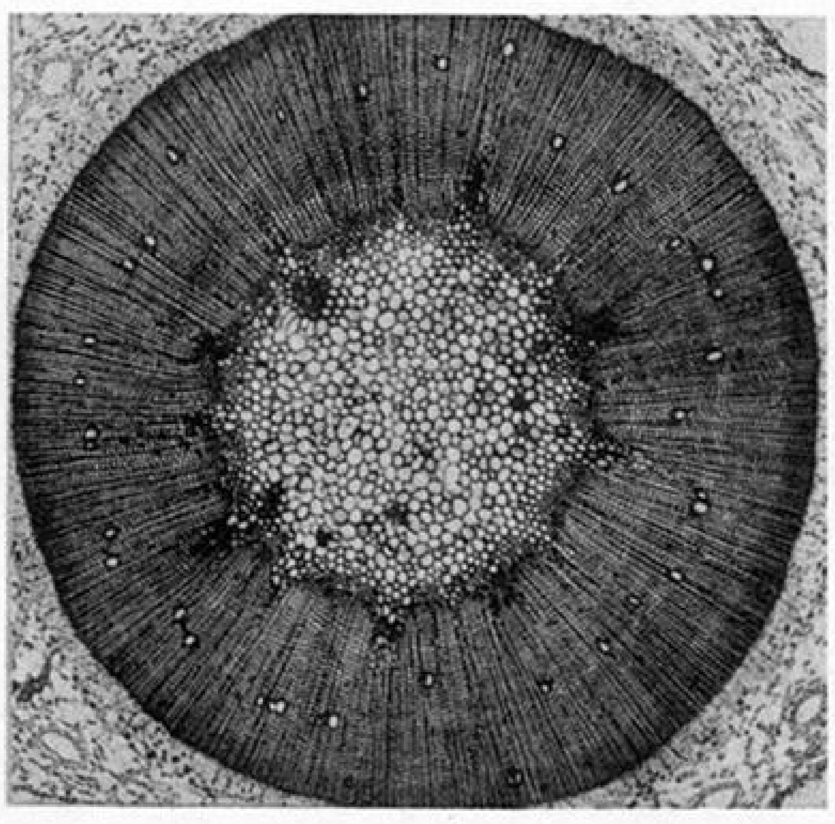

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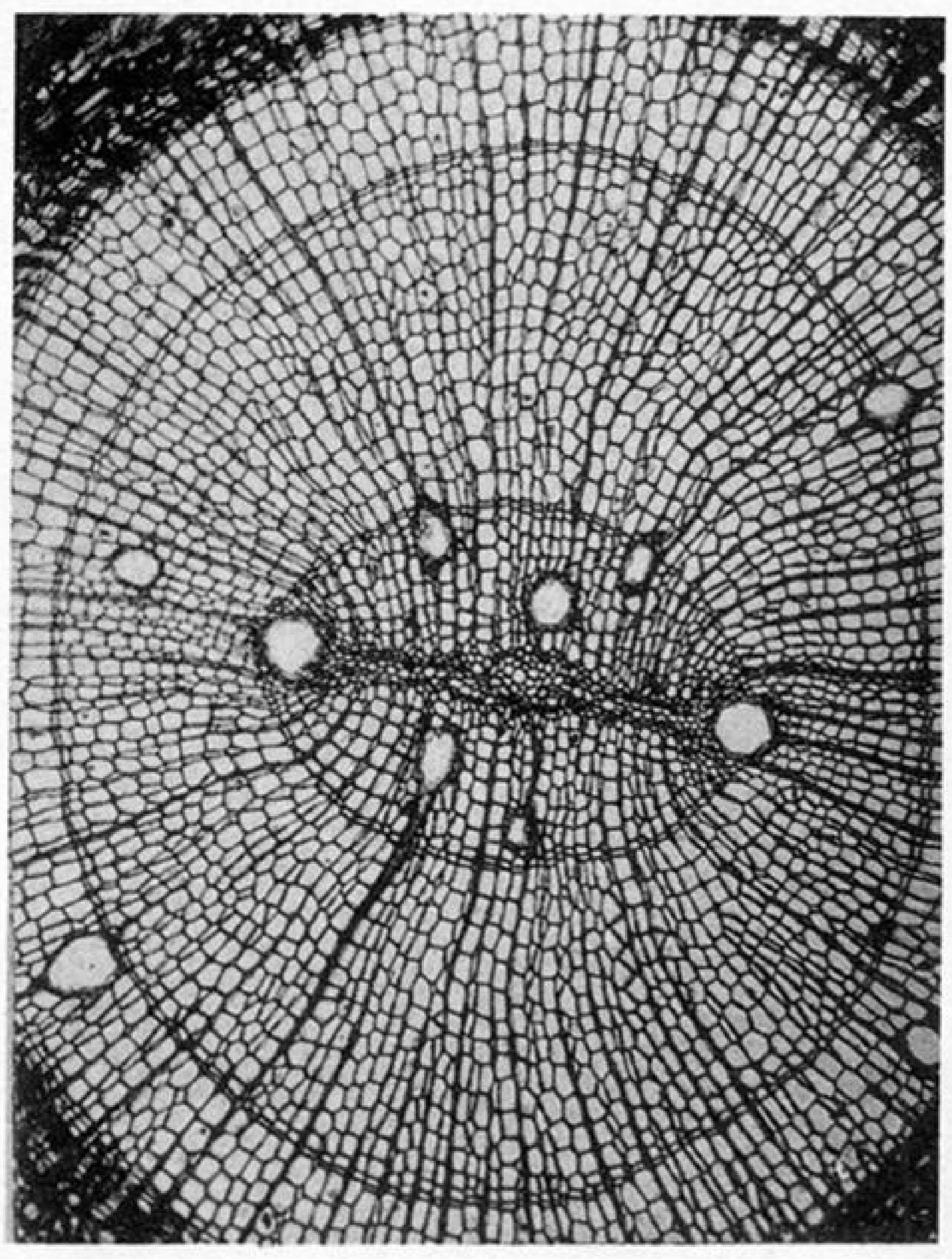

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PLATE 13.

PHOTO. 57.—*Picea canadensis.* Transverse of tap root of same plant as those of Plate 5. × 15. Wound and tangential series of resin canals.

PHOTO. 58.—*P. canadensis.* Transverse of stem of same plant. × 15. Injury to branch connected with resin canals in fourth year's growth of stem (as illustrated in fig. 4, Nos. 7 and 8).

PHOTO. 59.—*P. canadensis.* Unwounded branch from same node as Photo. 58. × 35.

PHOTO. 60.—*P. canadensis.* Transverse of stem of same plant. × 15. Wound at lower right of the ring with many resin canals. Secondary wood in pith.

PHOTO. 61.—*P. canadensis.* Transverse showing same wound as that in Photo. 60, but at a different level. × 35.

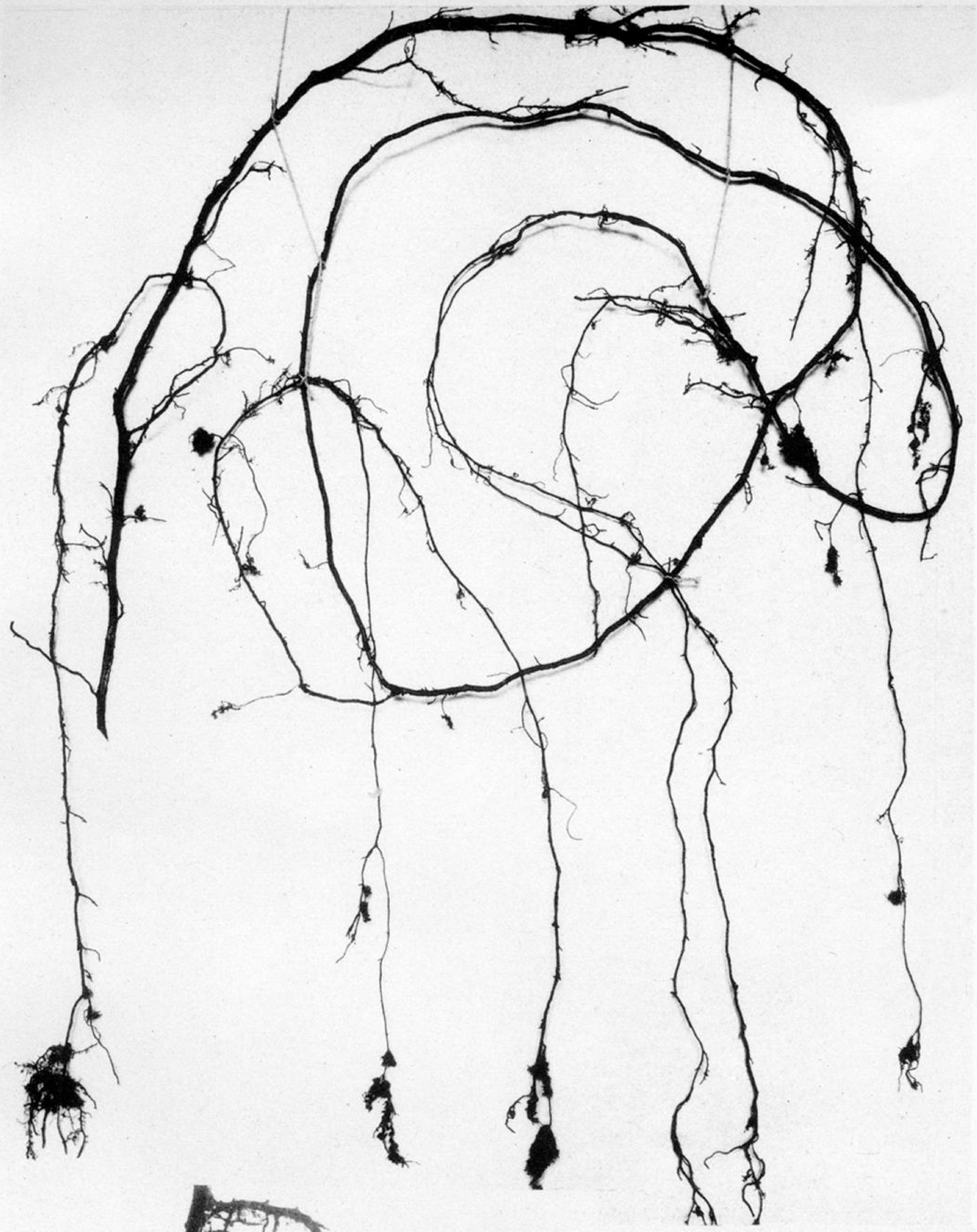
PHOTO. 62.—*P. canadensis.* Transverse lower down in same node as Photo. 60. × 35. Secondary wood forms a circle in pith.

PHOTO. 63.—*P. canadensis.* Another region of secondary growth in pith. × 95.

PHOTO. 64.—*P. canadensis.* Secondary growth in pith showing cambium at right. × 250.

PHOTOS. 65 and 66.—*P. canadensis.* Transverse of leader of a plant 27 years old. × 15. Scattered resin canals and false annual rings.

PHOTO. 67.—*P. canadensis.* Transverse of a side root of an old tree at a considerable distance from the trunk. × 35. Five resin canals in secondary wood of the inner year's growth.



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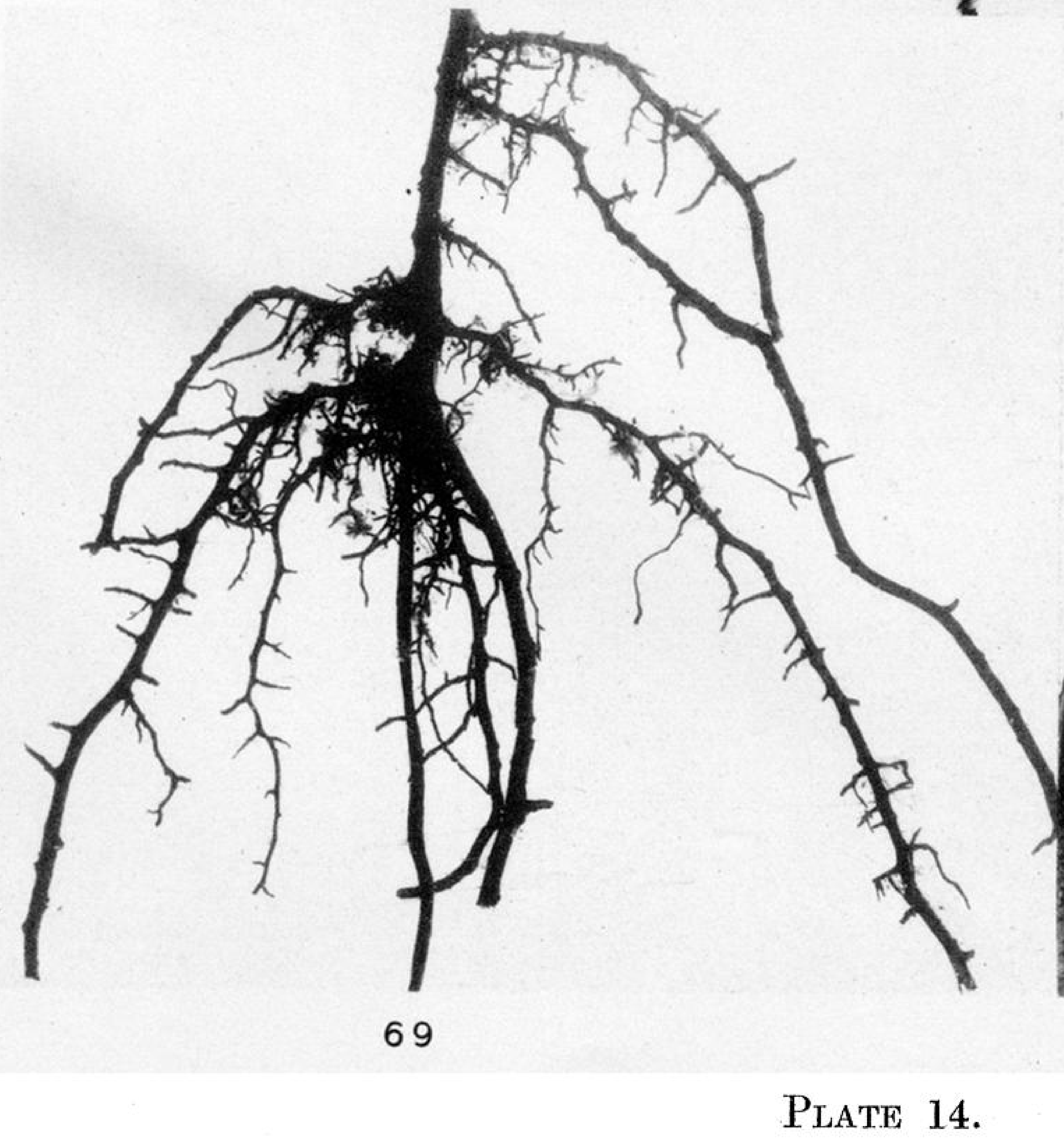

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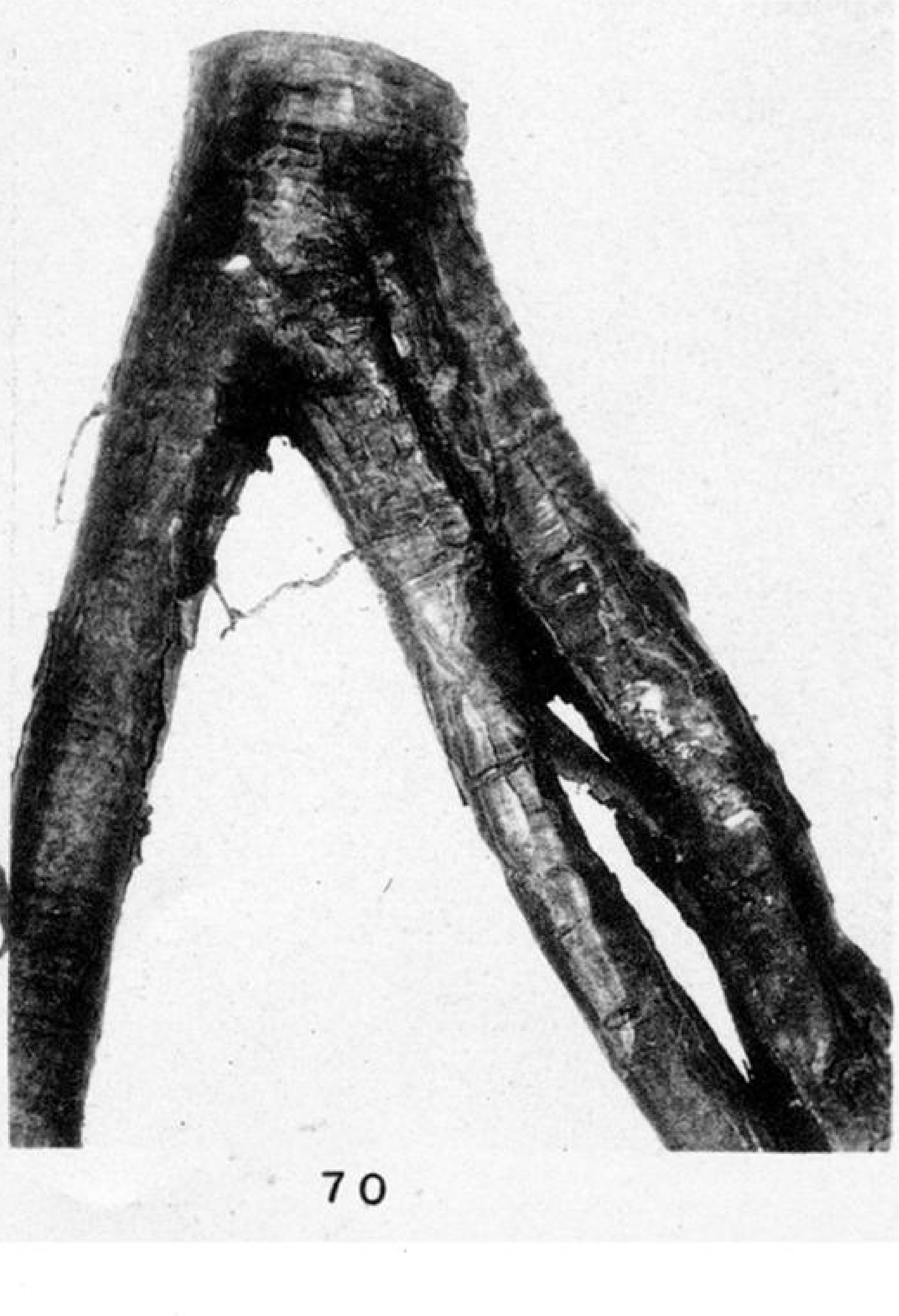

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PLATE 14.

PHOTO. 68.—*Picea canadensis*. Long lateral root from an old tree, much reduced, showing numerous rootlets at tips of branches. Most of the rootlets have been lost from the older parts.

PHOTO. 69.—*P. canadensis*. One of the tip clusters from the root shown in Photo. 68—about natural size.

PHOTO. 70.—*P. canadensis*. Roots, natural size. Splitting has occurred between the two parallel branches.