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The Histology of the Cell Wall with Special Reference to the Mode of Connection of Cells. Part I. The Distribution and Character of "Connecting Threads" in the Tissues of Pinus sylvestris and Other Allied Species

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II. *The Histology of the Cell Wall with Special Reference to the Mode of Connection of Cells.*

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Part I.

The Distribution and Character of "Connecting Threads" in the Tissues of Pinus sylvestris *and other allied Species.*

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[Plates 31–35.]

Introductory Note to Part I., by W. Gardiner.

When in 1897 I communicated to the Royal Society a preliminary paper "On the Histology of the Cell Wall with Special Reference to the Mode of Connection of Cells," I hoped that no long period would elapse before the publication of a more detailed account, dealing with "connecting threads" generally.

The pressure of official duties, and to some extent, also, the difficulties of the research, have so militated against my schemes that the full paper still remains unwritten.

In October, 1898, Mr. A. W. Hill, of King's College, commenced to assist me in the research, and has since that time worked in my laboratory as my colleague. Besides our investigations in common, on the whole subject of connecting threads, Mr. Hill on his own account made a special study of the histology of the vegetative tissues of *Pinus sylvestris* and *pinea*, with a view of following the precise mode of communication of the various cells and tissues throughout the body of the plant.

I had arranged that the full paper should be published in three parts as follows, viz., first the part dealing with methods, written by myself; then an account of the occurrence and distribution of "connecting threads" in *Pinus sylvestris* and its congeners, by Mr. Hill; and, lastly, the general results of the research written by us conjointly. While unpropitious circumstances have frustrated my plans and hindered the appear-

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ance of the first and last, the second is now practically completed, and appears in the present communication as Part I.

The tissue of the Coniferæ, which has so often been the subject of important anatomical and physiological research, happens to form particularly favourable material for the investigation of the minute histology of "Connecting threads"; and the study of the distribution and character of these threads is materially assisted by the unusually complete knowledge, already accumulated, of the structure and function of the several elements of which the various tissues are composed.

In the following paper it is proposed to investigate the more important histological features presented by connecting threads in the tissues of representatives of the genus *Pinus*, and, for the most part, the two species *Pinus pinea* and *Pinus sylvestris* have supplied the material for the research.

For the examination of the threads in germinating seedlings and young plants, *Pinus pinea* has been used, while in *Pinus sylvestris* the stem, roots, and leaves of the mature plant have been submitted to detailed examination.

The Methods.—For the methods employed in the research, a reference to the papers already published by GARDINER must for the present suffice, since the fuller account of the technique is still in process of being written; but the papers already published sufficiently set forth the main principles upon which the later methods, still to appear, are in all essentials based.*

I. CONNECTING THREADS IN *Pinus pinea.*

The Structure of Germinating Seeds and Young Plants in Pinus pinea.

Owing to the absence of any good account of the structure of the embryonic tissues, the earlier part of the paper will be somewhat lengthened by anatomical details, which are, however, of an interesting character. The endosperm will be dealt with first, and will be followed by a description of the cotyledons, hypocotyl, and root.

The Endosperm and the Germinating Seedling.

A. *The Endosperm.*

The relations of the embryo and endosperm are already sufficiently well known to render any detailed account superfluous. A transverse section of the sheath-like wall of the endosperm, which surrounds and protects the young embryo, shows the following structure: The internal tissue is bounded by a single well-defined layer

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* GARDINER, 'Roy. Soc. Proc.,' vol. 62, 1897 'Camb. Phil. Soc. Proc.,' vol. 9, Pt. VIII.

of cells which have their external or free walls thick and pitted, and within this is the ordinary endosperm tissue; which in the immediate neighbourhood of the embryo is broken down, and represented by a layer of much compressed, disorganised cells, whose contents have been absorbed by the developing embryo.

On treating a section with iodine, the cell walls turn blue,* whilst the contents, consisting of aleurone grains and oil, assume an orange tint, due mainly to the deep staining of the crystalloids of the aleurone grains.

The general tissue of the endosperm appears at first sight to be composed of fairly large cells, more or less rounded in outline, with intercellular spaces at the corners; but on shaking out the contents, these cells are seen to be divided up into two, four, or more daughter-cells, which have been formed by internal divisions subsequent to the formation of the mother-cell.

After staining a section of tissue (from the cells of which the contents have been removed by shaking), the difference between the young and old walls is very noticeable, owing to the difference in the distribution of the connecting threads; for in the young, thin walls the threads are for the most part scattered all over the surface (though sometimes showing a slight tendency to grouping), whilst in the old walls they appear in surface view as well-defined groups of darkly-stained dots situated in shallow pits; each pit having the threads arranged in little circles of five and six, or in small squares or triangles. (Fig. 1, Plate 31.)

This arrangement of threads in pits, which is characteristic of all the old walls, is brought about by the peculiar growth of the cell wall during development, by means of which groups of threads remain collected together, owing to the comparatively little surface growth in the places where the thread groups occur, while considerable extension takes place in the portions of the wall between them, accompanied also by considerable growth in thickness of these portions.

Towards the cotyledons, the endosperm cells are smaller and do not show internal division; the threads also are thicker and show traces (when the seed is germinating) of ferment action.

In the outermost bounding layer the external or free wall, although provided with numerous pits, shows no threads leading through the wall to the exterior.

The importance of connecting threads in endosperm has already been remarked by all the numerous observers who have worked on this tissue, from TANGL† downwards.‡ Not only do the ferments from the cotyledons pass into the endosperm by the threads, but it is by these paths that the dissolved food material travels to the developing embryo.

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* This is somewhat exceptional. For other instances see GARDINER, "On the Constitution of the Cell Wall and Middle Lamella," 'Camb. Phil. Soc. Proc.,' vol. 5, Pt. II.

† "Ueber offene Communication zwischen Zellen des Endosperms," 'Prings. Jahrb.,' vol. 12, 1880.

‡ The literature of the subject will be given in Part II. A list of papers to 1891 is given in KEINITZ GERLOFF'S paper, 'Bot. Zeit.,' 1891.

B. *The Seedling.*

(1.) *The Cotyledons.*—The cotyledons,* some eight to twelve in number, form a ring around the apex of the young stem, and are enclosed within the endosperm, in which the tips remain embedded until the greater part of the reserve materials have been absorbed. If the tips by accident grow through the endosperm during germination, the seedling stops growing, so that it appears evident that the apices of the cotyledons function as the absorbent organs, and an examination of longitudinal and transverse sections also affords proof that this is the case.

Transverse sections were taken near to the tip† of a cotyledon belonging to a seedling whose radicle was about four inches long. The outline of the section forms roughly an isosceles triangle, with the side next the endosperm (that is, the lower side of the leaf) forming the base. (Fig. 2, Plate 31.)

The cotyledon is bounded by a well marked slightly cuticularised epidermis with stomata on the two slopes, which represent the upper side of the leaf. There are no stomata on the basal side, where also the epidermal cells differ from those situated at the sides of the leaf, in being much shorter and possessing thick and more mucilaginous walls.

Below the epidermis on the lower side of the leaf come two or three layers of short hypodermal cells, while on the upper sides only one or two rows are usually present. The stomata, where present, are sunk below the surface of the leaf and interrupt the hypodermis. The guard cells show signs of cuticularisation on their free walls, and the side walls dividing them from the neighbouring epidermal cells are markedly thick and well developed, except where a small pit occurs at the base of this wall. (Fig. 3, Plate 31.)

The resin canals, which are situated among the hypodermal cells just below the epidermis, vary in number from two to five in the young cotyledon. Two canals are always present adjoining the epidermis of the lower side of the leaf, and their early formation and their close proximity to the endosperm suggest that they play an important *rôle* in the tissue during development.‡ At the apex of the cotyledon one median or two lateral canals are present, and in some cases all three occur. In very young specimens, although the apical canals are not yet developed, the two at the base are found to be already fully formed.

The Palisade Tissue.—The hypodermal cells are succeeded by a broad band of

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* *Cf.* figures in SACHS' 'Vorlesungen' (of Pinus seedlings).

† DAGUILLON, "Recherches morphologiques sur les feuilles des conifères," 'Rev. Gén. de Bot.,' vol. 2, 1890, pp. 272–276, gives a brief anatomical description of the cotyledons and primary and adult leaves of *Pinus pinea*.

‡ In the very young root the positions of the young xylem bundles are just indicated by resin canals alternating with the primary phloem, a further suggestion of their importance.

palisade tissue, consisting of shallow cells with rounded outlines provided with intercellular spaces, occurring at the corners where the cells meet.

A median radial section shows about four rows of these cells between the hypodermal tissue and the endodermis on the lower side (which corresponds to the under side of the leaf); while on the upper side of the leaf the cells are more numerous, and the palisade tissue is deeper.

Within the well-marked endodermis lies the single collateral vascular bundle, and between this layer and the bundle a few rows of short parenchyma cells occur, which represent the pericycle, and are most numerous around the spiral elements of the xylem. In the mature cotyledon the majority of these cells become lignified to form the characteristic transfusion tissue, but some remain unlignified and serve to unite the phloem with the cortical tissues, so that the stelar area is seen to be very similar to that of the mature leaf.

The phloem, which forms the greater part of the bundle, is very conspicuous. Reference to the photograph (fig. 2, Plate 31) shows that it is composed of two portions, an inner part consisting of regularly arranged rows of cells formed by cambium, and an outer horse-shoe shaped group of primary phloem, which is separated from the pericycle by the well-marked sheath.*

The xylem appears in section as a small triangular patch composed of spiral vessels, some of which show developing bordered pits. In older cotyledons the xylem is considerably increased by the cambium, and becomes much more important in consequence of its relation to the transfusion tissue.

Before considering the distribution and character of the "connecting threads" in the tissues of the cotyledon and seedling, it will be well to make certain preliminary remarks concerning the mode of occurrence of these structures in cells generally.

In most parenchymatous cells, owing largely to differences in the growth of the walls, there is a different arrangement of the threads in the end and the side walls. The end walls when examined in surface view are usually seen to be closely covered with fine threads, which appear as dots, and which may either be uniformly distributed or may exhibit a tendency to be aggregated in small groups. On the side walls, on the other hand, threads are almost always found in large groups separated by intervals of clear membrane, an arrangement depending on the great growth in length of the cell, and the groups usually occur in pits, whose size varies in the different cells and tissues of the plant. In large pits the threads are usually seen to be broken up into several smaller or secondary groups.

The length of the threads is naturally equal to the breadth of the membrane which they traverse, and in the young walls of the *Pinus pinea* seedlings since the pit-closing membranes measure from 1 μ to 2 μ across, this also represents the measurements of the threads. The threads are seen to be very fine, and may or may not show a dot or swelling at the point where they cross the middle lamella.

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* Similar arcs of primary phloem can be seen in transverse sections of very young roots.

In order to obtain an approximate idea of the actual size of the threads, the pit-closing membranes of both fresh and stained sections of parenchymatous cells of *Pinus sylvestris* (three-year-old stem) were measured, and also the number of stained threads corresponding to one micrometer division was noted. From the data so obtained, after allowing for the increase by artificial swelling, the dimensions of the individual threads appear to be in length about 1·8 μ and 0·3 μ, the size of the threads especially as regards length, increasing with the age of the cell.

To return now to the cotyledon, we may deal first with the *epidermis.*

The marked difference previously noticed between the cells of the lower and upper epidermis of the cotyledon is further emphasised by the distribution of the connecting threads.

All the epidermal cells show their end walls covered with threads usually distributed uniformly, but sometimes also aggregated into small groups, and in the radial walls threads occur in groups which unite the several cells of the layer together. In the case of the epidermis of the lower side of the leaf the threads are everywhere much more numerous and more conspicuous, and the pits themselves are larger and contain more threads, which threads appear thicker and more darkly stained than those of the epidermal cells situated on the sloping sides, corresponding to the upper side of the cotyledonary leaf. (See figs. 3, 4, 5, Plate 31.)

In a longitudinal radial section, the two sides of the leaf can immediately be distinguished by the number of the groups of threads, apart from the differences in the size of the cells; and the epidermal cells of the lower side have every appearance of being the absorbent layer, into which the reserve materials of the endosperm are taken, by diffusion through the outer wall, and then passed on into the inner tissues of the leaf by means of the innumerable connecting threads between the epidermal and hypodermal cells. (Fig. 3, Plate 31.)

The swollen character of the cell-walls as well as the thicker and more darkly staining threads of the lower side are probably due to the influence of ferments, which must be constantly passing from the cotyledon to the endosperm.

No threads occur in the free or external walls of the epidermis,[*] and this one would be prepared to expect, in view of our knowledge of their origin from the persistent nodes of achromatin fibres,[†] seeing that the epidermis is the outermost layer of the embryo.

The outer cells of the resin canals are also directly connected with the epidermal and hypodermal cells by numerous thread groups (fig. 5, Plate 31); groups of threads are also specially numerous on the tangential walls of the several concentric layers of cells which immediately surround the resin duct, and thus form paths from the hypodermal and epidermal cells to the cavity of the canal.

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[*] In this connection *cf.* W. GARDINER, 'Roy. Soc. Proc.,' 1897, vol. 62, fig. 6, where threads are represented as going to the cuticle.

[†] W. GARDINER, 'Roy. Soc. Proc.' 1900.

The character of the resin canal threads will be dealt with in greater detail when considering the hypocotyl.

The guard cells of the stomata* are quite the most difficult cells to investigate. Only a few threads pierce the pit-closing membrane, and numbers of sections may be examined before the one spot, where threads occur, is found. Eight or nine clear cases have been seen showing about four very short threads in section in a deep pit connecting the guard cell with the neighbouring epidermal cell, the pit being situated just at the base of the epidermal cell. (Fig. 6, Plate 31.)

The longevity of the guard cells in tissues after their severance from the plant, and the difficulty of removing starch from them,† would possibly lead one to expect that the connection between them and surrounding cells would be very slight, and actual observation most certainly seems to show that this is the case. The cells beneath the epidermis exhibit the usual thread arrangement of ordinary parenchyma already described, the end walls showing scattered threads, whilst on the side walls they occur in the slight pits which are elongated in the horizontal direction, (figs. 3 and 4, Plate 31). The pit threads of the side walls generally appear thicker and more deeply stained than those in the end walls, and are usually shorter. Further, they are also, as has already been noticed, more numerous on the lower than on the upper side of the cotyledon, and evidently indicate the path of nutritive materials to the phloem. This is especially noticeable in a radial longitudinal section. (Fig. 3, Plate 31.)

The palisade tissue in these young cotyledons appears to be a storing-place for the reserve materials brought over from the endosperm, and their cells are well connected by threads (also in pits) with those of the outer tissues of the leaf. Connections with one another by means of large pits with numerous short threads occur in plenty in the radial and tangential direction; the former being very noticeable in longitudinal sections. (Fig. 3, Plate 31.)

The history of the threads in relation to the separation from one another of the cells of the palisade parenchyma is of some interest. It is of course well known that in the adult leaf tissue—and the same is true of the tissue of the cotyledon—the parenchyma separates into plates of tissue which, seen in longitudinal section, appear as a series of separate rows of cells standing at right angles to the vascular bundle, and that in young tissue these plates are closely opposed, forming a solid tissue mass.

Preparations made with a view of demonstrating the threads show that in the early stages, when the walls, which will ultimately separate, are still intact, they are freely traversed by numerous groups of threads. But as the tissue separates into plates, involving the cleavage of the walls along the region of the middle

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* Kohl, 'Bot. Centralbl.,' vol. 72, No. 8, figures threads to the guard cells in *Viscum*. *Cf.* Kuhla, Bot. Zeitg.,' March, 1900.

† Leitgeb, "Beiträge zur Physiologie der Spalt-Öffnungs-Apparate," 'Mittheilungen Bot. Inst. zu Graz,' Heft 1, 1886.

lamella, the splitting which first begins at the places where several cells meet gradually extends until, at length, the palisade tissue becomes separated into isolated plates of cells connected together tangentially and radially but having no communication in the vertical direction. (Figs. 3 and 7, Plate 31; *cf.* also fig. 34, Plate 35.) In the young cotyledon to which the figure refers this separation is taking place, and in some cases the short half-threads can be actually seen in the two separated portions of the formerly united wall.

With sections of slightly older cotyledons, the two half-walls appear quite homogeneous, and show no trace of threads having been present; so that it seems probable either that the protoplasm is able to fill up the canals occupied by the threads, and thus render the wall imperforate, or that the same end may be attained by local mucilaginous change in the cell membrane.

A similar case to that presented by the palisade cells occurs with the epithelial cells of the resin canals, where the cavity of the canal has arisen schizogenously, and the outer thin walls of the cells are really only half-walls.* In accordance with this mode of origin, we should expect to see short half-threads connecting these epithelial cells with the cavity of the canal, but in no case has a satisfactory observation of such threads been made. The walls are very thin, and appear mucilaginous in character, and are moreover usually covered by minute granules. Small canals may be present as in other cell walls, but these may either not be occupied by permanent strands of protoplasm, or the wall may have become mucilaginous and the canals filled up, so that the secretion formed in the epithelial cells has to pass into the canal through a practically imperforate membrane, instead of being poured in through fine pores.

The Endodermis.—This layer, to which the innermost palisade cells are joined, shows a vast number of groups of threads in shallow pits, and since it is the layer with which all the palisade cells communicate, it serves as the passageway not only from the cortex to the stele, but also from the palisade cells above to those below: a means of communication otherwise impossible, seeing that in the adult condition the tissue consists of a series of isolated plates as already described. Besides these connections in the radial and vertical directions, there is also an adequate connection tangentially between the various endodermal cells by means of the numerous threads traversing the radial walls. The distribution of the threads in this layer is thus of very great interest, and increases our knowledge of its physiological importance.†

The Pericycle.—The short parenchymatous cells of the pericycle, occurring between the endodermis and the phloem, are very similar to those of the former tissue, both in the distribution and character of their connecting threads.

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* STRASBURGER, 'Practicum,' Eng. ed., p. 123. Also SACHS'S 'Text-Book of Bot.,' 2nd ed., p. 94, fig. 78, an excellent figure of developing resin canals.

† Compare the structure of the endodermis of the older hypocotyl, p. 102, and of the mature leaf, p. 118.

The thread groups, which are usually oval or elliptical in shape, are arranged with their long axes at right angles to the length of the cell. In some cases the groups are almost circular in form, or they may be drawn out into a narrow elliptical figure; or the large groups may be broken up into smaller aggregates; but all are enclosed in a large general pit, and thus exhibit features which are commonly found in all parenchymatous cells (fig. 13, Plate 32, which, however, is a section of the hypocotyl).

On the phloem side of the vascular bundle the pericyclic cells described above are usually three or four cells deep, whilst on the xylem side they occupy a much larger area, for all the cells between the endodermis and xylem are apparently pericyclic.

The character of the thread areas gradually changes from fairly large groups in the cells near the endodermis to smaller elliptical areas in those around the wood vessels. The innermost layer of the pericycle shows numerous small thread-groups connecting this tissue to the sheath cells of the phloem.

The end walls of the pericyclic cells, which are provided with the usual arrangement of scattered threads, are often seen to be oblique, and this is probably due to the unequal growth in length of the side walls of these cells, owing to their proximity to the greatly elongated phloem elements.

The Phloem.—The structure of the phloem and its relation to the rest of the tissue may now be considered.

The phloem is separated from the pericycle by a well-marked sheath, and a longitudinal section shows that the sheath cells belong to the phloem, since they are long elements with horizontal end walls, and are thus easily distinguished from the short pericyclic cells. Within the sheath is situated the primary phloem and still more internally the secondary phloem; the cells becoming smaller and thicker-walled, and finally merging into the meristemmatic tissue situated between the phloem and xylem.

In transverse section the inner or secondary phloem, which is bounded internally by the cambium, is somewhat oblong in shape, and is seen to be composed of a number (eight to nine) of radial rows of sieve tubes, and accompanying the sieve tubes medullary rays. At either flank is situated a group of albuminous cells. The primary phloem, which is composed of a number of large irregular cells, and occurs outside the inner phloem, is bounded externally by a well-marked horseshoe-shaped limiting layer; the ends of which impinge on to the two groups of albuminous cells already mentioned.

With reference to this arrangement, a point of some interest should be mentioned here, namely, that the limiting layer, supplemented by the two albuminous groups, forms a definite cordon of cells intercalated between the phloem and the pericycle, so that any connection between these two tissues must take place through the cells of the composite investing layer.

It will be seen later on that, as a matter of fact, it is the albuminous cells which are of especial importance in forming the connecting link between the pericycle and phloem.

The arrangement of the connecting threads in the phloem sheath of the cotyledon is particularly interesting. The cells of the sheath are much smaller than those of the primary phloem, and in transverse section resemble parenchyma cells, but in longitudinal section they are long and somewhat like sieve tubes.

Their end walls are fairly thick, and are pierced by numerous threads with a dot or swelling at the point where they cross the middle lamella, and small thread groups are scattered on the walls adjoining the pericycle and the phloem, thus affording a means of communication in either direction. The most numerous, however, are those occurring on the walls connecting the cells of the sheath with one another, and they are especially noticeable between the cells which are situated at the sides of the primary phloem, and lead up to the albuminous groups. (Fig. 8, Plate 32.)

This appears to point to a concentration at one place of the material received from the palisade cells, namely, the region of the young albuminous cells on either side of the inner phloem, and the reason for this arrangement and concentration of the threads in this way is further elucidated in the older cotyledon.

In the very young cotyledon, entrance to the phloem is possible through any of the sheath cells, and no doubt reserve material in solution is poured in from all sides; but in the older stages, owing to the lignification of several of the pericyclic cells at the sides of the phloem, to form the "transfusion" tissue, there are only a few possible paths left open by which the plastic food materials elaborated in the palisade cells can reach the phloem tissue, namely, either at the top of the phloem, or else along the lateral cells of the sheath, and so to the albuminous cells flanking the sieve tubes; or a shorter path still is from the endodermis to the sieve tubes through the pericycle and abuminous cells. (Fig. 8, Plate 32; *cf.* also fig. 36, Plate 35.)

A cotyledon from a plant whose plumule is well developed and bears several leaves shows the primary phloem cells disorganised and useless; having been supplanted by a vigorous growth of radially arranged sieve tubes which communicate with the outside tissue solely by the albuminous cells.* (Fig. 8, Plate 32.)

The Primary Phloem.—With regard to the tissues of the primary phloem, the following points deserve mention: The somewhat large cells of the primary phloem appear rectangular or hexagonal in shape, as seen in transverse section. (Fig. 2, Plate 31.)

The thread areas on the side walls are exceedingly numerous. They are usually oval in shape and are placed with their long axes either at right angles to or parallel with the long axis of the cells; in some cases also they are circular. In the greater number of groups, the threads usually separate into several irregular secondary aggregates; the particular arrangement being dependent on the amount of growth that has taken place in the cell.† In section the connecting threads are seen stretching right across the wall, and are longer than those found connecting parenchymatous cells, but pits can scarcely be said to be present.

* *Cf.* with the adult leaf, p. 118.

† *Cf.* p. 87.

The threads are very fine and packed closely together, and usually show granules adhering to their free surfaces,* and the median dot is always visible.

The tissue being of a mucilaginous nature swells readily, and under these circumstances the threads are easily broken up into rows of granules.

The end walls, at first horizontal, become oblique owing to the unequal growth in length of the cell (fig. 9, Plate 32), and the older the tissues, the more oblique the wall is found to become, so that in the hypocotyl, to be described later, the end walls have been dragged out to such a length that they appear almost parallel to the side walls (*vide* p. 99).

The end walls are richly provided with threads, which in longitudinal section usually present a somewhat confused appearance of threads and dots overlying one another and intermingling, owing to the fact that the walls slope and undulate in such a manner that a preparation which shows a portion of the threads in accurate longitudinal section cuts the remainder obliquely. (Fig. 9, Plate 32.)

The Secondary Phloem.—The structure of the secondary phloem may now be described. Radial rows of sieve tubes, together with a few medullary-ray cells, compose this tissue.

The thicker walled cells appear in transverse section, similar to adult sieve tubes, and agree with them also in possessing numerous threads on the radial walls. Only a few small sieve plates or groups of threads occur on the tangential walls, so that the radial communication which is possible in the outer primary zone, does not take place here to any extent (fig. 9, Plate 32), but in longitudinal section the phloem elements of the young cotyledon differ from the sieve tubes of *Pinus sylvestris* in possessing distinct and thick horizontal end walls, which latter are pierced by long and numerous connecting threads. These threads are beautifully curved; they are thickened in the middle and taper towards the two free ends, and the median thickening is probably similar to the granule always present in sieve tube threads, although here it forms a much more conspicuous feature. (Fig. 9, Plate 32.)

The cells at the junction of primary and secondary phloem apparently show no thread groups on the tangential walls which connect them with the primary phloem, and the advantage of this isolation is obvious as the cotyledon increases in age, since by this arrangement the active secondary tissues are completely cut off from the compressed and disorganised elements then no longer functional.

The similarity of the square-ended sieve tubes of the inner phloem of the cotyledon to those characteristic of dicotyledons is very striking, and if any conclusions can be drawn from histological details, or from embryonic tissues, respecting the affinities or ancestry of a group of plants, the appearance of these sieve tubes, with their thick horizontal end walls pierced like sieve plates, suggests that some relationship may possibly exist between the Coniferæ and the Dicotyledons.

Returning to the structure of the inner phloem, a tangential section across this

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* *Cf.* p. 98.

tissue shows that the sieve elements, which occupy the central portion, consist of fairly long tubes, and that the albuminous cells at the two sides are distinctly shorter and are always full of contents. These cells which, as we have already mentioned, form the passage cells from the mesophyll to the sieve tubes, *vià* the localised cells of the pericycle, possess curious fan-like groups of threads on their radial walls.

In this respect they resemble the threads between adjoining sieve tubes, which are also usually arranged in a fan-like manner, and this structure seems indeed to be also characteristic of many of the lateral sieve plates (*cf.* the lateral sieve plates of *Phaseolus*, *Cucurbita*, &c.).

The position of these fan-like thread groups may be readily recognised in normal tissue not yet subjected to swelling and staining, since both the radial and tangential walls are seen to be covered with spherical knob-like thickenings, and it is these thickenings which are traversed by the threads. (Fig. 38, Plate 35.)

The arrangement of the several threads upon which the assumption of the fan-like figure depends, is both interesting and peculiar, for instead of the threads being convexly curved outwards, so that the whole group would form a barrel-figure (figs. 22 and 23, Plate 33)—which is the usual condition of things—they are curved concavely, so that the group is narrowest at the middle and broadest at the ends. The more centrally placed threads are also the longest, in consequence of the rounded contour of the nodular swellings. (Fig. 8, Plate 32; *cf.* also fig. 36, Plate 35.)

Any individual group of connecting threads may not inaptly be compared to a wheatsheaf, whose separate pieces of straw have been pulled out at each end to form a rounded top and bottom to the whole sheaf.

In some of the smaller groups the arrangement of the threads on either side of the middle lamella differs; for on one side they may be fanned out, whilst on the other side they remain straight, thus resembling a fan with a handle, and frequently also the wall is thicker on one side of the middle lamella than on the other, causing a similar difference in the length of the two portions. Each thread shows a well-marked dot at the region of the middle lamella.

Owing to the occurrence of these unsymmetrical thread groups on the variously inclined lateral walls their definite orientation is not easily seen, but the greater number appear to be so arranged that the firmer or denser half of the wall, with the threads more closely packed, is directed towards the pericycle, and the more swollen half with the threads more loosely arranged and more markedly fan-like away from it* (fig. 8, Plate 32). Where, in consequence of unequal thickening of the two halves of a composite wall, the middle lamella is nearer one side than the other, the sheaves of threads which form the thread groups are also necessarily composed of two portions of unequal length, and in such cases the collection of shorter pieces

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* *Cf.* with mature leaves where the orientation is quite definite, with the denser half outwards.

appears to consist of threads which are finer and more numerous than the longer ones which traverse the thicker portion of the membrane. The portion of the wall traversed by the shorter threads stains faintly, while the wall through which the longer segments of the threads go remains uncoloured, and is bright and highly refractive, so that the difference between the two sides is the more emphasised. This portion indeed appears somewhat of the nature of a callus, though observations show that it does not answer to the usual callus reactions.* The longer threads generally appear to be broken up into strings of darkly-staining granules, owing doubtless to the character of the membrane which, being mucilaginous, is easily swollen.

In some transverse sections of the inner phloem a young medullary ray may occur, the cells of which may be distinguished by the fact that radial threads are present piercing the tangential wall. The young medullary-ray cells appear at first to consist almost entirely of companion or albuminous cells; but in the older cotyledons starch-containing medullary-ray cells are also present.

The cambial zone between the phloem and xylem is composed of thin-walled rectangular cells in whose walls threads have not yet been very successfully demonstrated, though they are without doubt present.† Russow states that he has seen threads with ease in cambium,‡ but this statement needs further confirmation.

The Xylem.—The xylem is the less conspicuous portion of the bundle, and consists of few vessels arranged in a broadened V-shaped mass (fig. 2, Plate 31). The existence of connecting threads in the wood vessels and cells is difficult to demonstrate, and remains as yet an unsolved problem, one of the difficulties being that most protoplasmic stains also colour the lignified tissues.

As far as one can see, it is possible that threads are present when the vessel is young, and that they then become obliterated either by being covered over by the layers added to the cell wall, or that they suffer mucilaginous or other change, and so disappear.

Regular groups of dots observed in the middle of the wall between two young vessels seen in a tangential section lend some support to this view, which will be referred to again when other questions of lignification are discussed (see description of the xylem of the hypocotyl, p. 100).

Structural Changes in the Mature Cotyledon.—In order to study the alterations that occur in the distribution and character of the threads as the cotyledons grow older, material was obtained from seedlings whose plumule was about 2 inches long and well supplied with young foliage leaves.

Transverse sections show that the internal tissues have become stronger, and that a good deal of lignification has occurred within the endodermis. So far as the epidermis and hypoderm are concerned, there is little change as regards the distribution

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* *Cf.* mature leaves, p. 118, and results obtained by special staining.

† *Cf.* W. Gardiner, 'Roy. Soc. Proc.,' 1900.

‡ Russow, 'Sitzber. d. Nat. Ges. Dorpat,' 1883, pp. 573 and 574.

of the threads, except that there is not that marked difference which we had previously observed between the lower and upper sides of the cotyledon. This is largely due to the growth in length which the cotyledon has undergone, which causes the wall to become thinner and the thread groups to be separated. It is also possible that in the process of thickening of the hypodermal cells, and during the formation of the intercellular spaces, some thread areas may have been obliterated.

In the palisade tissue the principal change is the separation of the cells from one another to form the plates of tissue already mentioned,* and the ease with which the walls concerned in the separation part from one another, notwithstanding the fact that they are well connected by threads, is certainly most striking. The obliteration of the threads which follows this separation takes place very quickly, and there appears to be no communication between the intercellular spaces and the cell content, but whether the pores in the walls persist, or whether they become filled by mucilage or cellulose, cannot be observed, since the threads at this stage no longer stain. The free surfaces of the halved walls are, however, covered by a thin, darkly staining cuticularized layer, which clothes and protects the newly exposed membrane (fig. 7, Plate 31).

The tissues of the pericycle undergo a good deal ot modification ; a large number of cells becoming lignified, leaving those with unaltered cellulose walls irregularly scattered amongst them, and it was observed that the changes associated with lignification take place with great rapidity. In sections taken from that portion of the cotyledon just emerged from the endosperm, the pericyclic cells show traces of incipient lignification ; doubtless connected with the function of these cells in relation with the quick passage of water to the leaf mesophyll.

Where two transfusion cells adjoin, they communicate with each other by means of bordered pits, but where such a cell abuts on a living pericyclic cell with cellulose walls, a thin lignified layer is developed which extends over the cellulose membrane (fig. 11, Plate 32). When this layer has only just been formed, connecting threads can still be seen in the cellulose portion of the walls extending as far as the lignified layer upon which they impinge, and which apparently blocks their free ends, cutting them off from any direct communication with the dead transfusion cell.

Examination of slightly older stages shows only faint traces of threads in the wall (fig. 11, Plate 32), and the lignified layer becomes the more conspicuous as the age of the leaf increases (*cf.* the adult leaf of *Pinus sylvestris*, fig. 36, Plate 35).

(2.) *The Hypocotyl.*—For the examination of the connecting threads in this region, seedlings of various ages were examined. The seeds were sown on the 12th of November, and from the crop of young plants thus produced material was preserved on the 6th and 12th of December, and the 28th of the following January. In the oldest plants, which were, therefore, about two and a-half months old, most of

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* *Cf.* pp. 89 and 90. These changes are seen commencing in longitudinal sections of the cotyledons which have just emerged from the endosperm.

the root had become woody, and the plumule showed a few young leaves; while plants about one month old had their cotyledons just free from the endosperm, and their roots still soft and white.

In these younger seedlings sections of the hypocotyl show that near the apex the bundles are arranged collaterally, but that, at a slightly lower level, a separation of the xylem and phloem commences, and still lower down the bundles present a radial structure, which then persists, and which, indeed, is characteristic of the greater portion of the hypocotyl.

In the oldest seedlings, sections of the hypocotyl show a collateral structure, but this is of secondary origin, and similar in development to that which arises in a thickening root.

Returning to the young seedling, the structure of which may be followed in further detail, a transverse section of the lower portion of the hypocotyl shows the following arrangement of the tissues (fig. 12, Plate 32):—

The epidermis, protected by a thick cuticle, is interrupted at intervals by stomata sunk in depressions, and below it come two or three layers of hypodermal cells, which are smaller and more closely packed than the main mass of the more internal cortical cells, and possess but few intercellular spaces. The middle lamella is very prominent, and darkly staining, especially at the angles formed where several cells join, and where the walls tend to thicken and become slightly collenchymatous.

The resin canals occur just below the epidermis, and are the continuation of the canals seen at the lower sides of the cotyledons.

The cortex, which is about fifteen to eighteen cells deep, is composed of fairly large celled tissue provided with intercellular spaces.

The limits of the cortex are indicated by the endodermis, which may be readily recognised even in thin sections, since the cell-contents are usually retained (fig. 12, Plate 32). Inside this layer, cells which are smaller, thin-walled, and angular, and with few intercellular spaces, form a band of tissue of varying thickness and indefinite outline representing the pericycle,* within which come the radial bundles and a well-developed pith.

The phloem bundles of the hypocotyl are interesting, since they are similar in structure to the phloems of the cotyledonary bundle, and a like type is also found in the very young root, so that the same type of phloem prevails throughout the whole embryo.

The phloem, as seen in transverse section, consists (as in the cotyledonary leaf) of two parts, namely, an outer portion composed of large, radially elongated cells forming an arc, which externally merges insensibly into the pericycle;† and of an inner portion, consisting of a narrow band of thick-walled, fairly rectangular cells.

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* Bower, 'Practical Botany,' p. 248, "The Pericycle."

† The distinction between the pericycle and phloem can only definitely be seen in longitudinal section.

On the pith side of this inner portion cambial activity is seen to be commencing, associated with tangential divisions in the adjoining pith cells, so that a regular band of meristemmatic tissue is formed on the inner side of the phloem, and ultimately passes above the xylem groups to form a complete ring. The much smaller primary xylem groups alternating with the phloem show a resin duct on their outer sides. The pith cells around the bundles are small and thin-walled, but in the centre are similar to the cortical cells.

The distribution of the connecting threads is, in general, similar to that found in the cotyledon. In the epidermis, threads are not easily met with in transverse section owing to their relatively sparse distribution. End walls in surface view are also rare.

In actual structure the groups on the side walls show that the closing membrane of the small pits is traversed by a group of eight to ten short threads, often broken up into groups of four or five threads each. The end walls, on the other hand, show their characteristic arrangement of scattered threads, which, however, in this epidermis are not numerous.

The cortical cells are shorter than those of the epidermis; and their end walls present a most beautiful appearance, being full of fine curved threads, which pass without a break through the double wall. (Fig. 13, Plate 32.)

The side walls in surface view (as seen in longitudinal section) show large and small oval or spindle-shaped shallow pits, each with its long axis at right angles to the long axis of the cell. When stained, these areas are seen to be covered by dark dots, which, when quite small and round, are the ends of the connecting threads themselves, but more frequently they are darkly stained granules which cover them. These granules render the pits very conspicuous in surface view, but also give a false picture of the size of threads.

Transverse sections show threads equally numerous in the radial or tangential direction, and very large numbers of fine threads traverse the closing membrane of any single pit, in which they are usually distributed in three or four separate groups. So numerous are the threads, that a general coloration is given to the pit-closing membrane, and it is difficult to distinguish them as separate fine lines if the sections have been deeply stained (*e.g.*, by the acid violet method).

Each thread uniting the cortical cells shows usually a very small dot or swelling at the middle lamella, and these dots, which are also seen as more conspicuous objects on the sieve tube threads, appear to be the persistent nodes of the achromatin fibres, which are continued as threads during the formation of the cell wall after nuclear division.*† The end walls are covered by a vast number of points representing the ends of threads.

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* W. GARDINER, 'Roy. Soc. Proc.,' 1900.

† When the cell walls are over-swollen, separation takes place along the middle lamella, and the threads rupture at the position of these dots.

The *endodermis*, which shows only a few threads, and appears also to be slightly lignified, will be considered more fully where the older sections are described, when it will be found to have undergone some interesting changes. In the young material it is difficult to be always certain which cells belong to this layer.

The tissues of the *pericycle* are like those of cortical or other parenchymatous cells as regards the distribution of the connecting threads. The cells, however, are smaller and the threads shorter.

When the *phloem* is reached (especially if a radial section is examined) a marked change is noticed, for the cells are very long, and the thread areas which are large and darkly stained are placed parallel to the long walls of these elements and therefore at right angles to the direction of the thread groups of parenchyma cells. (Fig. 13, Plate 32.)

Often in these sections surface views are seen of walls covered with innumerable groups of threads irregularly distributed, the greater part of which are always out of focus, showing that the wall is not all in the same plane. Further examination shows that these walls are the oblique end walls of the primary phloem, and that they resemble the similar tissues already described in the cotyledon. (See fig. 9 and fig. 10, Plate 32, which latter is a longitudinal section of a root.)

In certain instances the end wall is so oblique, owing to the growth in length of the cells, that in places they actually run almost parallel to the side walls. Except that they are more numerous, the threads traversing these walls resemble in structure and appearance those described in similar tissue of the cotyledon, but as the phloem of the hypocotyl is much larger in quantity, many more of these curious and striking "end walls" are seen in transverse section.

Connecting threads are also seen in large and small groups on the radial and tangential walls, and all the threads show the median dot.

That portion of the phloem (viz., the inner phloem) which forms a band three or four cells deep on the inner side of the above mentioned primary group consists of thick-walled and easily-swollen elements, which present the appearance of ordinary sieve tubes in transverse section, and possess groups of threads on the radial walls only. The end walls of these elements when examined in surface view are seen to be covered by numerous fine threads.

As well in longitudinal as in radial section the young sieve tubes appear to be similar to those already described for the cotyledon. The sieve plates on the radial walls show a large number of very fine threads arranged in a slightly fan-like manner, and similar threads in smaller and fewer groups unite the outer and inner portion of the phloem.

In the tangential walls near the dividing pith cells several threads may be seen scattered at intervals throughout the membranes, which are here unpitted. Some of the walls which have recently been formed by tangential divisions show fine scattered threads, and these walls may be either the tangential walls of young sieve tubes, or the tangential walls of the cells of the commencing medullary rays. It is a point worth notice that the tangential walls of the latter tissue are always found to be similar to the end walls of the ordinary parenchyma cells, in the character and distribution of the connecting threads.* (*Cf.* fig. 13, Plate 32, and fig. 36, Plate 35.) The tangential walls of the developing sieve tubes quickly lose all trace of their radial connecting threads. If this was not so, all the sieve tubes would be seen to be in radial communication with one another up to the cambium, but the canals of the threads situated radially are probably filled by mucilage, and an imperforate wall is formed, as we have noticed in other instances.

In the case of the medullary rays the numerous scattered threads which traverse the tangential walls are persistent, notwithstanding that the origin of these cells is similar to sieve tubes, namely, by tangential divisions from the cambium. Thus it appears that though threads are always initially formed as a consequence of nuclear division they need not necessarily be retained, unless of value.†

The Xylem.—The *xylem* patches consist of groups of lignified spiral vessels, some of the youngest elements of which show a few bordered pits. A resin duct occurs on the outer side of the xylem a little distance from the vessels, and such ducts—like those in the cortex—show threads very clearly, connecting the protoplasm of the various cells which surround the canal.

The distinct orientation of the connecting threads with regard to the duct is very noticeable. The main thread groups which run in the radial direction connect the duct by the shortest route with the neighbouring tissues and point to an easy passage of material towards the canal. The cells which surround the duct are connected with one another, and are thus linked together to form a circle by means of small groups of threads. The end walls also show the usual arrangement of numerous scattered threads. (Fig. 14, Plate 32.)

The epithelial cells show connections with one another both in the vertical and tangential direction, and in the neighbouring cells, also, tangential connections have been well seen (especially in canals of *Pinus sylvestris*).

The question of the existence of pores between the epithelial cells and the cavity has already been referred to, and no further evidence bearing upon this point was obtained from the hypocotyl.

The vessels of the *xylem* show no threads either between one another or connecting them with the surrounding parenchyma, but whether any remains of overlaid threads do actually exist between the various xylem elements, like those seen in the walls of a few elements of the cotyledonary xylem, must for the present be left an open question.

In some of the youngest of the xylem elements developing bordered pits may be

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* *Cf.* with the adult tissues of *P. sylvestris.* In the older hypocotyl several medullary rays occur.

† *Cf.* W. GARDINER, *loc. cit.*

observed, and these were closely examined in all cases. The cells were found to be full of protoplasm, which was very closely applied to the torus, however much it was contracted away from the wall in other places; and this circumstance, although it makes the young bordered pits conspicuous objects, also causes them to be very difficult to examine. (See figs. 15 and 16, Plate 33.) In some a few threads appear to cross the torus, and in surface view several pits showed small groups of dots within the border (fig. 17, Plate 33). (The drawings were made from preparations of the developing wood of *Pinus austriaca.*)

Since, as STRASBURGER has shown, the bordered pits are homologous in position and arrangement to the sieve plates of the phloem, connecting threads would certainly be expected to be present, especially as the young cells are full of protoplasm, and the few successful observations already referred to, though certainly needing further confirmation, tend to establish the view that threads do occur, at any rate, when the tracheids are young. With increasing age the thread canals in the torus probably very soon get obliterated, and it then becomes an imperforate membrane.

Both RUSSOW* and STRASBURGER† noticed the way in which the protoplasm sticks to the torus, and the former observer states that the primary pits of the cambium and young wood are undoubtedly perforated, and concludes that as the pit membrane is shut in older tracheids the pores must have been stopped by cell substance, and he considers that certain of the striæ on the old torus may mark the scars of former perforation.‡

The cells of the *pith* exhibit similar arrangements of the connecting threads to those found in the cortex, but the groups on the side walls are not always quite so large.

In sections of the hypocotyl of plants six weeks older than those just described, the chief difference is seen in the increase of the tissues of the vascular bundles, which, moreover, owing to the development of secondary thickening, have become collateral.

The tissues of the secondary phloem are seen to be composed of radial rows of sieve tubes all connected with one another by the groups of threads in the radial walls. The primary phloem which was so conspicuous in the young hypocotyl is seen to be greatly compressed and no longer functional, having been replaced by the vigorous development of the secondary elements.

Medullary rays showing numerous threads on their tangential walls pass through both phloem and xylem to unite the pith and cortical cells.

The *endodermis* has become lignified, but passage cells are left at intervals which possess cellulose walls, and through these cells the connection between the cortex

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* RUSSOW, 'Sitzber. d. Nat. Ges. Dorpat,' 1883.

† STRASBURGER, 'Bau und Wachstum,' p. 42 *et seq.*, Taf. II.

‡ RUSSOW, 'Bot. Central.,' 1883.

and stele is still maintained. Connecting threads occur in some numbers in the walls of such cells, and can also be seen abundantly distributed in the walls of the neighbouring cells on each side of the endodermis. (Fig. 38, Plate 35.) The passage cells are most frequent outside the phloem. The radial walls of all the cells of this layer are strongly lignified,* and it is, therefore, almost impossible to see if there are any threads in them. The protoplasm is, however, frequently found to be closely applied to these walls. The threads in the cortex appear quite similar to those already described.

Still older stems are found to agree in almost every respect with *Pinus sylvestris*, the tissues of which will be described presently.

The Seedling Root.—The distribution of connecting threads in the root tip is, if possible, more interesting than in the stem. The longitudinal section of the root tip of *Pinus pinea* shows the usual typical structure, namely, the plerome with the periblem covered externally by the "root cap."

The cells of the latter form a layer three to five cells deep, which stretches a good distance up the sides of the root proper. The cap is seen plainly on placing a section in iodine, as its cells contain starch, which is not found in the more internal tissues. Besides the presence of starch there is also a strong contrast between the thin walls of the periblem cells and the thick, easily-swelling walls of the larger cap cells. The latter at the region of the root apex are irregular in shape, although fairly isodiametric, while at the sides they are oblong, and further from the tip, along the sides of the root, they are quite long and also narrow in proportion to their length.

The results obtained by the Safranin method were confirmed by those given by the acid blue method.

Numerous threads are very easily seen in the cells of the cap; the end walls show the threads scattered singly or in groups of two or three all over their surfaces, and in section they appear long and well curved, and easily break up into granules when the wall is much swollen.†

On the side walls the threads are arranged in narrow deep pits with a thin pit-closing membrane, so that when a section possessing cell contents is mounted in iodine, the appearance of direct continuity is given by the two opposite pit processes.

The thread groups are quite small and fusiform in outline, being only some two or three threads broad and ten to twelve long, and they occur usually at right angles to the long axis of the root (fig. 18, Plate 33). The distribution of the threads in the "root tip" is striking, since they are obviously arranged with reference to the apex ofthe root proper, which represents the centre to which the threads lead.

From the root-cap apex their main direction is vertical, whilst proceeding up the

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* *Cf.* the endodermis of the leaf of *Pinus sylvestris*, p. 118.

† The strongest swelling agent used was 1 per cent. sulphuric acid with a solution of iodine in potassium iodide.

sides it becomes inclined until at the level of the growing point the threads lead in horizontally, and so continue up the side of the root. (Fig. 19, Plate 33.)

Examination of the free surface of the root cap shows that the outermost cells are continually wearing away and breaking down into a mucilaginous slime which covers the surface. In the uninjured walls of the cells next the free surface, threads can be seen abutting on to this slime, which by this means is in a position to communicate with the living protoplasm of the root cap, and the same arrangement can also be observed all along the sides of the cap. The lateral thread groups though small are very numerous, and in section two or three or sometimes only single threads can be seen traversing the closing membrane of the pits, which are here exceedingly narrow.

Between the cells of the cap and the periblem, threads are also visible, but these are better shown in the roots of other plants, *e.g.*, those of *Vicia Faba.*

As regards the cells of the root proper, a longitudinal section of the upper end of the root tip (fig. 19, Plate 33) shows connecting threads in surface view, but the walls are often too thin to enable the delicate, faintly staining threads to be seen in section. In the periblem the groups are small and lenticular, and placed fairly close together in the younger cells, though separating as they grow older.

Just internal to the cortex come the longer cells of the young plerome with very numerous rounded or slightly elongated thread areas all over the walls, and this narrow region is apparently the developing phloem. The centre of the plerome is occupied by the long cells of the young pith, provided with small and narrow thread areas at intervals, which, like those of the cortex, are at right angles to the long axis of the root, but are less numerous.

Fig. 9, Plate 32, represents a longitudinal section of the primary phloem, showing the curious oblique end walls richly provided with threads.

In a transverse section of the upper end of the root tip the cells, which form the thick-walled tissue of the cap, show on their tangential walls numerous threads, each with its median dot. Some of the radial walls appear to have been recently formed by division, judging from the scattered threads seen all over them; divisions which, indeed, would be needed as the root increases in diameter.

Both the number and the distribution of the connecting threads in the root cap suggest that they must have no small physiological significance.

The root cap appears to perform two important functions, namely, those of a sensitive organ and those of an organ of absorption :—

(*a.*) As a sensitive organ—

The researches of PFEFFER* and CZAPEK† have shown that the root tip is the place where the stimulus of gravity is felt; the part of the root answering

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* PFEFFER, 'Annals of Botany,' 1874; *vide* also DARWIN, 'Physiology of Plants,' § 205, A.

† CZAPEK, 'Jahrb. für Wiss. Bot.,' vol. 27, 1895.

to the stimulus occurring a little above this point. It seems highly probable that the numerous connecting threads of the "root cap," which focus themselves on the growing point of the root, form of the channels by which the stimulus is transmitted, and that the part of the root which can respond to a stimulus lies in the neighbourhood of the actual growing point itself. The value of the sensitive root cap to a young and tender root growing in a soil full of obstacles is obvious, since a stimulus produced by contact with a foreign body (*e.g.*, with a stone) on being transmitted to the place where bending can occur might cause a deflection of the root away from the obstruction.

(*b*.) As an absorbent organ—

The root cap also seems to be an organ of first importance in connection with the absorption of water into the seedling root.

It seems probable that the cells of the root cap, which, as we have seen, extend a long way up the sides of the root, largely function as the means by which water enters.

The slime surrounding the cap is capable of absorbing water, and the threads which have been described as extending to the free surface and abutting on the broken down mucilaginous slime appear to be the principal agents for conducting the water to the tissues of the young root.* The cells of the cap alongside the periblem show threads to the surface, which are as numerous as those situated nearer the tip, and there is good connection across the few cells of this region to the periblem, whose cells communicate with the root cap by pits containing threads.

Once within the cortical tissues thread areas of the ordinary type abound, by which the absorbed water can be passed to the xylem or to the other tissues of the young root.

Some time after the above results had been worked out with the root tips of *Pinus pinea*, our attention was drawn to a paragraph in the middle of a long paper by CZAPEK† on "Geotropic Stimulus Perception." Using the root tips of the *Vicia Faba*, he says, "The way of stimulus transmission takes place from cell to cell by means of 'connecting threads,' which in the root tip are clearly seen (when examined with homogeneous immersion lenses) in *living* roots, or well seen if the sections are treated with weak iodine solution."

In consequence of these statements the root tips of *Vicia Faba* have been examined, and the results with figures are appended, as they are useful to compare with *Pinus* already described.

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* Root hairs are usually absent in *Pinus pinea*.

† CZAPEK, 'Prings. Jahrb.,' vol. 32, 1898, p. 218 *et seq.*; also pp. 302–308.

It seems quite certain that CZAPEK was in error with regard to these connecting threads, for they cannot be seen either in sections of living material or in those mounted in weak iodine solution. Since, however, the pits are deep, and the protoplasm filling them becomes stained with the iodine, the various cells appear to be directly connected through open pits; for the small pit-closing membrane, though invariably present, is hard to see and also stains slightly.

There is little doubt that it is this *appearance* of a direct continuity, which he describes, and it is easy to understand his mistake if the memoir of KEINITZ-GERLOFF* was his guide. His general conclusions, although they rest on inaccurate observation, are probably correct.

The root of *Vicia Faba*, when examined by the special methods necessary for the demonstration of connecting threads, turns out to be particularly favourable material. The root cap is much smaller than that of *Pinus*, but like it the cells are prolonged some distance up the side of the root as long thick-walled tissue. At the apex of the cap the outer thick-walled portion is fairly sharply marked off from the inner part, which consists of thin-walled cells. The outer cells and those along the sides of the root have deeply pitted walls and usually retain their contents. Small groups of threads are usually found in the pits connecting the cells together, so that in section only a few threads can be seen; but in some parts the pits are larger and the threads more numerous. As the cell walls at the edge of the root cap are very mucilaginous, the threads are easily broken up into small granules.

The lateral thread areas, which are narrow and pointed, are very closely packed together in the younger cells, becoming separated as the cell grows in length and breadth. The unpitted end walls are occupied by a good number of long threads.

The root-cap cells at the side of the root show deep and fairly broad pits on the side walls, and similar pits occur between the cap cells and cortical cells of the root (fig. 19, Plate 33); and the threads are in all cases curved and form barrel-like figures. The thin-walled cells of the root cap immediately below the growing point are interesting, because they show how the distribution of the threads is affected by the growth of the cell wall. Such cells (see fig. 20, Plate 33) show threads in surface view scattered irregularly over the face of the walls, and the side and end walls in section appear very similar. A little further away, where only a slight amount of growth in length has taken place, the threads on the side walls have become so arranged that they are distributed in small groups over the wall, and such threads are found to be situated in small pits.

In the more externally situated tissue, the cell walls thicken and the deepening pits are moved further apart.

The root cap of *Vicia* shows threads to the free surface very clearly. The young cortical cells are also well provided with threads, and surface views of cells of various

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* KEINITZ-GERLOFF, 'Bot. Zeit.,' 1891.

ages show interesting gradations from a wall where threads are irregularly scattered with scarcely any indication of grouping, to those where threads are distributed in the usual narrow fusiform areas.

II. "CONNECTING THREADS" OF *Pinus sylvestris.*

The anatomy of the adult stem, leaves, and root of *Pinus sylvestris* is so well known and has been so well figured by STRASBURGER* and others that no further description is necessary here. The distribution and character of the threads in the parenchymatous and vascular tissues of the stem will first be described. The root will then be similarly treated, and finally the leaf.

The Stem.—The summer material of *Pinus sylvestris*, which was taken from a robust three-year-old stem, was not preserved until the 4th of August, when the activity of the cambium was over.

All the younger material (and this was of *P. austriaca*) which had been preserved in June for stages in the formation of wood and bast, was found to be so badly preserved, owing to the use of a faulty fixative, that it was almost useless, and from this unfortunate circumstance it follows that the many interesting results which will certainly be obtained when the cambium and developing phloem and xylem are successfully examined, cannot be dealt with in the present paper, but must be reserved for a future communication.

Pinus sylvestris material was also preserved in January, but excepting the callus development of the sieve tubes, there is little difference, as regard threads, between the tissues in the summer and winter condition.

In certain cases the threads are fairly easy to see. Radial sections of material taken in August, which was merely placed in iodine and examined in this re-agent, showed without further preparation traces of threads, which appeared distinctly as dark lines in the end walls of the cortical cells, and also in the tangential walls of the medullary-ray cells.

The parenchyma cells of the pith, if mounted in weak iodine containing about 10 per cent. sulphuric acid, show the cellulose walls blue, excepting where the pits occur, where the closing membrane is stained yellow.† On closer examination, the middle lamella of this region is seen to be marked by groups of dots, and definite groups of striæ can also be seen crossing the closing membrane and corresponding to the dots above mentioned. In some cases the pit-closing membrane remains entirely unstained either with iodine and sulphuric acid, or chlor-zinc iodine; the cell wall alone becoming coloured and assuming the characteristic blue.

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* STRASBURGER, 'Leitungsbahnen,' 'Practicum,' &c.

† *Cf.* W. GARDINER, 'Phil. Trans.,' 1883, p. 880, "On the Nature of the Pit-closing Membrane.

Curiously enough, threads in the end walls could not be seen in surface view with this treatment. A difference in staining of the cell walls and pit-closing membrane is often equally apparent, when sections are mounted in RUSSOW'S callus reagent in place of iodine and sulphuric acid. Here also the pit-closing membrane becomes yellow or remains colourless, whilst the cell wall stains blue-violet.

RUSSOW* using these reagents noticed the same effects, and considered the non-staining of the closing membrane to be due to its peculiar physical or chemical constitution, and he thought (and this was written before his discoveries on the perforation of the wall) that it consisted of a modified cellulose, which is more easily permeable than the pure cellulose of the wall.

These different reactions suggest, either that there is some essential primary difference between pit-closing membrane and cell wall, or else that the nature of the former has become changed subsequently to its formation; but it is also possible that the presence of the protoplasmic threads in the membrane may have some influence.

More detailed examination of the side wall pits of cortical cells in radial section showed the pit-closing membrane covered with bright, glistering, angular, and rounded granular particles, and the ends of the basal walls of the cortical cells, and also apparently the surface of young sieve plates, are similarly covered.

These granular particles, which can also be seen in the general cell protoplasm and are protoplasmic or proteïd in nature, are here, as in the sections submitted to further preparation and stained with aniline dyes (see p. 98), not the real ends of the threads, but granules attached to them. With RUSSOW'S callus reagent they are also stained brown.

For accurate and reliable observations concerning the distribution of connecting threads in the tissues of the stem, simple treatment with iodine is not sufficient, and the sections must be carefully prepared and stained by either the safranin or acid violet method.

The Cortex.—The general distribution of threads in the three directions (*i.e.*, vertical, radial, and tangential) can be most easily seen in a transverse section.

The horizontal or end walls present the usual feature of numerous threads, but in the older walls there is a tendency to occasional grouping and slight pitting.† In all places where cell division has recently occurred, the walls are thin and show numerous scattered threads (fig. 21, Plate 33). The threads traversing the pit membranes of the tangential walls are hard to make out, since the pits have but thin-closing membranes and are sparsely distributed.

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* RUSSOW, 'Sitzber. d. Nat. Ges. Dorpat,' 1882, pp. 250–360.

† A longitudinal section shows some of the end wall threads grouped together in shallow pits, and these are usually situated around the edges of the walls, whilst other threads occur more or less singly or in pairs and are no longer than those of the pit groups, since the end wall is somewhat lenticular in section.

When successfully observed, the threads appear numerous and very fine, and show sometimes a median dot. (Fig. 21, Plate 33.) They also frequently appear much thicker than they really are, owing to the stain massing together groups of fine threads. Further, the pit membranes are so arranged with regard to the tangential walls, that there is considerable difficulty in showing them in accurate sectional view, and they appear partly in section and partly oblique, so that the darkly-staining granules at the ends of the threads become confused with the threads themselves, which gives an erroneous impression of thick threads.

On the radial walls, pits are found in abundance with the threads arranged in them, in large and small groups (*cf.* the parenchymatous cells of the hypocotyl, fig. 13, Plate 32), and the whole group forms the usual barrel-figure.

In transverse section the pits are long, since they run horizontally, *i.e.*, at right angles, to the long axes of the cell. (Figs. 22 and 23, Plate 33.) From the above, it will appear that, excluding the cells just below the cork, the distribution of the threads in the cortical cells generally is comparable to that found in the sieve tubes, except that with the latter the pits are known to occur on the radial walls only.* But in the cortex there is a certain amount of radial communication, as well as that in the tangential direction. Thus the cortex, as seen in transverse section, appears to be formed of a series of irregular concentric bands of tissue, all the cells of which are closely united in the tangential direction by threads through the radial walls.

From the above description, and bearing in mind the numerous threads of the end walls, it is seen that so far as the cortex is concerned, and excluding the special cases of the medullary-ray tissue and that of the cork cambium described below, the directions in which communication take place most easily are the vertical and tangential, so that movement is chiefly vertical or spiral.

In consequence of this arrangement, it is obvious, as RUSSOW† pointed out, that the greatest number of threads can be seen in tangential sections of the cortex.

The cork and cork cambium are situated at the exterior of the cortex. The tangential walls of the cork cambium, which are fairly thick and mucilaginous, swell with great ease and are pierced by numerous long curved threads, which latter stretch without a break right across the middle lamella from cell to cell (fig. 23, Plate 33), though easily broken up into granules if the wall is over-swollen.

The older walls in this region show a tendency to an arrangement of the threads in shallow pits (fig. 23 (*a*)). The change in direction of the threads in this cork cambium when compared with the rest of the cortex is very marked, and the radial arrangement is obviously due to the fact that the cells which have become meristemmatic have originated by tangential division.

The radial threads are here persistent, and appear to be of value in conveying food material and water to the developing cork. On the radial walls of the cork cambium

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* It is possible that a somewhat analogous arrangement may also exist in the xylem.

† RUSSOW, 'Sitzber. d Nat. Ges. d. Dorpat,' 1883, p. 565.

cells deepish pits occur, through which a very large number of very fine threads unite the contents of adjoining cells. (Figs. 22 and 23, Plate 33.)

The *resin canals* appear as separate systems in the general cortex although well connected with it. The cortical cells surrounding the duct are arranged in concentric layers some five cells deep, and the most obvious threads are those distributed radially, which occur in groups, leading towards the cavity of the canal. In some cases scattered threads are seen on the tangential walls where cell division has recently occurred.

Tangential connection between the several cells of each concentric layer is effected by threads which occur in scattered groups, and are seen less frequently in transverse section than the groups on the radial walls; the end walls also show the usual scattered arrangement of threads.

The epithelial cells are well connected with the circle of cells outside them and also with each other vertically and tangentially, and the free walls are usually covered with stained granules, but no threads can be seen.

The *medullary-ray cells*, as compared with the general cortex, show another change in the main direction and distribution of the connecting threads, for here it is the threads, traversing the tangential wall, and therefore running in a radial direction, which are especially well developed, thus indicating the value of these cells as passage-ways through the xylem and phloem to the cortex. The tangential walls are riddled with numerous curved threads without any pits (like the young end walls of the cortical cells), and the basal walls have oval patches of threads in shallow pits connecting the cells of the ray together in the vertical direction. (Fig. 24, Plate 34.)

The interesting relations between the starch-containing cells, which form the bulk of the medullary-ray tissue and the bast-parenchyma, and between the sieve tubes and the albuminous cells, will be considered when the phloem is described.

The medullary-ray cells get shorter the nearer they approach the cambium from which they arise; but their character is unaltered, and all through the wood the darkly-stained tangential walls form conspicuous objects. There the cells are much longer, and a radial section shows that the starch-containing cells of the ray are fewer than in the phloem. The wood medullary-ray cells are connected vertically by a few groups of threads. (Fig. 30, Plate 34.)

The question of the existence of threads in the cellulose walls of the pits between the medullary-ray cells and the tracheids will be discussed when the xylem is described.

The medullary ray has now brought us to the pith, which occupies only a small space in a three-year-old stem. The cells are similar to ordinary parenchyma; their end walls have numerous scattered threads, and pits occur in the side walls provided with threads which stain very deeply. The general direction of the latter is radial, especially in the neighbourhood of the primary medullary rays. The pith is in close communication with the ring of resin canals at the inner edge of the secondary wood, the cells of which canals show a large number of threads arranged in the usual manner.

The Phloem.—The phloem of *Pinus sylvestris*, which is figured in the various works of STRASBURGER,* is made up of sieve tubes and of cambiform or bast-parenchyma cells. The albuminous cells, which usually accompany the medullary rays, may also be conveniently described with the phloem.

A study of the distribution of the connecting threads in the phloem and in the medullary-ray cells associated with it, brings out the striking fact that the sieve tubes never communicate directly, either with the cells of the bast-parenchyma, or with the starch-containing cells of the medullary ray, and that the following relations exist, namely, that the sieve tubes are connected with the albuminous cells and the bast-parenchyma with the starch cells of the medullary ray. Both these latter are, however, connected with the albuminous cells, the starch cells freely and the bast-parenchyma to a much less degree, and from this it follows that the albuminous cells perform the important function of affording the only means of communication, and this an indirect one, between the sieve tubes and the rest of the parenchymatous tissues which compose the bast and medullary rays.

In a transverse section the absence of any connection between the starch-containing medullary-ray cells and the sieve tubes is at once apparent (fig. 24, Plate 34); while, on the other hand, in places where a tangential band of bast-parenchyma cells is cut across by a medullary ray, numerous threads between the two cells can be seen, which threads are situated in fairly deep pits and present the well-known barrel-figure, with the outer threads of the group curved in the usual manner. (Figs. 24, 25, and 26, Plate 34.)

Proceeding tangentially along a band of bast-parenchyma cells, the absence of "connecting threads" between them and the sieve tubes is as noticeable as between the latter and the starch medullary-ray cells just mentioned. The cells of the band are very well connected together by groups of threads in pits, and the end walls are seen in surface view to be covered by dots, which are the ends of threads arranged like those in the tangential walls of the medullary-ray cells, or like those of the end walls of the cortical cells.

The bands of bast-parenchyma cells in the older phloem amongst the empty sieve tubes still retain their contents and also their threads, which connect them with one another and with the medullary-ray cells.

Occasionally a medullary ray of square cells, each one being very little larger than a sieve tube, is seen in the transverse section, having their tangential walls pierced by scattered threads, which are not so numerous as those of the starch-containing ray cells, and these are the albuminous cells, which differ from the starch cells in showing connections with the sieve tubes.

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* STRASBURGER, 'Leitungsbahnen,' Taf. I.; 'Bau und Wachstum.,' Taf. III.; 'Bot. Practicum,' figs. 47, 49, and 50.

The sieve tubes, as both RUSSOW and STRASBURGER observed, only possess connecting threads in the radial walls, and these threads stain more easily than the connecting thread in any other tissues.

The walls turn blue with iodine alone, which indicates their mucilaginous nature, in virtue of which they swell easily, and thus enable the dye to penetrate into the threads.

Owing to the very great readiness with which the younger walls swell, the youngest sieve tubes are difficult to observe, although some fairly young elements were seen, in which the threads form an entire undivided group between the two pit processes. Examination of older material shows the group broken up into four or five secondary groups, separated from one another by the thicker portions of the membrane, and it is to these secondary pits (fig. 27, Plate 34) that the characteristic appearance of a sieve plate in surface view is due. (Fig. 28, Plate 34.)

All the threads of the sieve tubes show the median dot or swelling which has been noticed both by RUSSOW* and STRASBURGER, and figured by the latter.† The dot is more conspicuous in the older sieve tubes, while in the young ones it is quite small and faint. (Fig. 29, Plate 34.) In the older the dots appear to swell and coalesce, causing the formation of a darkly stained plate in the centre of the sieve. The precise function of these dots can only be determined by further research. They certainly appear to be of the same nature as the rest of the thread, judging from staining reactions; but whether they are a help or a hindrance to the passage of soluble matter must for the present be left an open question. The way in which they tend to coalesce in old sieve plates suggests a comparison with GARDINER'S figure of the endosperm in a germinating seed of *Tamus communis*,‡ where the ferment corrodes along the middle lamella and along the threads, producing a result not unlike that found in sieve tubes, in which ferments also occur in abundance. These ferments very probably have some effect on the connecting threads, by means of which they no doubt pass from one cell to another.

A radial longitudinal section (fig. 30, Plate 34) shows the various connections of the medullary-ray cells in great perfection, and the drawing of such a section is all the more striking when compared with the ordinary figures of a radial section of *Pinus sylvestris*,§ where the cell walls are thin and contracted owing to the use of alcohol material.

The numerous curved threads of the tangential walls of the starch medullary-ray cells have already been noticed in the description of the transverse section; and they are well seen in the sections cut radially. In the vertical direction, connection

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* RUSSOW, 'Sitzber. d. Nat. Ges. d. Dorpat,' 1882, p. 270.

† STRASBURGER, 'Bau und Wachstum,' figs. 36 and 38, Taf. 4; 'Leitungsbahnen,' figs. 33 and 34, Taf. 2.

‡ GARDINER, 'Roy. Soc. Proc.,' 1887, fig. 3, p. 106.

§ See STRASBURGER, 'Leitungsbahnen,' fig. 1, Plate 1.

between the cells of the ray takes place by means of small groups of darkly-staining threads in shallow pits.

The albuminous cells, which link the sieve tubes with the starch-containing medullary-ray cells, are connected with the latter by many groups of threads in slight pits. These pits are rather more pronounced than those between the ordinary cells of the ray, and there is a great concentration of threads to the albuminous cells, from the longer cells of the ray, below or above, as the case may be. (Fig. 30, Plate 34, and fig. 26, Plate 34.) Between themselves (*i.e.*, in the radial direction), they show a large number of short, rather faint threads in the tangential walls, which are not packed together like those of the ordinary ray cells, but more irregularly scattered; the cells thus presenting the appearance usually associated with cells which have recently undergone tangential division.

The elongation of the walls also naturally tends to separate the threads.* In places where the contents of these cells have fallen out, small thread areas can be seen in surface view, which are the ends of the threads connecting the sieve tubes with them, and towards which they function as companion cells. The groups are similar to the sieve areas between two sieve tubes, but are smaller, and they are best seen in tangential sections of the phloem.

The sieve tubes show sieves or thread groups in surface view on their radial walls, as darkly stained circular areas composed of numerous small irregular aggregates.

Closer examination shows that the small groups consist in reality of darkly-staining granules which hide the true ends of the threads. Not infrequently the small secondary pits are left filled with their protoplasmic contents, which then appear as dark patches obscuring all the threads below (fig. 28, Plate 34; *cf.* also a transverse section of a sieve, fig. 27, Plate 34); but there seems little doubt that the actual threads can only very rarely be seen clearly in a surface view. STRASBURGER† figures sieve areas in surface view, and indicates the existence of only from three to six threads in each secondary pit, which end in a darkly staining spot or patch; his figure also of a transverse section‡ shows only some three groups of three threads each. But in sections prepared by our methods, the threads are more numerous than this, and also much finer (compare figs. 27 and 29, Plate 34).

The most complete study of the phloem can be made by means of tangential sections, and the various sections thus obtained present very different appearances, since they may be taken through the empty, or the active sieve tube region, or through one of the tangential bands of bast-parenchyma cells. These latter will be first dealt with, since the cells are, as has been pointed out, quite similar to ordinary

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* *Cf.* the description of these cells as seen in a transverse section, p. 114.

† STRASBURGER, 'Bot. Practicum' (Eng. ed.), p. 121, fig. 49; 'Bau und Wachstum,' fig. 39, Taf. IV.; also *cf.* the early surface view figures of sieve plates, De Bary (Eng. ed.), fig. 77, p. 180.

‡ STRASBURGER, 'Bot. Practicum' (Eng. ed.), fig. 77, p. 180.

parenchyma cells in the arrangements of their connecting threads. The end walls are full of darkly stained curved threads, exactly like the tangential walls of the starch medullary-ray cells, and if the section passes through two or three of these cells adjoining one another, they are seen to be well united by groups of threads, both large and small, in well-marked pits. (Fig. 25, Plate 34.)

The phloem parenchyma cells are much shorter than the sieve tubes, and possess square end walls. There are two kinds of these cells,* namely, those containing starch, which are similar to medullary-ray cells, and those containing crystals in a resinous-looking matrix. Connections between the latter and the starch cells are not easily seen, for the thread groups are indistinct and only stain faintly, which is due probably either to the fact that their contents do not stain with the reagents used, or else that the cells are now no longer living, but merely act as receptacles for calcium oxalate and resinous substances.

The medullary rays are very striking objects when they are in contact with bast-parenchyma cells, in consequence of the profusion of threads with which the walls are provided; the starch cells show a very large number of groups of dark threads situated in pits, and one or two groups of threads are also seen uniting the several cells of the ray (the ray in fig. 25 is a very small one). In the radial section recently described (see p. 112, and fig. 30, Plate 34) the pits were very shallow because the walls were young, whereas, in the tangential section mentioned above, the preparation was taken from an older region of the phloem, and the pits are consequently deeper owing to the increase in thickness of the unpitted portions of the wall. (Fig. 26 shows a tangential section of a piece of a fairly young medullary ray, *m.r.*) Since the whole of a tangential section will not be accurately tangential owing to the curvature of the stem, sieve tubes may be seen at the edges of sections and bast-parenchyma in the centre, or *vice versâ*; and in such sections the absence of any communication between these two elements is very noticeable. The similar lack of threads between the sieve tubes and starch medullary-ray cells is equally striking, so that where a ray touches a sieve tube on the one side and a parenchyma cell on the other a strong contrast is at once apparent. (Fig. 26, Plate 34.)

The distribution of their connecting threads appears to indicate the similar character of starch medullary-ray cells, bast-parenchyma, and ordinary cortical cells.

The albuminous cells are connected with the bast-parenchyma cells by numerous small groups of threads, like those uniting them with the ordinary starch-containing cells of the medullary rays (figs. 26 and 31, Plate 34), and since the albuminous cells act as the companion cells of the sieve tubes, they also offer an indirect means of communication between the latter and the bast-parenchyma cells.

Besides the crystalliferous and the starch-containing cells of the bast-parenchyma, there are longitudinal albuminous cells† which, in general appearance, are like the

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* STRASBURGER, 'Bot. Practicum' (Eng. ed.), p. 121.

† STRASBURGER, 'Leitungsbahnen,' p. 60 *et seq.*, figs. 27 and 32, Taf. II.

starch cells, but which when stained show the character of ordinary albuminous cells. (Fig. 31, Plate 34.)

The walls between both kinds of albuminous cells and the sieve tubes show pits, the slightly curved closing membranes of which (*cf.* sieve plates) are traversed by a large number of very fine threads like those of the sieve plates, arranged in a slightly fan-shaped manner, the convex surface of the membrane being usually on the sieve tube side. The median dot is not so characteristic as on the sieve tube threads; in some cases it was visible (fig. 31, Plate 34), and in others it was apparently absent (fig. 26, Plate 34).

Thread groups also occur between the albuminous cells and the bast-parenchyma cells, and such groups are usually smaller than those found between the albuminous cells and the sieve tubes, and the threads do not possess a median dot. STRASBURGER* figures a number of albuminous cells, and speaks of the "one-sided pits." His figures do not appear to agree very well with one another, and at first it seemed difficult to reconcile them with our results; but recently, while working at the albuminous cells of leaves mordanted by means of permanganate of potash and stained with safranin, results were obtained which seem to explain STRASBURGER'S drawings, for the thread groups between these cells and sieve tubes are peculiar in that they appear to be in two halves: the threads on one side of the lamella exhibiting different staining reactions, and being larger than those on the other (*cf.* fig. 8, Plate 32, and fig. 36, Plate 35). With some dyes (*e.g.*, gentian violet) both halves of the group are stained, but with the permanganate-safranin method only the fine threads on one side (viz., the cortical side) are brought into notice, and the appearance of one-sided groups is obtained. The age of the group also makes a good deal of difference, and in young material there is not this tendency to separate staining, so that the changes in one-half of the thread group seem to be of a secondary character.

The above results seem to explain why, in some cases, STRASBURGER figures threads passing right through the walls, while in others they only reach half-way. He draws end walls similar to those in our figure† (fig. 31, Plate 34).

The sieve tubes can be studied best in tangential sections. Some quite young stages are seen in figs. 26 and 29, Plate 34. The end of the young tube in fig. 29, Plate 34, is interesting, since indications of the formation of additional sieve plates can be seen, and as the young sieve tubes must necessarily grow in length before they reach maturity, the figure is probably a correct representation of the process of providing the additional groups of threads that would be required. At x the protoplasm filling the lowest visible pit shows two apical points, from which fans of threads diverge, leaving a small piece of cellulose wall between; while in the next pit, y, bifurcation of the

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* STRASBURGER, 'Leitungsbahnen.'

† With *Damara australis*, results have also been obtained by our methods which are like those observed in *Pinus*, and the appearances, figured by STRASBURGER, can be similarly explained.

protoplasm makes two distinct secondary pits. The other four pits figured show a distinct paired arrangement, and suggest their origin from a single pit by division, like that seen in progress at x and y.

To furnish a sufficient number of threads when a pit divides, the threads may possibly be able to divide or split longitudinally, an idea put forward by RUSSOW.

There is a good deal of similarity between the wall of the young Coniferous sieve tube and the lateral wall of a dicotyledonous sieve tube, such as is found in *Phaseolus multiflorus* and *Cucurbita maxima*,* where the thin-curved pit-closing membranes with the fan-like arrangement of threads separated by thick portions of the cell-wall also occur. A comparison has already been made (p. 93) between ordinary dicotyledonous sieve tubes and those of the young seedling of *Pinus pinea*.

With regard to the origin of the sieve-tube threads, RUSSOW† speaks of fine puncturings occurring on the surface of the young primordial pit, and these he considers to be the rudiments of the threads, and he regards these young threads as boring their way through the wall, so that in two neighbouring sieve tubes, the threads on opposite sides of the pit membrane meet one another at the middle lamella to form complete "connecting threads."

STRASBURGER‡ agrees with RUSSOW, and considers that in the fully-developed sieve tubes, the threads lose their protoplasmic character, for he says, "Comparison of surface views and sections show that the fine points correspond to pores filled with protoplasm, and the threads which are at first thin, became thicker later on, and also longer as the wall thickens. This condition quickly passes, and the fine plasma threads, which fill the canals of the sieve plate, are changed into callus substance. In consequence of this change the threads become thicker and now form the callus rods."

There appears, however, to be no ground for the hypothesis that the sieve-plate threads have a different mode of origin to ordinary threads. It seems probable that they are formed during the radial divisions in tangential rows of cells, the products of the division being two sieve tubes, with radial sieve plates between them, so that the origin of the threads is *ab initio*, and is not due to subsequent boring through the already existing pit-closing membrane.

Referring to the median dots ("*Knötchen*") on these threads, STRASBURGER§ expresses uncertainty as to their nature, but considers them swollen places of the pit-closing membrane, and thinks that their presence indicates a closing of the active sieve pores, an hypothesis not held by RUSSOW. He also thinks the question

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* *Cucurbita* sieve tubes; *cf.* SACHS's 'Text-Book Botany,' 2nd ed., fig. 99, the wall 1. The appearance of this wall is practically correct. Drawings were exhibited at the Roy. Soc. Conversazione, 1899, of the lateral sieve plates of *Cucurbita* perforated like those described for *Pinus*.

† RUSSOW, 'Sitzber. d. Nat. Ges. Dorpat,' 1882, p. 279 *et seq.*

‡ STRASBURGER, 'Leitungsbahnen,' pp. 69 and 70.

§ STRASBURGER, 'Leitungsbahnen,' p. 71.

of closing is settled, because if not closed, these knobs must be supposed to be pierced by still finer threads, which would probably be of no value for the transference of materials.

Our methods of preparation throw no new light on the question of the special nature of the median dot, but it appears from its staining reaction and from its development* to belong to the protoplasmic thread and to be of the same nature.

The question of the formation of callus is another point which needs investigation by our methods, but the further consideration of this subject, concerning which Russow, Lecomte, and Strasburger have all written, must be deferred for the present.

The Xylem.—There is little to add here to the remarks already made in connection with the description of the lignified elements of the cotyledon and hypocotyl.

About twelve instances of the occurrence of apparent threads piercing the torus of the bordered pit have been seen, but these observations need further and more definite confirmation. The parenchymatous cells occurring as medullary rays, and those accompanying the resin canals, deserve some notice.

The medullary-ray cells, which are much longer and also fewer in number than those of the phloem portion of the ray, possess threads in the radial and vertical directions, which are of the same character as those of the starch cells already described; but whether any threads exist in the cellulose walls of the unbordered pits which are found between the medullary-ray cells and the tracheids, is a far more difficult question.

In some instances, threads have certainly been seen between the youngest tracheids and the medullary-ray cell, but in the great majority of cases such threads are not visible, and if they have existed at all it seems probable that they have been subsequently obliterated, so that diffusion through an imperforate membrane is the only means of communication between the tracheids and medullary-ray cells.

In support of the view, that no threads exist in the adult tissues between tracheids and medullary-ray cells, the absence of the threads between the latter and sieve tubes may be mentioned, and these cells are in a similar position with regard to one another as the medullary-ray cells are to the tracheids.

The resin canals are always accompanied by a certain amount of parenchyma, and are also always in contact with a medullary ray, with which the surrounding cells of the canal are in intimate connection.

These groups of parenchyma have their cells very well linked together by innumerable threads, so that communication between other parts of the stem, and with the resin canals of the wood, can be easily obtained by the medullary rays.

The Root.—With regard to the roots of *Pinus sylvestris* there is very little to

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* See also Gardiner, 'Roy. Soc. Proc.,' 1900.

add; the cortical tissue of old roots is not extensive, and the pits are not quite so numerous as in stems. The phloem characters are similar.

In the wood the resin canals are conspicuous objects and possess more surrounding parenchyma than in the stem, and in such canals the threads are very numerous.

As the conduction of material in the old root takes place almost entirely in the xylem and phloem, the small amount of cortical tissue is not surprising.

The Leaf.—The anatomy of the leaf of *Pinus sylvestris* is well known and needs no detailed description here. For the most recent drawing, the large figure given by STRASBURGER* in his 'Leitungsbahnen' will be useful for reference and comparison.

The mature leaf closely resembles the cotyledon, both in the arrangement of the tissues, and in the distribution and character of the connecting threads.

The epidermal cells, which are thick-walled and appear to be empty, show no trace of connecting threads; but in the hypodermal cells below, threads can be seen, though not in great numbers.

The hypodermal cell next the sunken guard cells of the stoma, often shows a small group of threads connecting it with the adjoining palisade cell below. It is difficult to see the precise manner in which the guard cells are connected with the hypoderm, but it seems likely (on the analogy of the cotyledons), that a small pit in which a few threads are present may occur connecting the two.

The Resin Canals occur around the edge of the leaf, and are surrounded by a ring of thick-walled strengthening cells, which encloses the epithelial cells. These thick-walled prosenchymatous elements are living, and communicate with the surrounding cells and with the epithelium by means of deep pits. The pits are funnel-shaped, and commencing with a canal of narrow bore broaden out over the pit-closing membrane, which is traversed by a large number of short curved threads. The protoplasm in these pits is frequently contracted, so that the peculiar shape of the pit is not noticed at first sight. (Fig. 32, Plate 35.)

The palisade cells in transverse section show numerous short dark threads in shallow pits, and connection between them in all directions (except the vertical) is very intimate. (Figs. 33, 34, 35, Plate 35.) There is no trace of any threads in the well-known buttresses of the palisade cells, and since they are only outgrowths from the walls this might have been expected. The preparation represented in fig. 35, Plate 35, shows the almost circular thread areas both in surface view and in section.

The palisade cells are bounded internally by the endodermis, with which layer they are intimately connected by threads in shallow pits, and by means of these threads the elaborated food material is passed in from the palisade cells.

The tangential walls of the *endodermis* are composed of cellulose, and numerous thread groups are found in them, which connect the parenchymatous cells of the

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* STRASBURGER, 'Leitungsbahnen,' Taf. I., fig. 13.

pericycle on the one side of this layer with the palisade tissue on the other. (Fig. 33, Plate 35.)

The radial walls are lignified, and the cell contents stick very closely to them, causing the endodermis to be very conspicuous in a transverse section of the leaf. There is also an appearance of threads traversing the pit-closing membrane, although owing to the dark staining it is difficult to be certain on this point; but it should be remembered that in the young radial walls of the endodermis of the cotyledon, connecting threads are very abundant.* (Fig. 33A.)

Wherever a parenchymatous cell of the *pericycle* abuts on to an endodermal cell the usual short darkly-staining threads can be observed in the tangential walls. These parenchymatous cells, situated as they are amongst the lignified transfusion cells, also show very numerous groups of threads, wherever they come in contact with one another, and they finally all connect with one cell which forms the passage-way to the albuminous cells of the phloem. (Fig. 36, Plate 35.) As far as can be seen, there are no threads in the walls between the dead transfusion tissue and the living pericyclic cells.†

A single group of albuminous cells occurs in connection with the phloem of each of the two vascular bundles of the leaf.‡ These albuminous cells are short and irregular in outline and the walls show the characteristic knob-like thickenings, which have already been described in other cases. As the material, from which the preparations illustrated in fig. 36, Plate 35, were made, was preserved in August, it seemed possible that the peculiar thickenings might be of the nature of developing callus; but in sections cut from tissue, which was preserved in the winter, no callus reactions could be obtained,§ and the knob-like swellings appear to be composed of slightly modified cellulose, which stains in a similar manner to the substance of ordinary pit-closing membranes. (Fig. 37, Plate 35.)

The thread groups which traverse the thickenings of the albuminous cell walls are similar to those described for the same cells in the cotyledon (*vide* p. 94) with the one-half of the thread, complex usually if not always the outer, shorter and more darkly stained than the other; when mordanted with permanganate of potash and stained with safranin, the appearance of a unilateral thread group is obtained, which reminds one of STRASBURGER's figures, but on re-staining with gentian violet the longer threads of the inner side of the thickening become visible (*vide* p. 114).

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* *Cf.* pp. 90 and 102.

† *Cf.* the pericycle of the cotyledon, p. 96, fig. 11, Plate 32.

‡ In the case of the single vascular bundle of the cotyledon of *Pinus pinea*, albuminous cells are present on each side of the phloem, and in *Picea excelsa* a similar condition exists (*vide* SCOTT, 'Structural Botany').

§ With corallin soda, water-blue, and RUSSOW's callus reagent no staining of the thickenings took place. With Congo-red the cell-walls stained pink, but the thickenings remained colourless. Ordinary pit-closing membrane also remains unstained.

It seems quite probable that the peculiar threads, which perforate the thickening, may act as a resistance to too quick a flow from the palisade cells, for the elaborated substances which result from the energy of the palisade cells are poured into the endodermis from all sides, and are then passed on into the parenchymatous cells of the pericycle. Here the stream is collected into smaller and smaller channels until finally the whole is poured into the passage cells on the outer side of each bundle (fig. 36, Plate 35, *pc.*). It is reasonable to suppose that the pressure of such a stream would be variable, according to circumstances, and then the effect of the unusually long and fine canals which pierce the curious localised thickenings of the walls of the passage cells might tend to give a uniform rate of flow to the substances in solution, which would thus gradually pass to the sieve tubes.

It will be noticed in the figure that several albuminous cells have to be passed through to reach the rectangular sieve tubes (fig. 36, Plate 35), with which they are connected by exactly similar groups of threads to those between the albuminous cells. As the sieve tubes are similar to those already described in the stem, they need not be dealt with again here.

The general distribution of the connecting threads must now be briefly discussed.

It has been noticed that the main direction of the threads in the cortex and phloem is the tangential one, so that it is the radial walls which are pierced; but in the phloem the divisions from the cambium take place, especially, in a tangential direction, and therefore, if the threads represent the persistent nodes of the achromatin fibres, they should be found in these walls; but the reverse is the case, and the inference is that such threads have only a transitory existence in the wall, which then quickly becomes a solid membrane.

The transitory nature of certain of the threads (in this case situated on the radial walls) also explains the absence of them between the sieve tubes and medullary-ray cells; and the marked difference in the distribution of the threads in the outer and the more internal portions of the cortex may possibly be explained in some similar manner.

In any case, the important fact comes to the fore that with the exception of the medullary ray and cork cambium cells, it is on the *radial* walls that the threads chiefly occur, and this further suggests the important conclusion that in the tissues of the Coniferæ submitted to examination the food supplies and the stimuli are both conducted for the most part in a tangential and vertical direction.

General Conclusions.

The research was undertaken with a view of ascertaining to what extent "connecting threads" are distributed throughout the body of any given plant, and for this purpose the endosperm and the various tissues of the stem, leaf, and root of the young seedling of *Pinus pinea*, and of the adult stem, leaf, and root of *Pinus sylvestris*, were examined.

The results show that the presence of such threads can be readily demonstrated in the case of all cells in which the wall retains its cellulose or mucilaginous character, and that in such young tissue as the growing point of the root all the cells are provided with connecting threads. When the lignified or suberised condition has supervened, it is difficult or impossible to identify threads, though even in such cases threads may be recognised in certain of the very young elements.

In *Pinus pinea* the tissue of the endosperm, equally with that of the germinating seedling, is well connected by threads.

The absorptive side of the cotyledon next the endosperm (corresponding to the lower side of the leaf) shows a certain histological distinction in that the walls of the cells both of the epidermis and the subjacent parenchyma are more richly provided with threads than are the similar tissues of the upper side. No threads, however, occur in the outer or free walls of the epidermis, so that diffusion only, as opposed to direct transference, can take place between the cell-contents of the endosperm and those of the cotyledon. In the stomata of the cotyledon threads have been seen in a few cases connecting the guard cells with the epidermal cells.

All the parenchymatous cells of the seedling plant show a general resemblance in the character of their connecting threads. On the end walls they are irregularly scattered, but on the lateral walls they usually occur in isolated groups, situated in shallow pits, mainly in consequence of the great growth in length which these walls have undergone.

The palisade cells of the cotyledon, which at first are united together in all directions, very soon separate, forming plates of tissue, and the threads in the walls, along which separation takes place, are very quickly obliterated. Similar obliteration of threads is seen to occur in those walls of pericycle cells which are situated between the cells which contain protoplasm and the young transfusion cells in process of lignification.

The phloem tissues of the young seedling of *Pinus pinea* present a distinct type, the peculiarities of which are treated of at some length. The large cells of the outer portion are characterised by long oblique end walls full of threads, whilst the thick walled cells of the inner part possess square end walls traversed by numerous long threads, resembling the sieve tubes of dicotyledons. All the sieve tube threads show a characteristic median dot.

The albuminous cells situated at the edges of the phloem of the leaves possess thread groups in peculiar localised thickenings on their walls. The threads, which are long and usually curved, stain in a peculiar manner, and these cells appear to have an important function as the passage cells from the mesophyll of the leaf to the phloem.

The root cap of the seedling root shows numerous threads connecting its cells together and also affording communication both with the free surface of the root as well as internally with the cells of the periblem. The function of the root cap as an organ for stimulus perception and as an absorbent organ is considered with reference to the abundance of the connecting threads.

In *Pinus sylvestris* the characters of the threads in the cortical tissues of the adult stem and root are similar to those of the seedling. Threads occur chiefly in the radial and end walls of these cells, but in the cells just under the cork, they are distributed in large numbers in the tangential walls.

In the phloem the absence of threads between sieve tubes and starch medullary-ray cells and also bast-parenchyma cells is very noticeable. The albuminous cells of the ray are, however, connected with all these cells, and threads also exist between the starch cells and bast-parenchyma. The medullary rays in both phloem and xylem show numerous threads all over the tangential walls and also small groups on the basal walls. The sieve-tube threads which are found only on the radial walls always show a median dot.

It seems probable that the torus of the young bordered pits is traversed by connecting threads which soon disappear.

The leaf of *Pinus sylvestris* shows a distribution of connecting threads similar to that of the cotyledon. The endodermis is seen to be very important as the layer connecting the tissues of the stele with those of the cortex by means of thread groups in the tangential walls. The living cells of the pericycle are freely connected together by threads; but no threads occur connecting them with the lignified cells of the transfusion tissue.

The albuminous cells are seen to agree in character with those of the cotyledon, and their function and peculiar properties are discussed.

The paper ends with some considerations on the general distribution of the connecting threads.

Explanation of Plates 31–35.

The lenses used were Swift's 1/8th and 1/12th apoc. with B.C. and 6 and 8 compens. oculars.

Figs. 1–14. *Pinus pinea.*

Fig. 1. Endosperm. Transverse section showing the arrangement of threads in the old and young walls both in surface view and section; *x*, an old wall in surface view shows 4–6 threads in small patches; *y*, a young wall with scattered threads. (× 730.)

Fig. 2. A transverse section of a young cotyledon. *l.ep.*, lower epidermis; *r.*, resin canal; *st.*, stomata; *pl.*, palisade tissue; *e.*, endodermis;

pc., pericycle; *s.*, phloem sheath; *p.p.*, primary phloem; *p.*, internal phloem; *x.*, xylem. (× 120.)

Fig. 3. Longitudinal radial section of cotyledon, lower side. *ep.*, epidermal cells next the endosperm; *pl.*, palisade cells showing commencing separation at the angles; between *ep.* and *pl.* cells of the hypoderm; connecting threads seen in section and surface view. (× 530.)

Fig. 4. Cotyledon. Lower side transverse section. *hyp.*, hypodermal cells. (× 730.)

Fig. 5. As 4, but including a resin canal, *r.* The orientation of threads with regard to the canal is well shown; at *x* threads are seen in the outer walls of epithelial cells. (× 530.)

Fig. 6. Cotyledon. A stoma in transverse section. *g.c.*, guard cells, a small deep pit containing four or five threads is seen connecting the guard cells with the adjoining epidermal cell; epidermal threads seen near *ep.*; threads in surface view in a hypodermal cell. (× 730.)

Fig. 7. Cotyledon. Longitudinal section of palisade tissue showing commencing separation into plates of cells; the half-threads are still visible in certain of the walls. The free surfaces of the separated walls are covered by a thin cuticularised layer, *x.*

Fig. 8. Cotyledon. Transverse section of phloem; the albuminous cells at the edge which join on to the parenchyma cells of the pericycle; the peculiar wheatsheaf like thread groups are well seen; the sieve tube side is that marked *x.* (× 750.)

Fig. 9. Cotyledon. Longitudinal radial section through the phloem; *p.p.*, the primary phloem with the peculiar oblique end walls, *e.w.*, showing numerous threads with a median dot; *p.*, the inner phloem, composed of sieve tubes like those of dicotyledons. (× 750.)

Fig. 10. Root. Longitudinal section of the phloem, showing a surface view of an oblique end wall, *e.w.*, of a primary phloem cell; in the cell above the elongated lateral thread groups are seen. (× 600.)

Fig. 11. Cotyledon. Longitudinal section through the pericycle; young transfusion cells showing lignification; at *y* the lignified layer has only just been formed; the threads are still seen in the cellulose wall; in the older wall, *x*, the threads are vanishing; at *z* an unlignified end wall is seen. (× 730.)

Fig. 12. Transverse section of a young hypocotyl of *Pinus pinea*. Lettering as in fig. 2. *P* = phloem bundle. (× 60.)

Fig. 13. Hypocotyl. Longitudinal radial section through inner cortex and phloem, showing the different direction of the thread groups in the two regions. A, cortical cells; B, pericycle and phloem; *e.*, endodermis; *s.t.*, sieve tube. (× 500.)

Fig. 14. A resin canal outside the xylem in transverse section; threads are seen going to the epithelial cells, and in one place an end wall of one of these cells is seen; three cell walls show signs of the recent division of a cell which they now separate into two; the threads are scattered and the walls swell easily. (× 700.)

Figs. 15–17. *Pinus austriaca.*

Figs. 15 and 16. Bordered pits in section, showing an appearance of threads across the torus between the darkly stained pit fillings of protoplasm; the cells are young, having just passed over from the cambium. (× 900.) The tracheid in fig. 15 is only partially lignified.

Fig. 17. Young bordered pits in surface view with the membrane covered by dots, which appear to be thread groups in surface view. (× 900.)

Fig. 18. *Pinus pinea.*

Fig. 18. Longitudinal section through root tip, showing the distribution of threads on the end and side walls; the end wall without threads should be like the other end wall, *e.w.* (× 750.)

Figs. 19 and 20. *Vicia faba.*

Fig. 19. Root tip. Longitudinal section. The connecting threads between the long thick-walled cells of the sheathing root cap *r.c.* and the thin-walled cells of the cortex *cx.* of the young root are well seen; also the connecting threads between the individual cells of both these tissues. (× 730.)

Fig. 20. Root cap. A section of the region where the cells are young and thin walled; the connecting threads are close together. On growth, these cells become like those *rc.* of fig. 19. (× 730.)

Figs. 21–37. *Pinus sylvestris.*

Fig. 21. Cells from the cortex. Transverse section. Three radial walls, *r.w.*, show by the numerous threads that cell divisions have taken place recently, and a more recent tangential division is shown by the wall *x*. The tangential wall, *tg.w.*, shows the usual obscure nature of threads in these walls. (× 750.)

Fig. 22. Shows a pit in the oblique radial wall with the membrane traversed by innumerable fine threads; on the side *c.* the over-swollen tangential wall just under the cork is seen with three threads visible. (× 750.)

Fig. 23. Cells under the cork of a three-year-old stem. The cell walls of the cork

cambium swell very readily, and the threads tend to separate into granules; the inner walls, *a*, show slight pitting with grouping of the threads; groups of threads are seen in the radial walls. The black walls, *c*, represent the cork cells (slightly diagrammatic). (× 500.)

Fig. 24. Phloem. Transverse section showing a medullary ray, *m.r.*, with tangential walls full of threads; connections occur between these cells and bast-parenchyma cells, *b.p.c.*; but there is no communication by threads between either of these cells and sieve tubes, *s.t.* (× 500.)

Fig. 25. Tangential section through the phloem through a layer of bast-parenchyma cells; *b.p.c.*, bast-parenchyma cells; *c.c.*, crystal sac; *m.r.*, medullary ray. (× 520.)

Fig. 26. Phloem. Tangential section; connections seen between sieve tubes *st.*, between sieve tubes and albuminous cells, also between starch and albuminous medullary-ray cells, and a bast-parenchyma cell, *b.p.c.*; the sieve plates show signs of division. (× 800.)

Fig. 27. Sieve tubes in transverse section showing sieve plates in the radial walls; the threads which form several groups all show a median dot (*cf.* fig. 28). (× 500.)

Fig. 28. A sieve plate in surface view showing sieve fields; the ends of the threads are obscured by pit fillings of protoplasm (*cf.* fig. 27). (× 750.)

Fig. 29. A young sieve tube in tangential section. The curvature of the pit-closing membrane and the fan-like arrangements of the threads is well seen; the median dot is quite small. A distinct paired arrangement of the four uppermost thread groups is noticeable, and the two lower ones, *x* and *y*, show commencing division, *x* being further advanced; still younger groups were out of focus. (× 800.)

Fig. 30. Radial section through the phloem and xylem along the line of a medullary ray; *s.c.*, the starch cells of the ray which extend through the xylem, *x.mr.*, and show threads in slight pits in the vertical direction, &c.; *alb.c.*, the albuminous cells above and below the starch cells, with which they communicate by threads in shallow pits; the connections in the tangential direction can also be seen. More sieve plates in surface view should have been drawn; *h.t.* horizontal tracheids. (× 500.)

Fig. 31. Longitudinal albuminous cells *alb.c.*, in tangential section showing fine connecting threads to a sieve tube on the side B, and to a bast-parenchyma cell on the side A; the threads to the sieve tube show a median dot. (× 520.)

Fig. 32. One of the thick-walled cells surrounding a resin canal of the leaf. Transverse section showing the peculiar pit with a broad closing membrane; numerous threads connect these cells with the epithelial cells, *ep.* (× 750.)

Fig. 33. The leaf. Transverse section showing the connection between palisade cells, *pl.*; the connection between palisade cells and endodermis *e.*, and between the latter and the pericycle *pc.*, forming a way to the phloem; *t.c.*, transfusion cell. (× 750.)

Fig. 33A. A pit between two endodermal cells in transverse section.

Fig. 34. The leaf. Longitudinal radial section, showing the lack of communication between palisade cells *pl.* in the vertical direction; *pc.*, pericycle; *e.*, endodermis; *ep.*, epidermis. (× 200.)

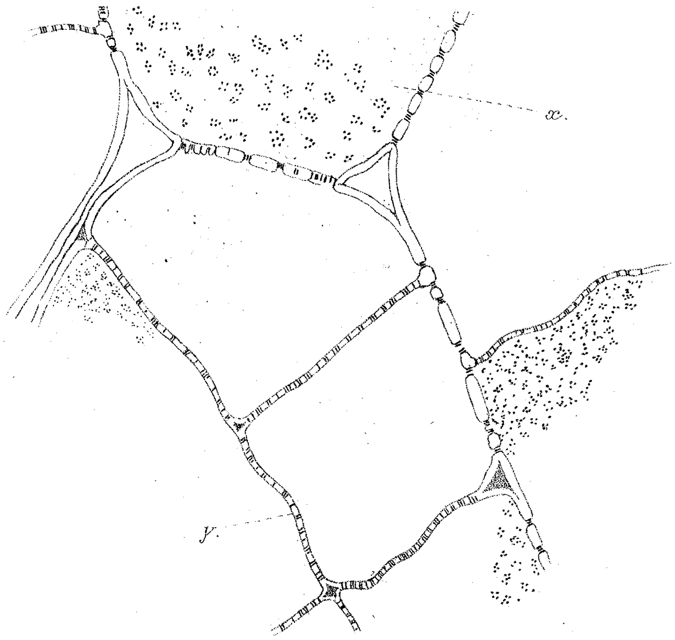
Fig. 35. A piece of the above more highly magnified, showing the arrangement of the threads; the vertical wall without threads is one of the buttresses in section, which are seen in fig. 33 to have no threads. (× 500.)

Fig. 36. Transverse section of the outer edge of the vascular bundle of a leaf. The albuminous cells, *alb.c.*, narrow down to a single cell, *px.*, to which also the living parenchymatous collecting cells of the pericycle converge; through this passage cell all the material passes from the palisade cells to the phloem; *f.*, fibres around the phloem; *x.*, xylem; to *e.* to endodermis; *P.*, phloem. (× 750.)

Fig. 37. Transverse section through the phloem of the cotyledon of *Pinus sylvestris*, showing the knob-like thickenings on the walls of the albuminous cells.

Fig. 38. *Pinus pinea.*

Fig. 38. Transverse section of an older hypocotyl of *Pinus pinea*, showing a passage cell *p.* of the endodermis with cellulose walls and connecting threads, on either side of which are lignified endodermal cells *e.*



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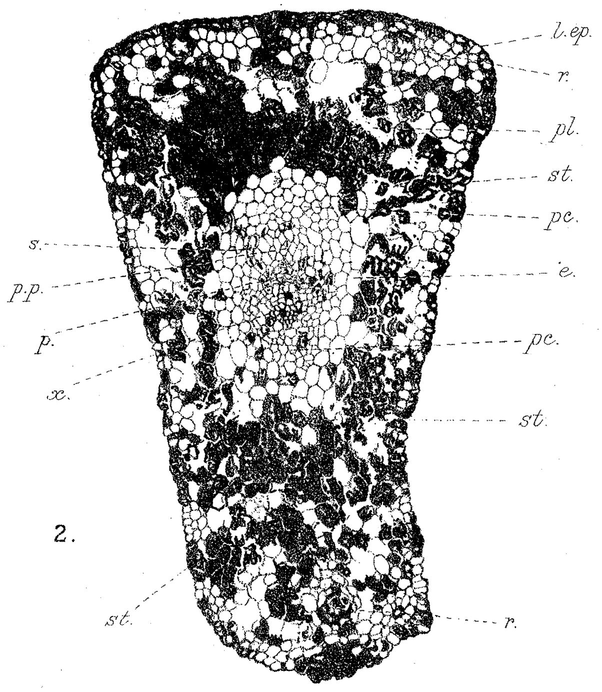

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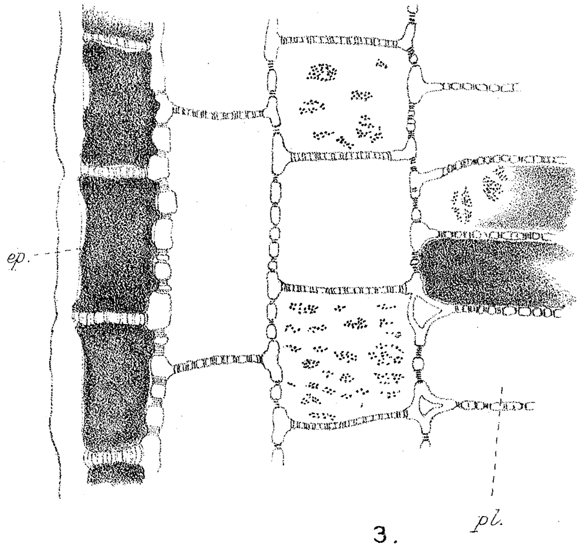

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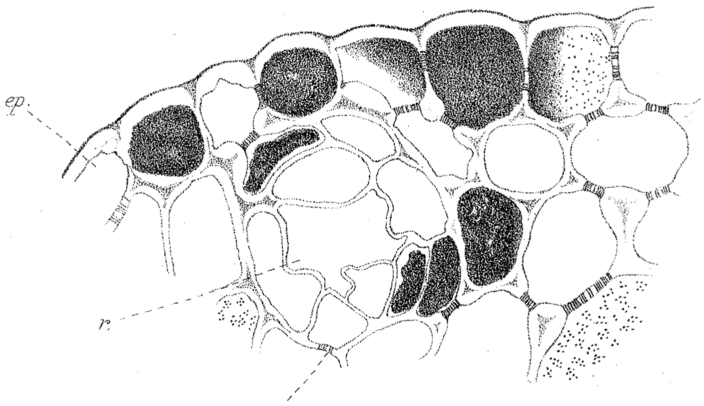

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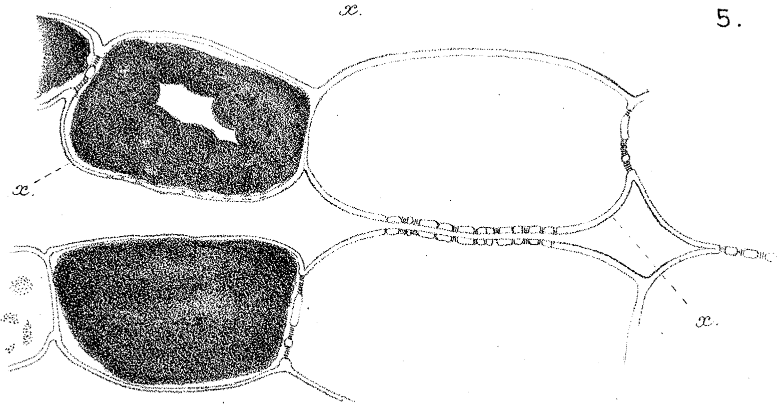

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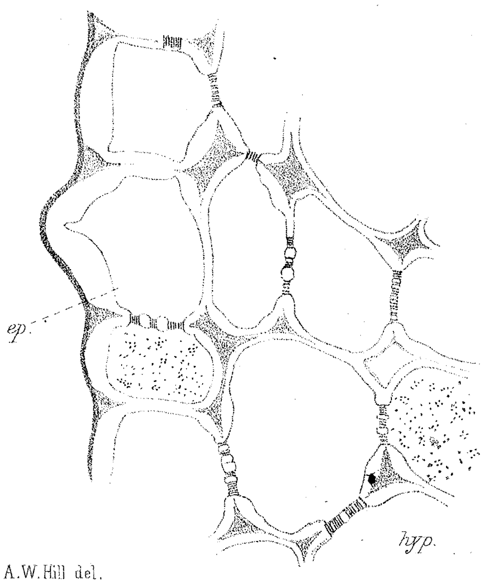

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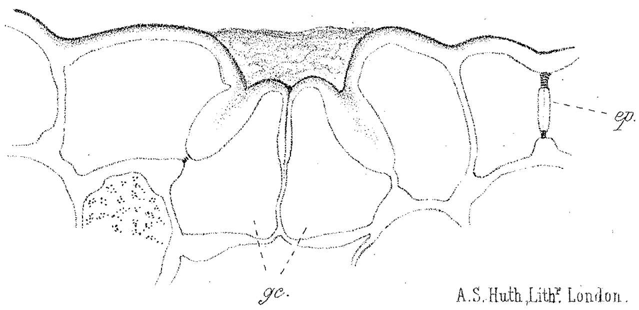

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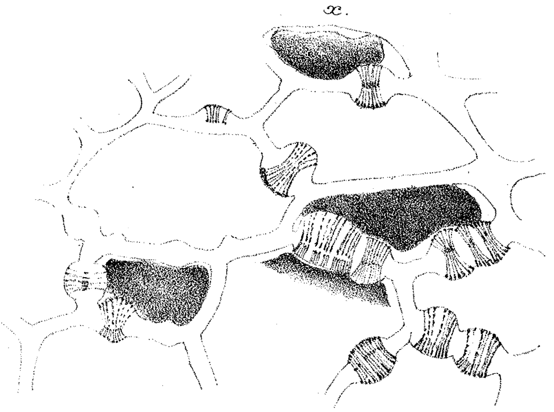

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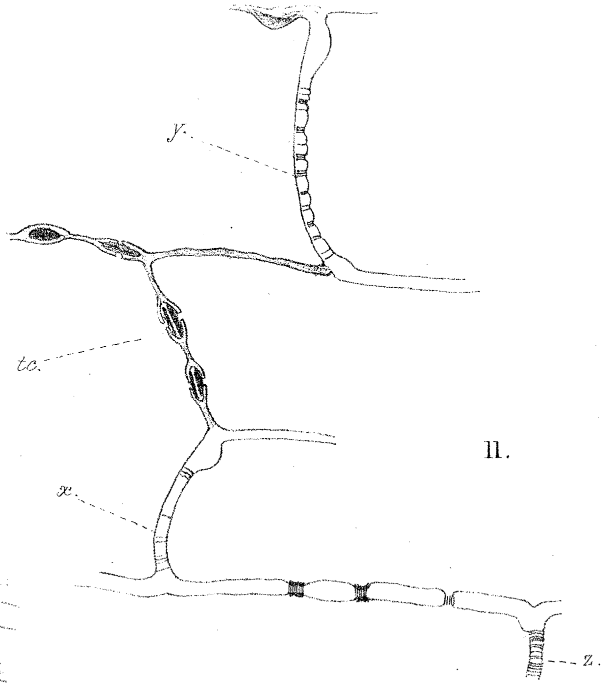

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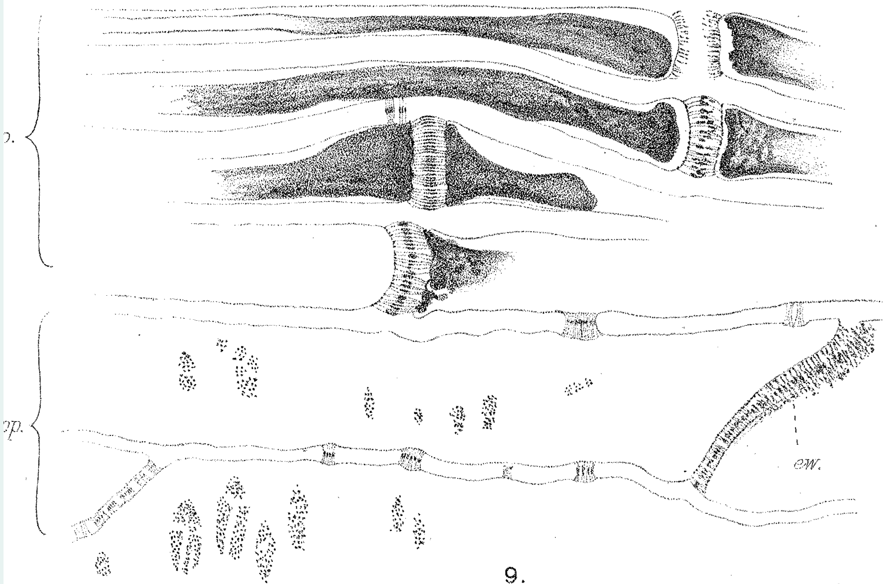

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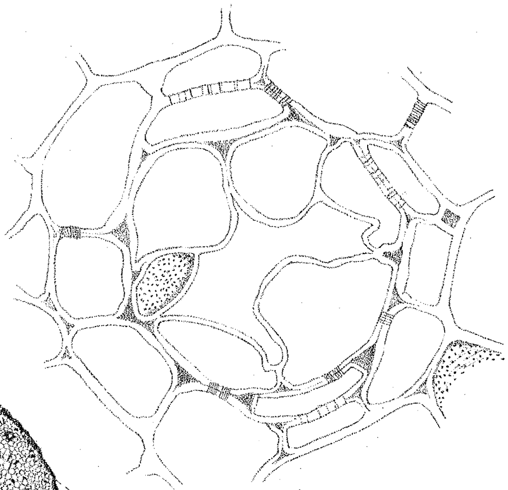

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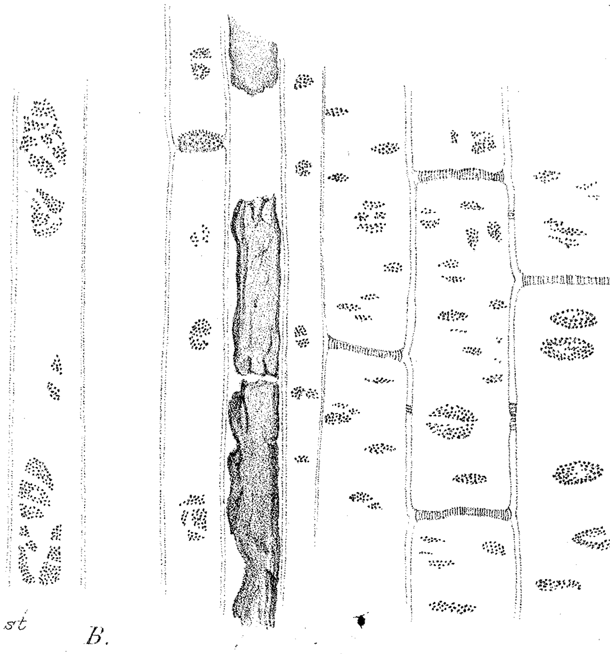

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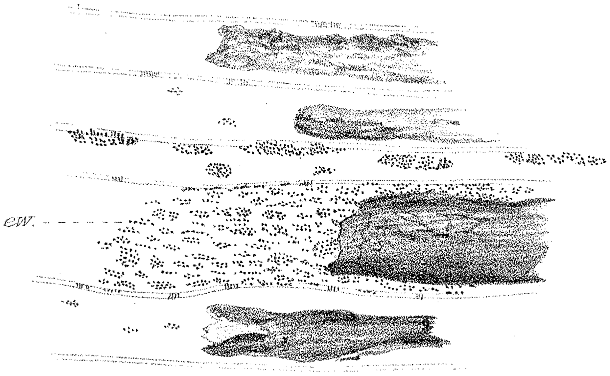

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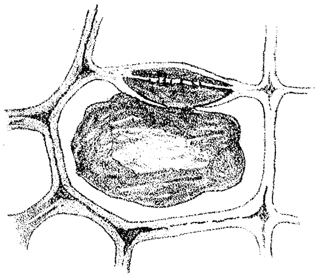

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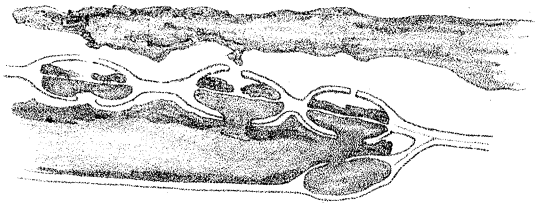

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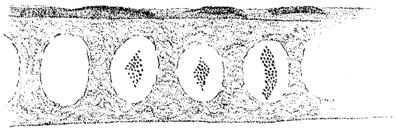

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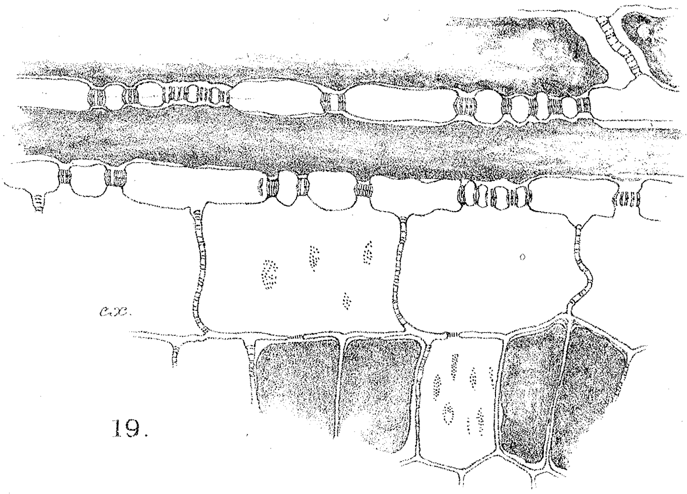

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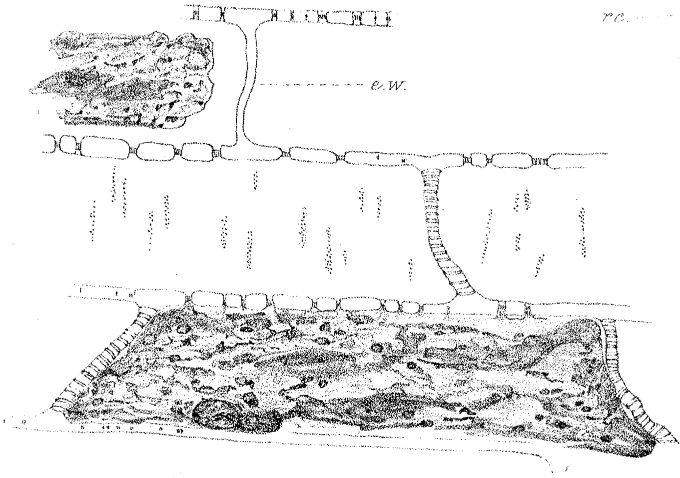

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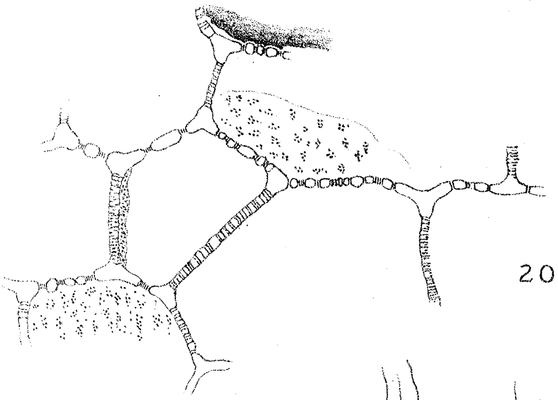

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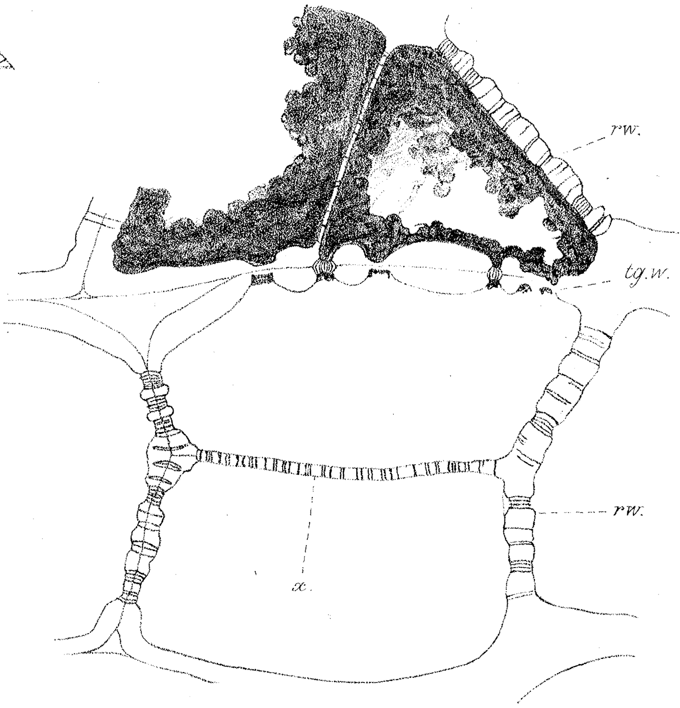

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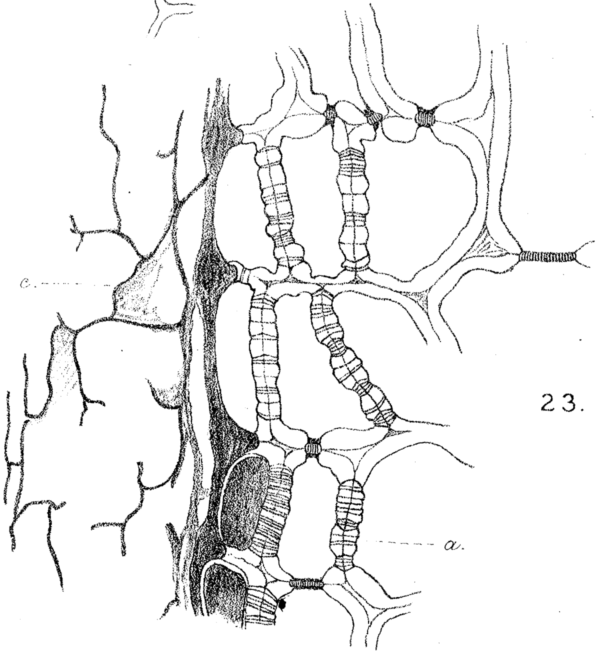

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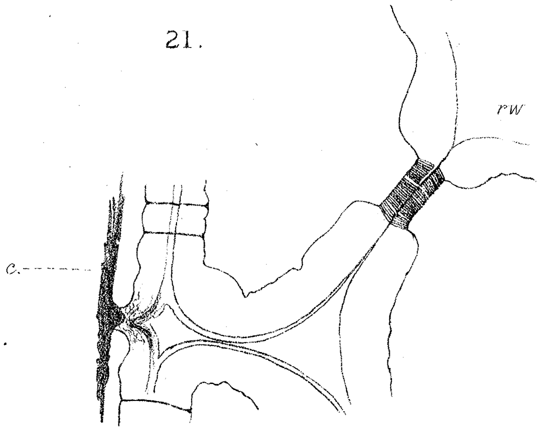

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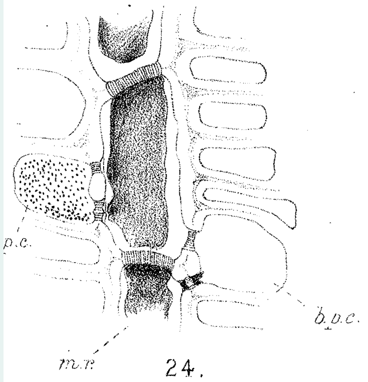

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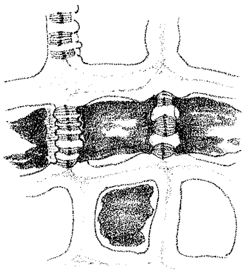

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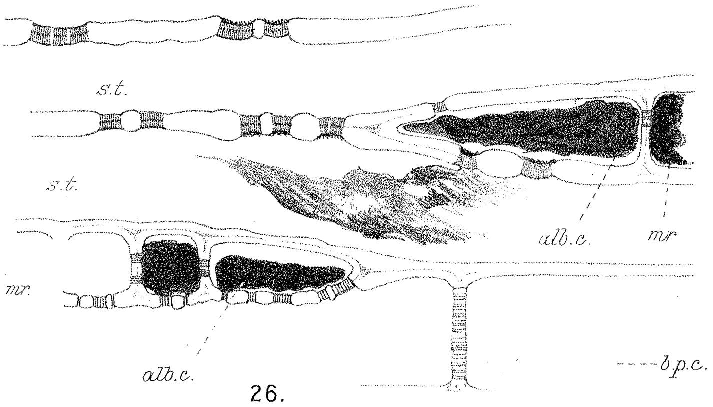

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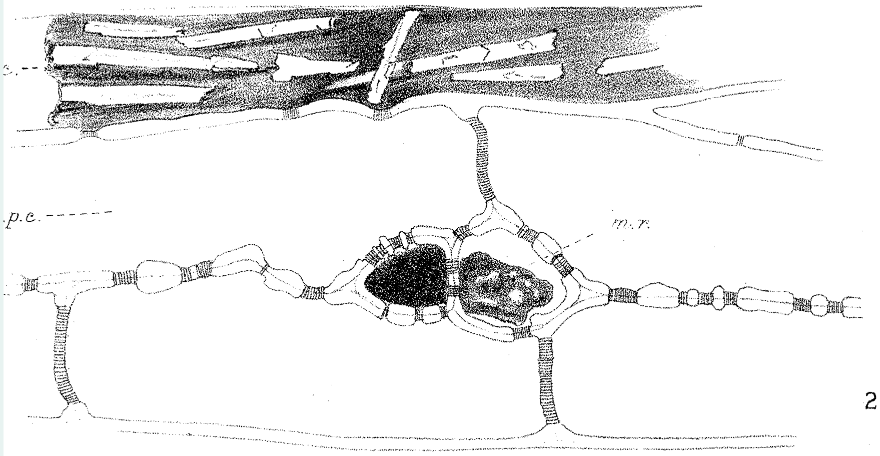

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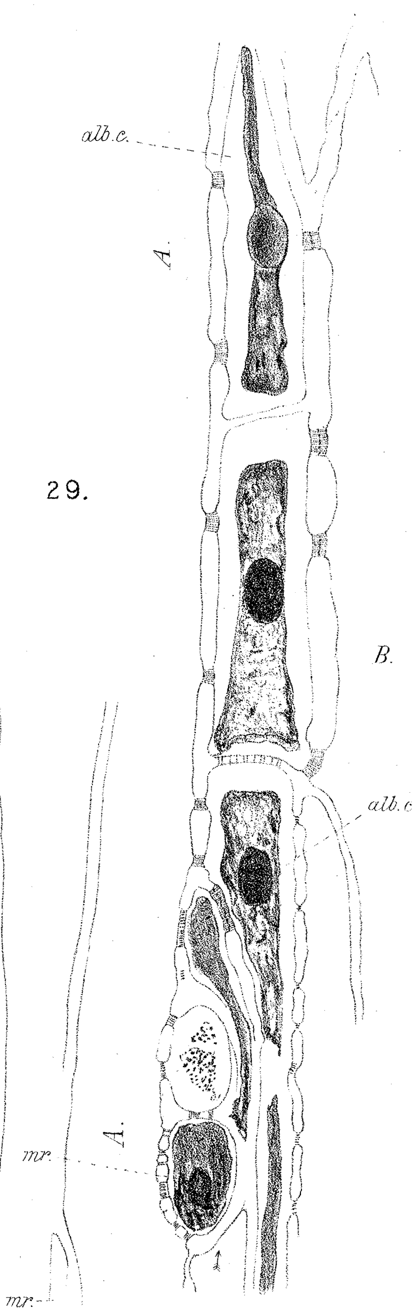

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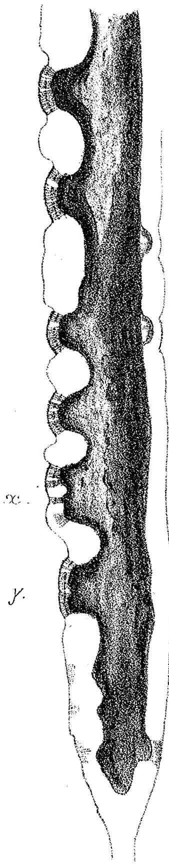

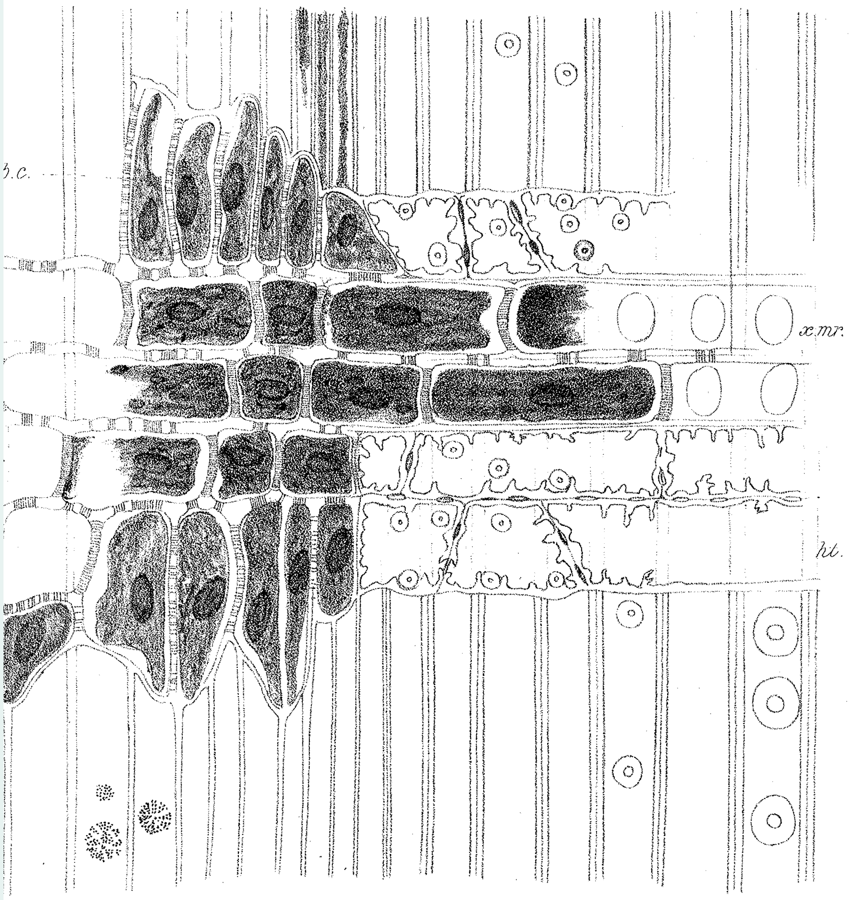

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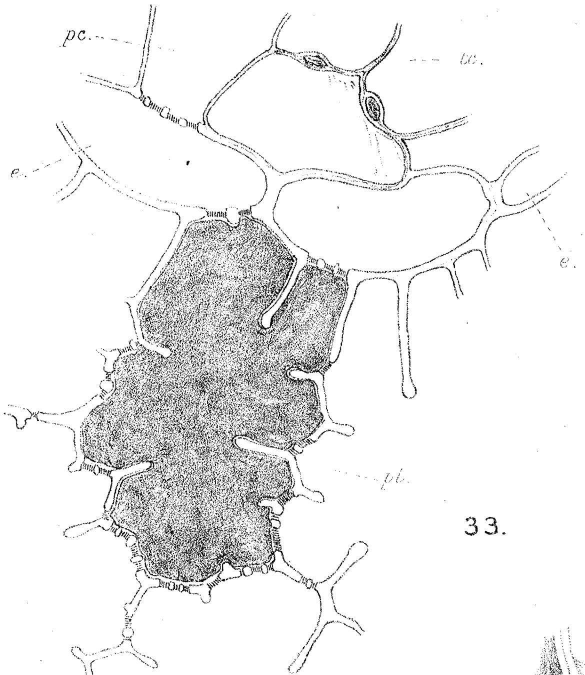

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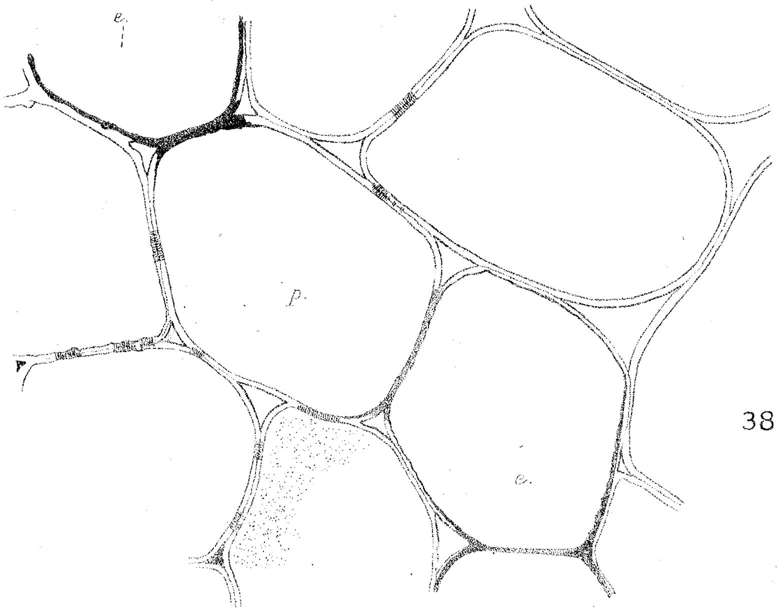

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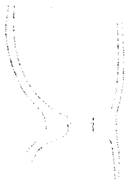

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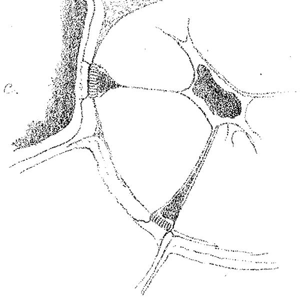

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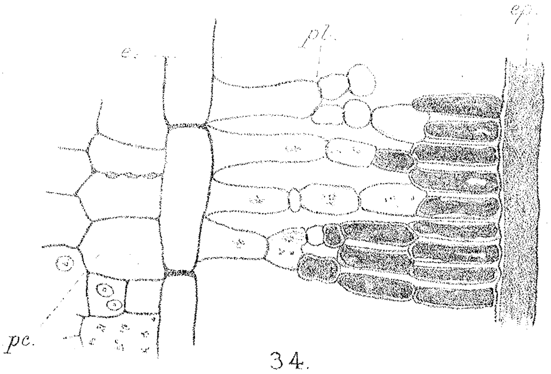

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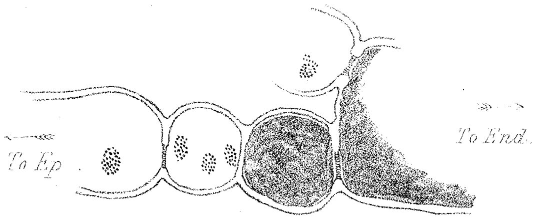

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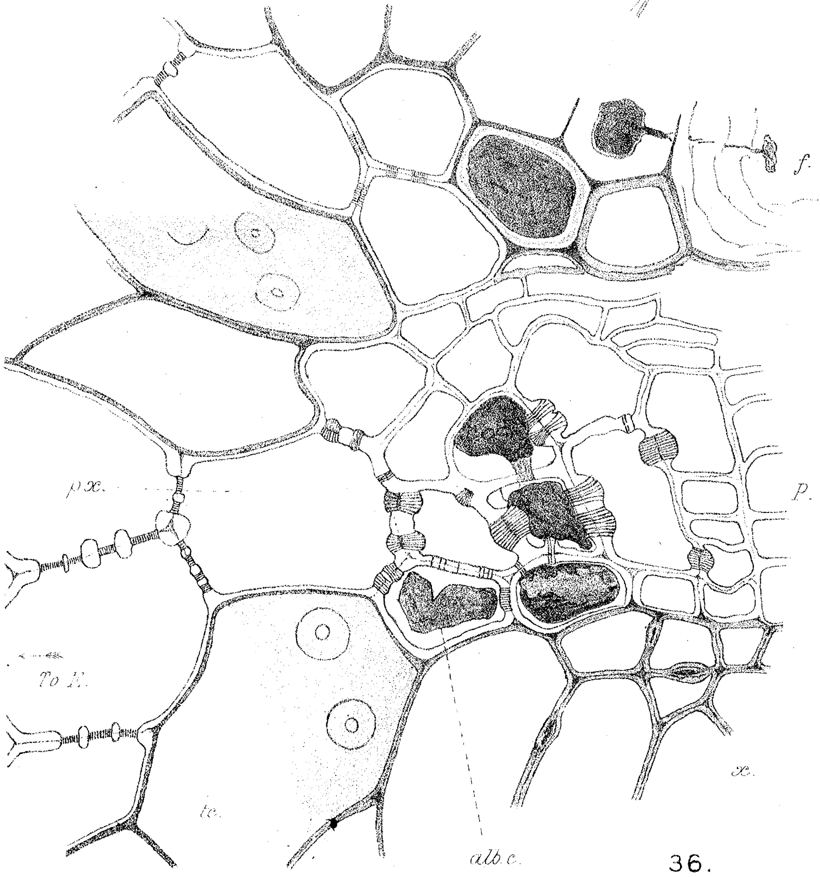

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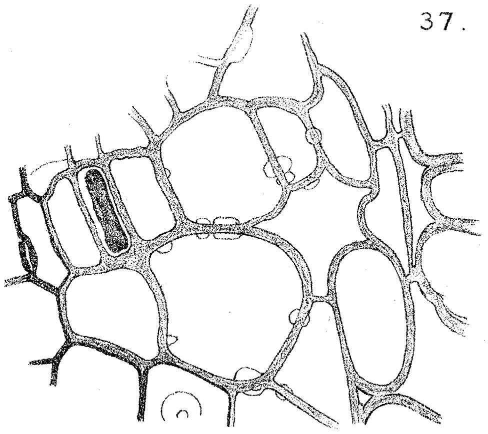

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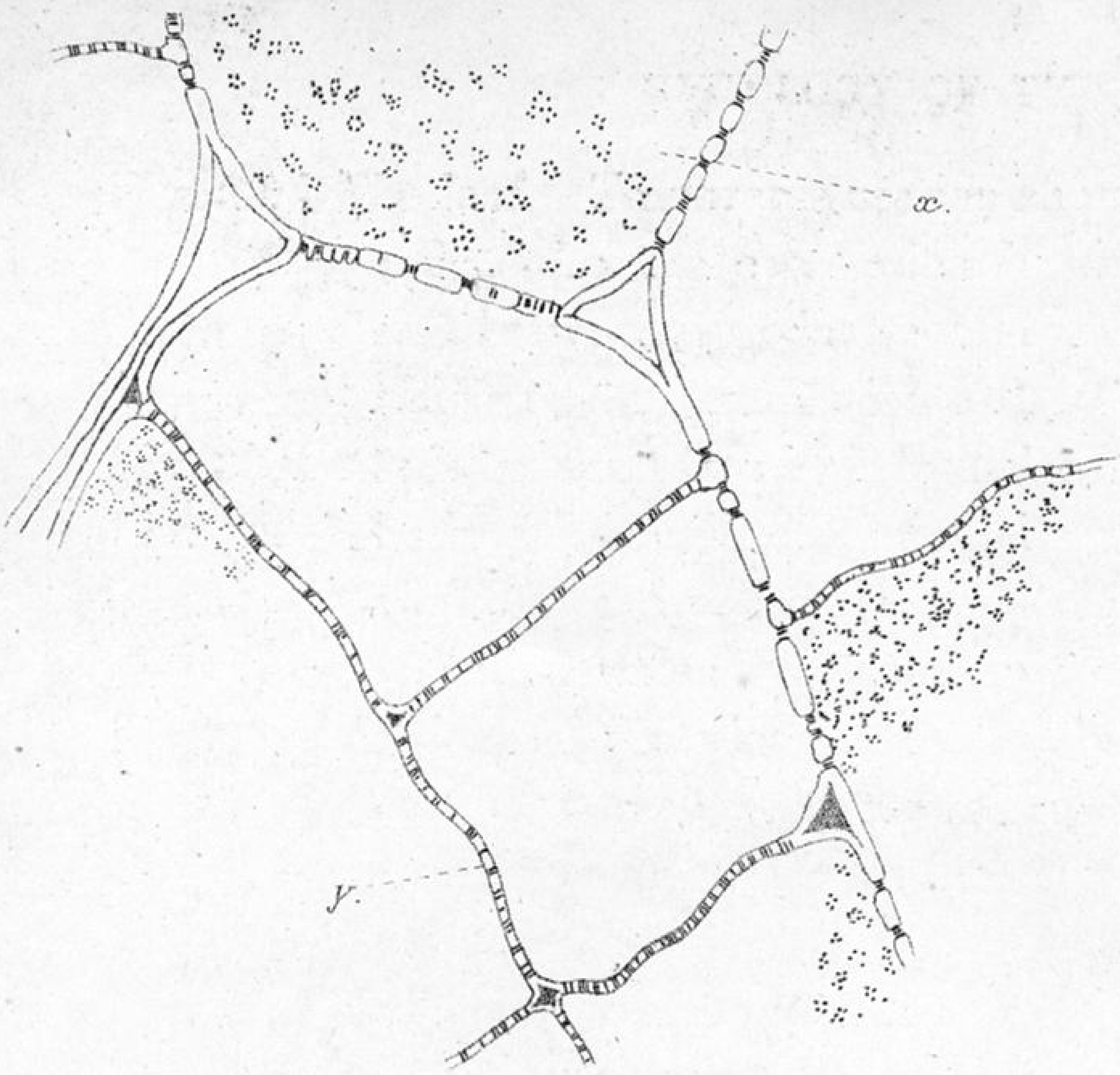
A. S. Huth, Lith^{r} London.



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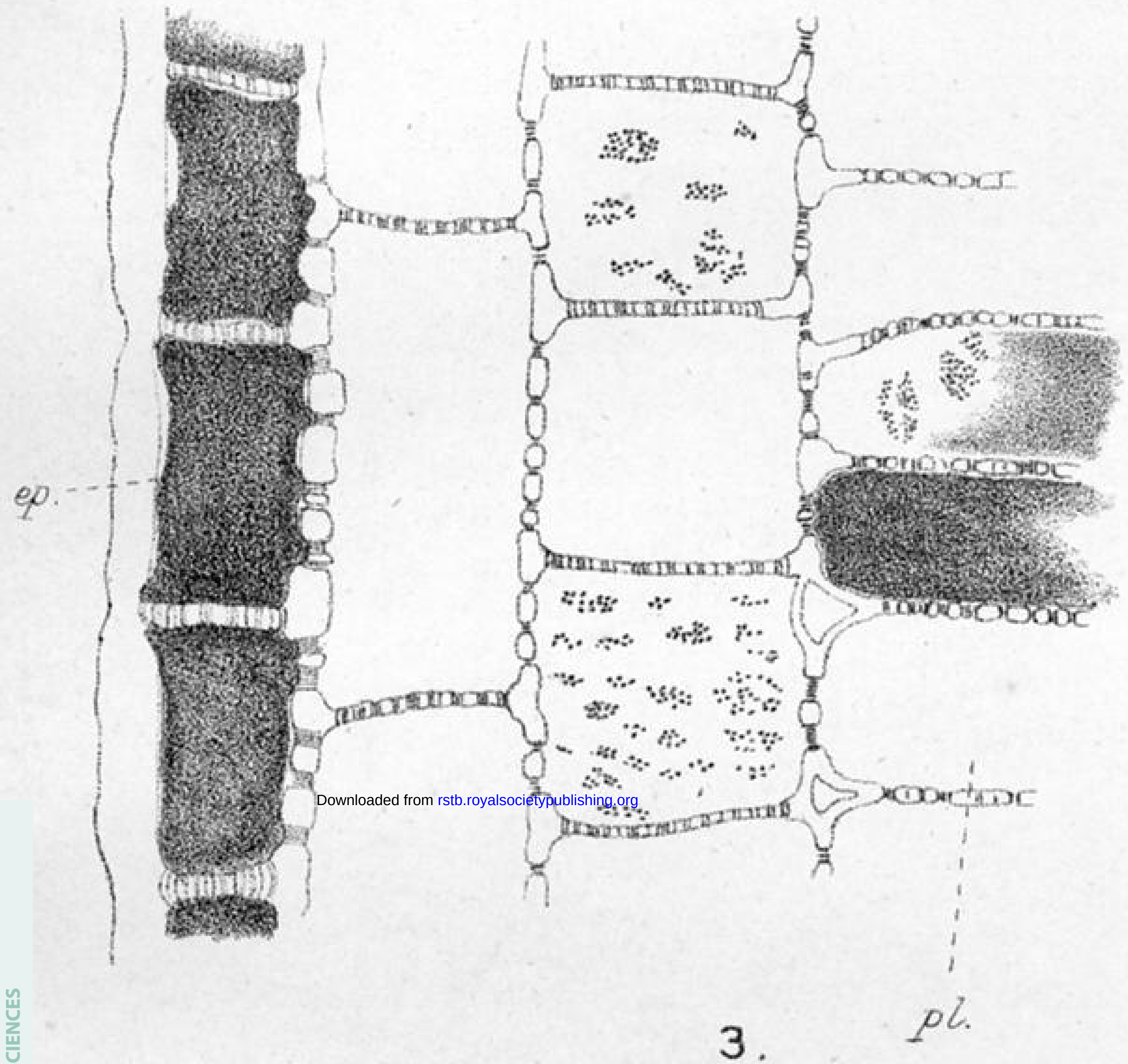

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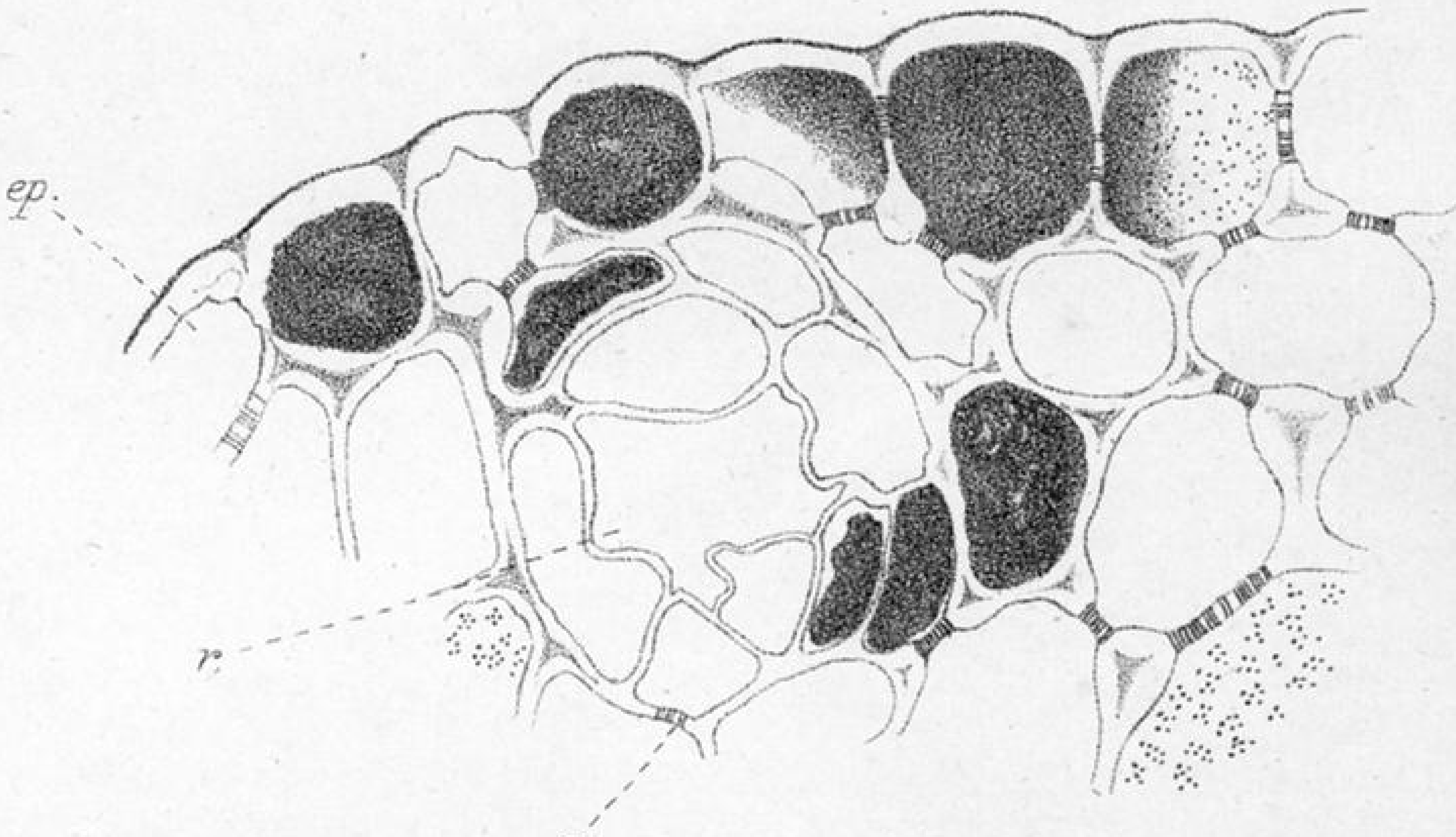

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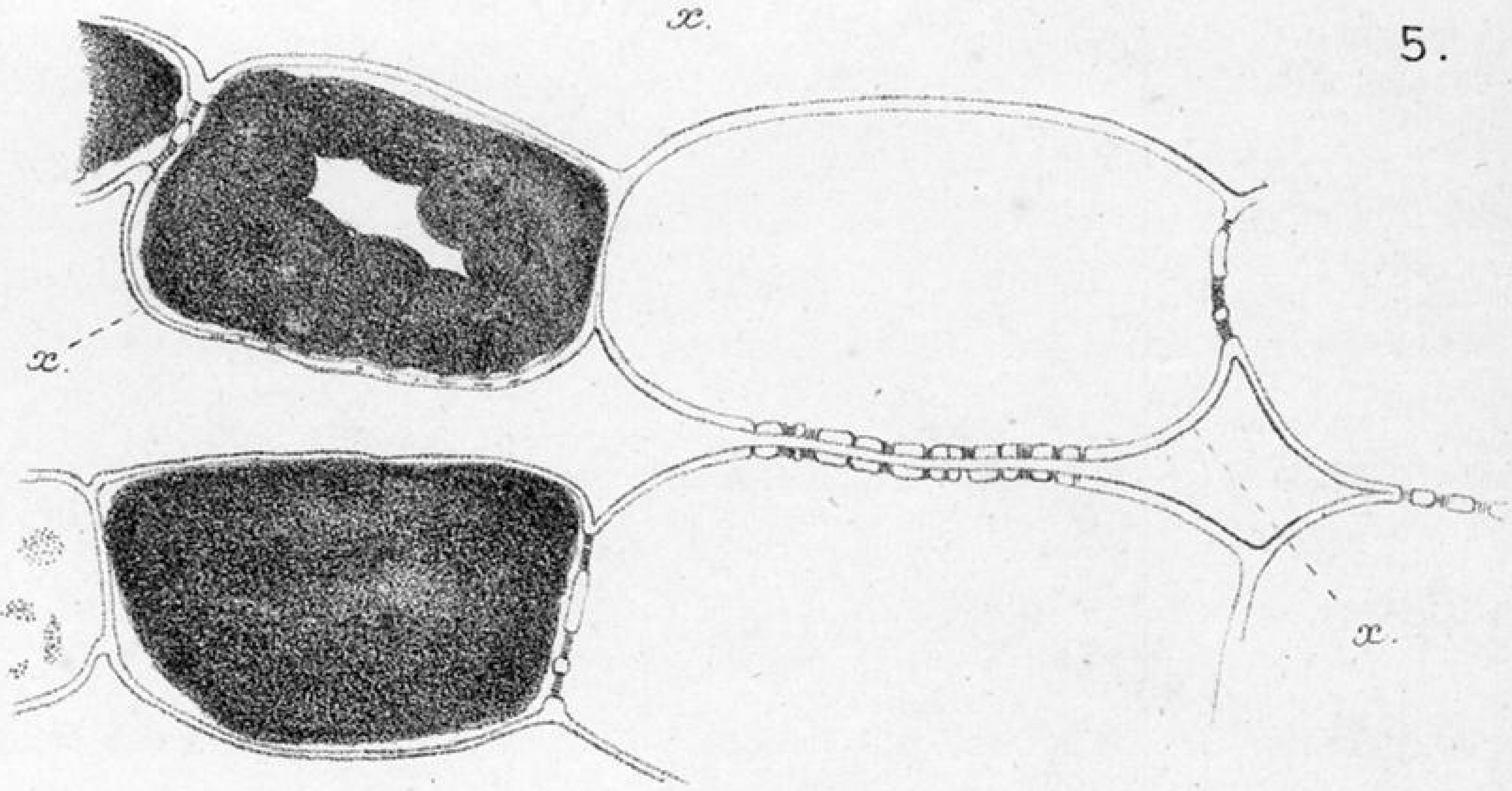

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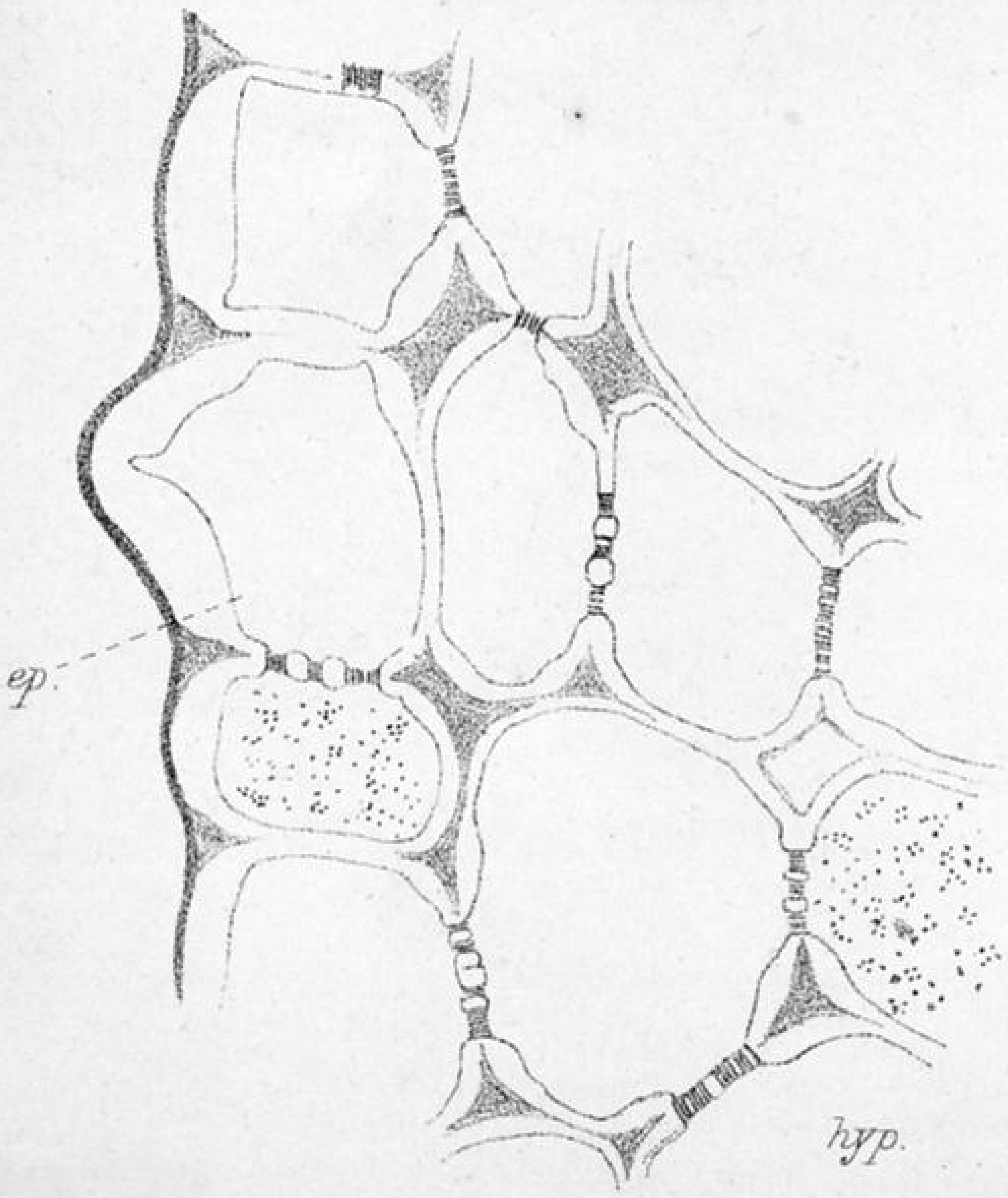

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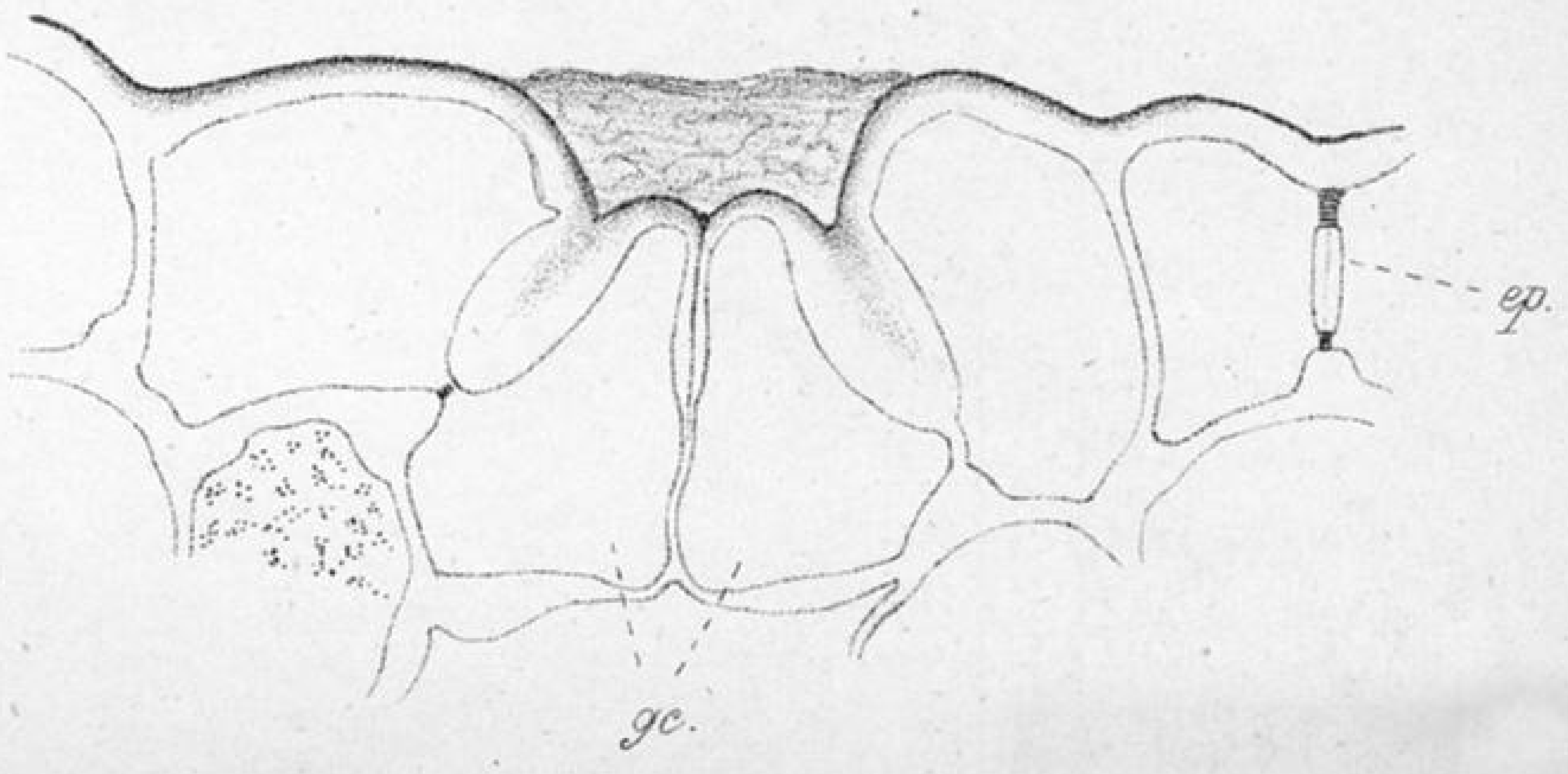

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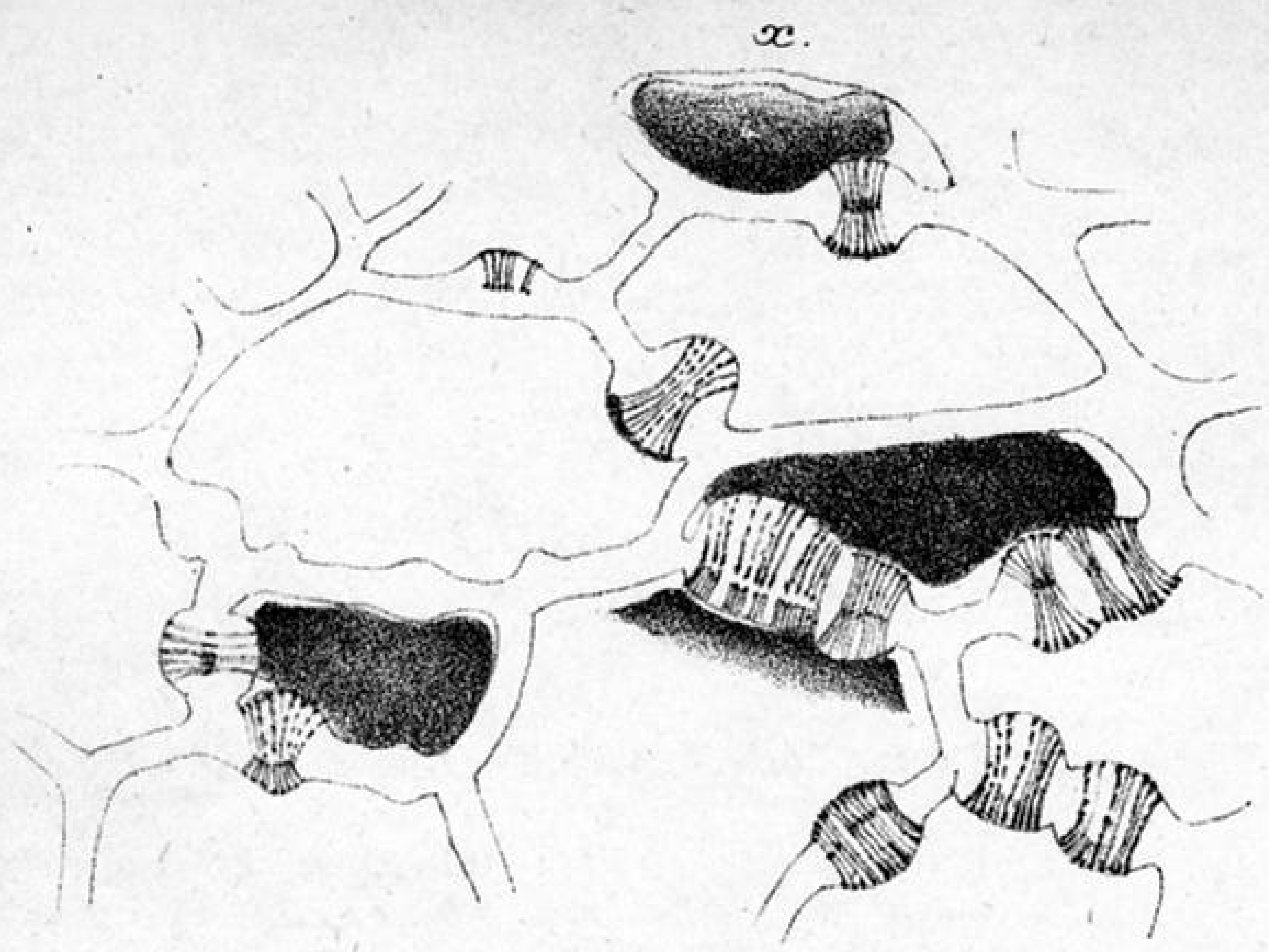

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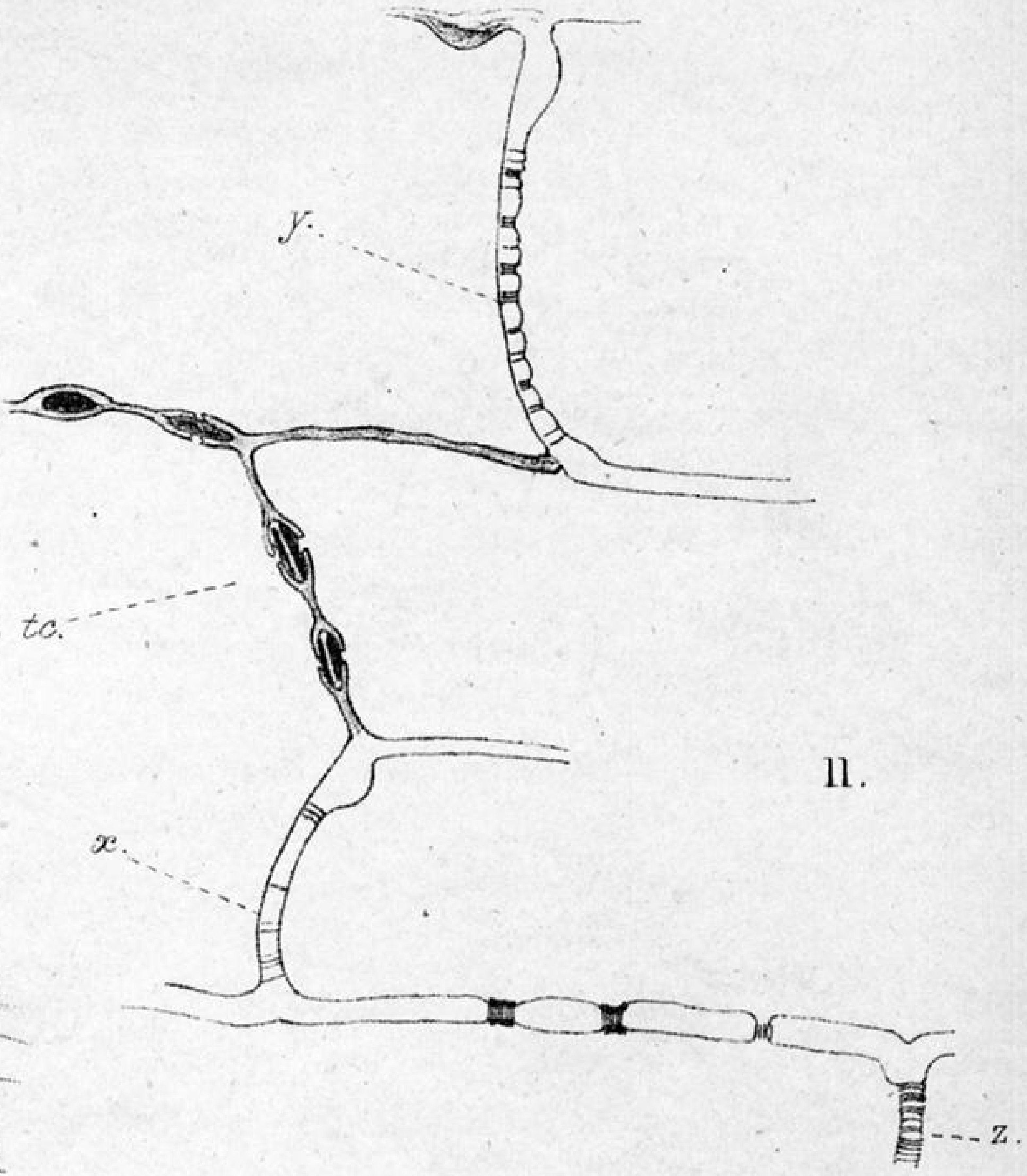

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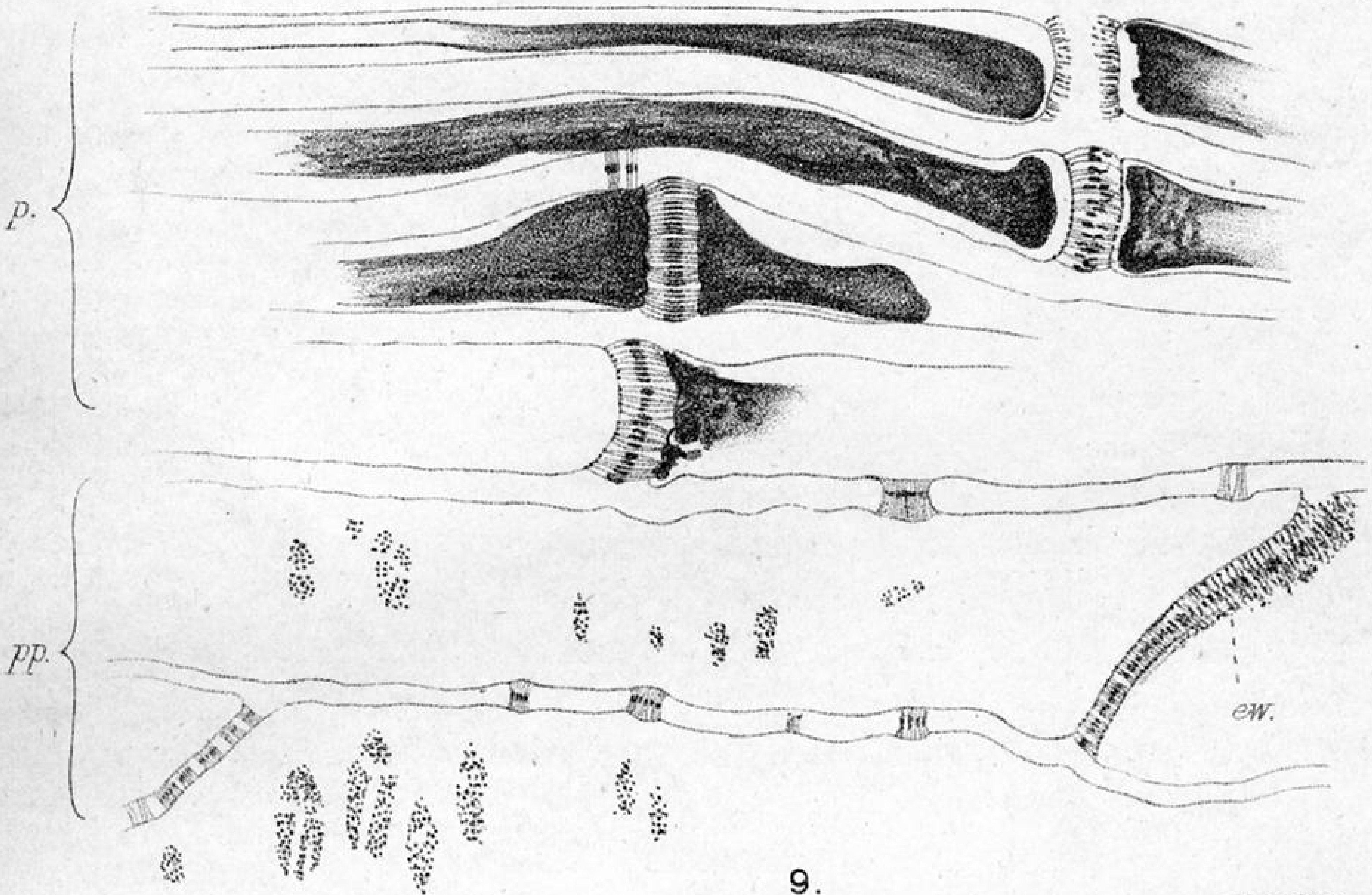

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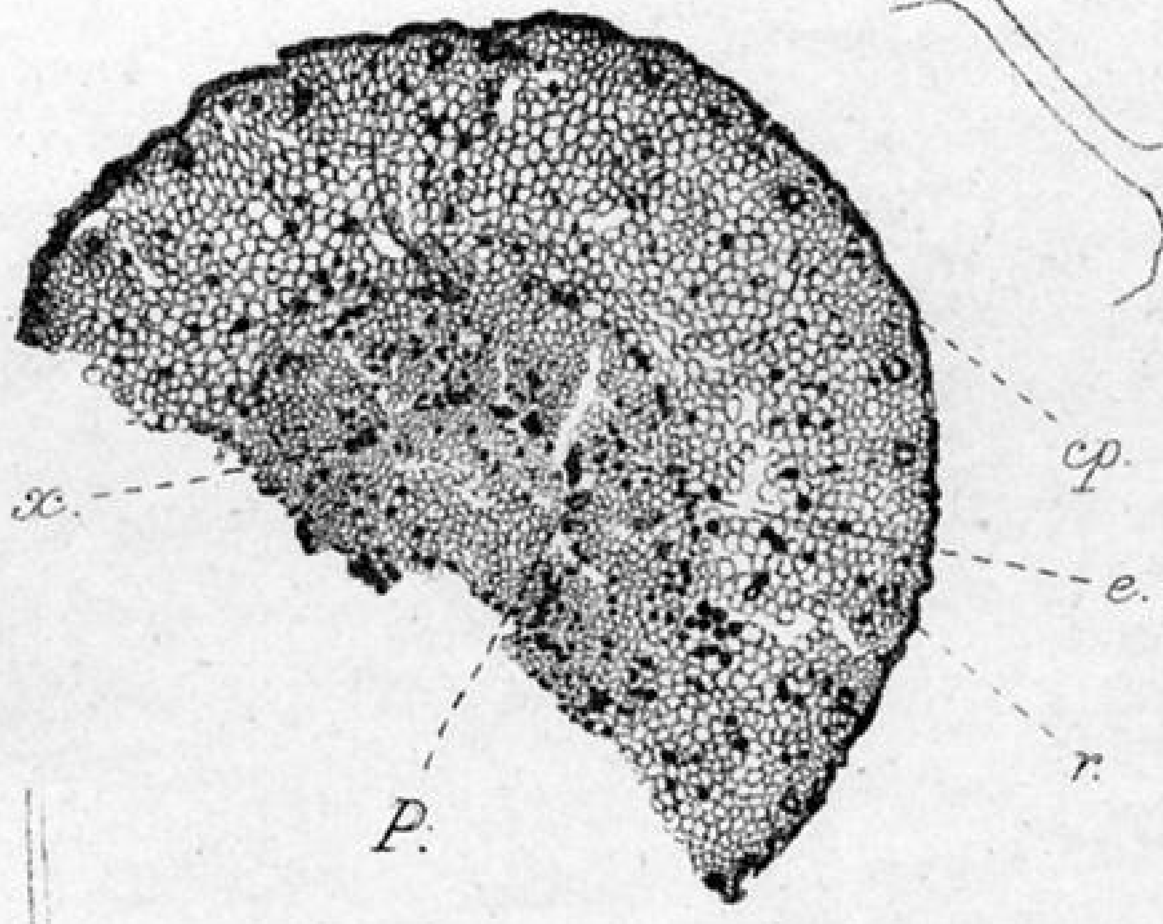

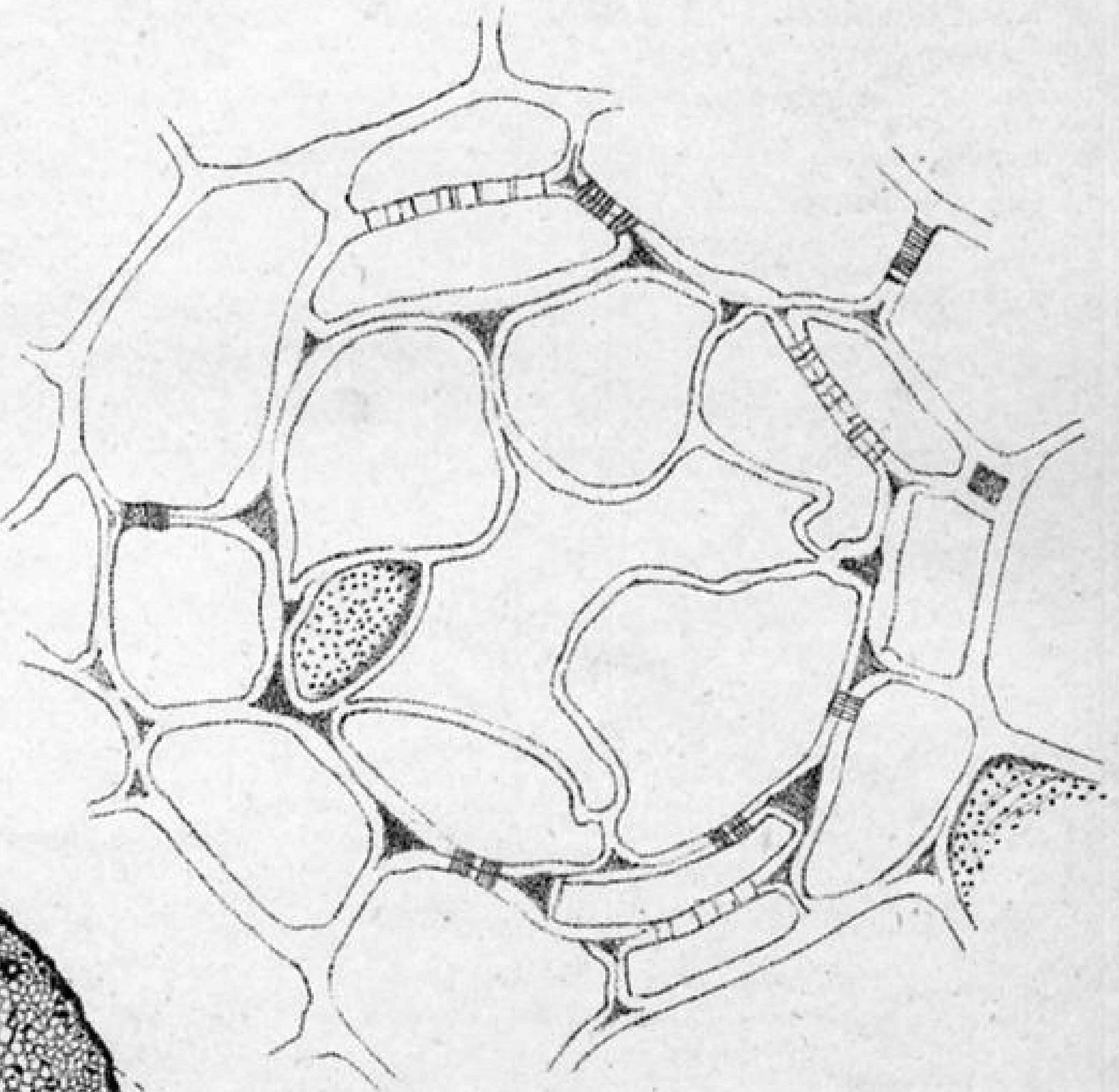

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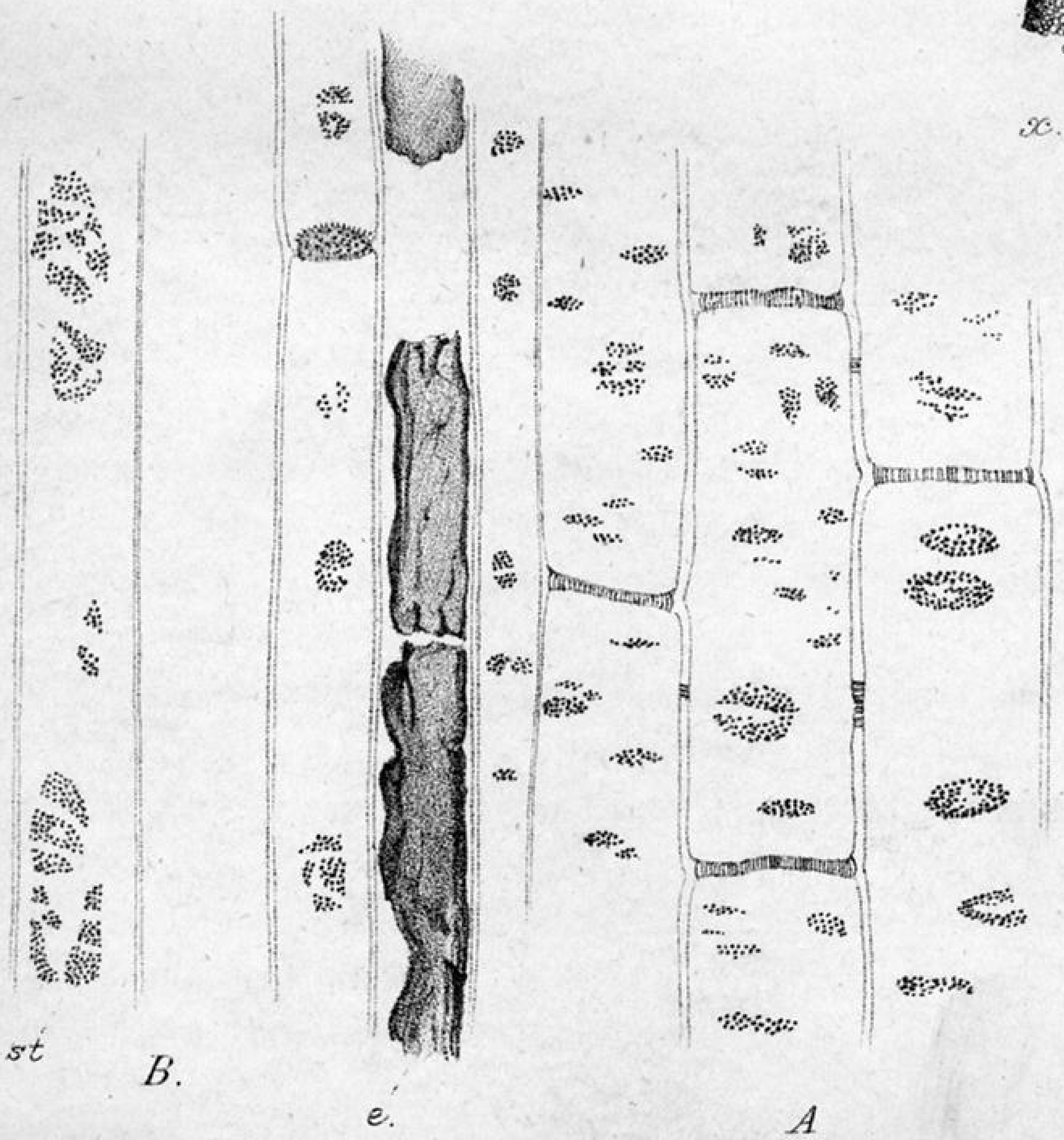

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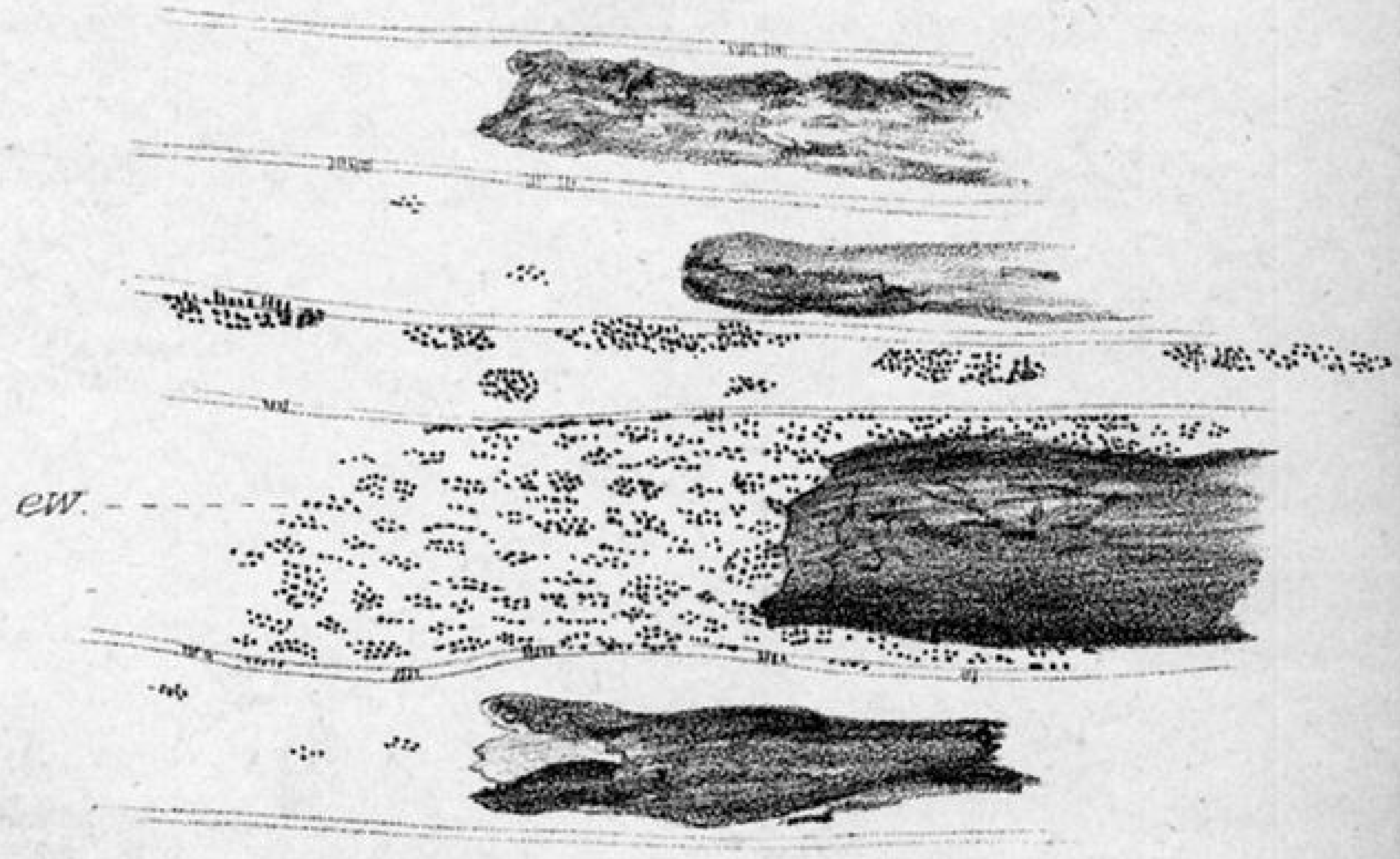

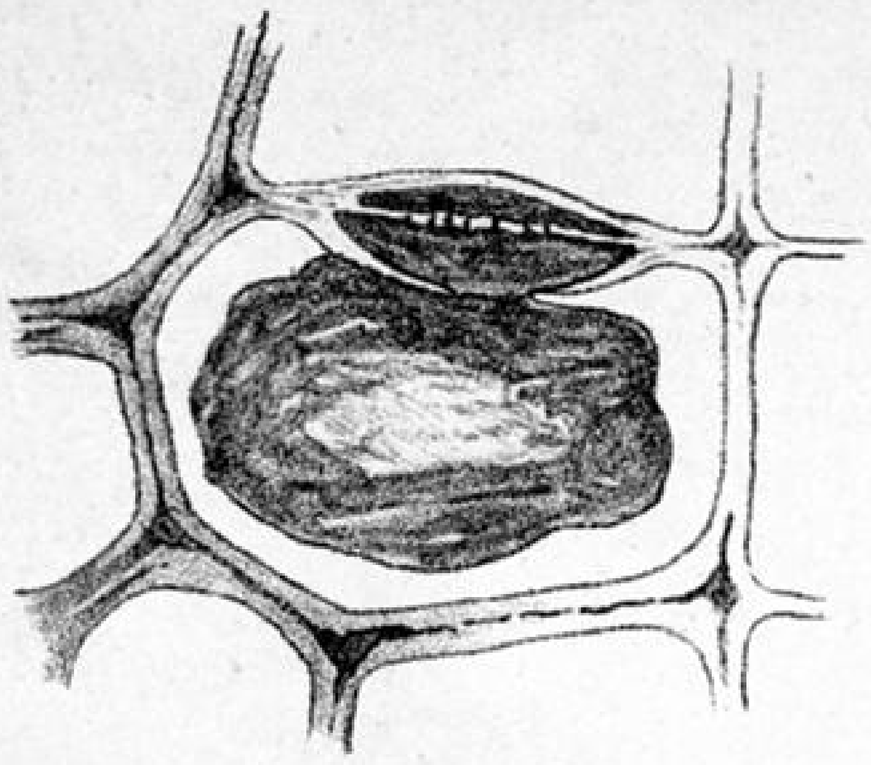

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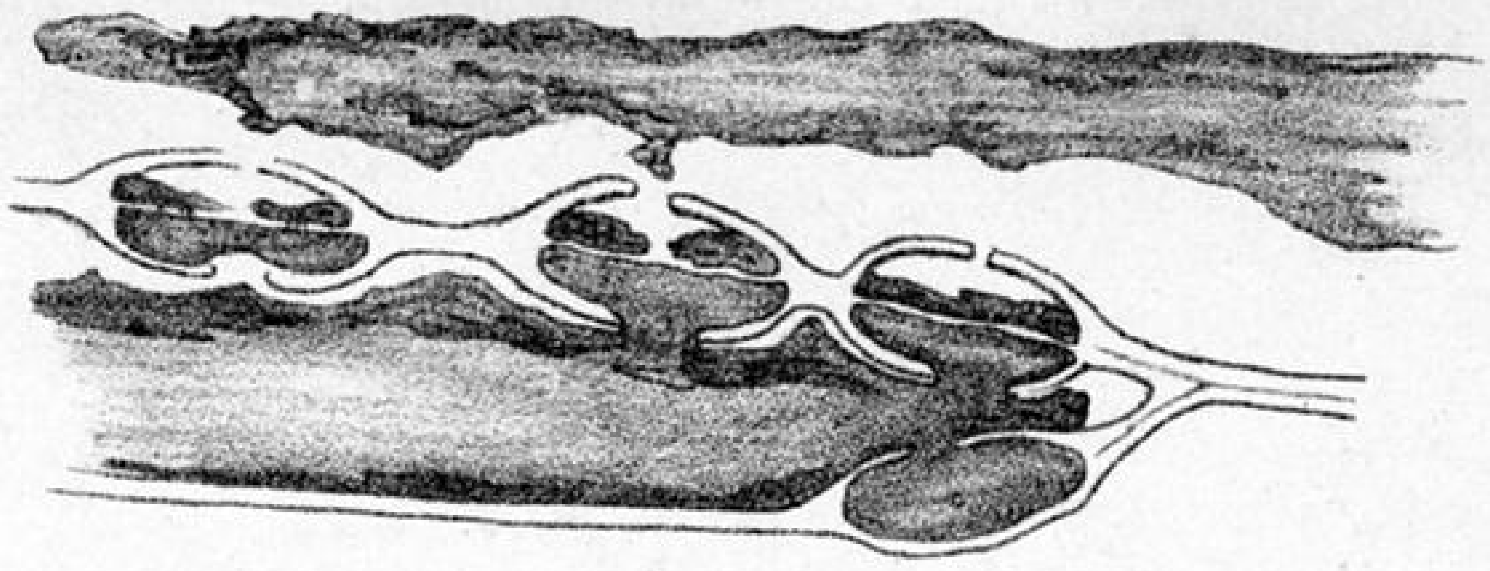

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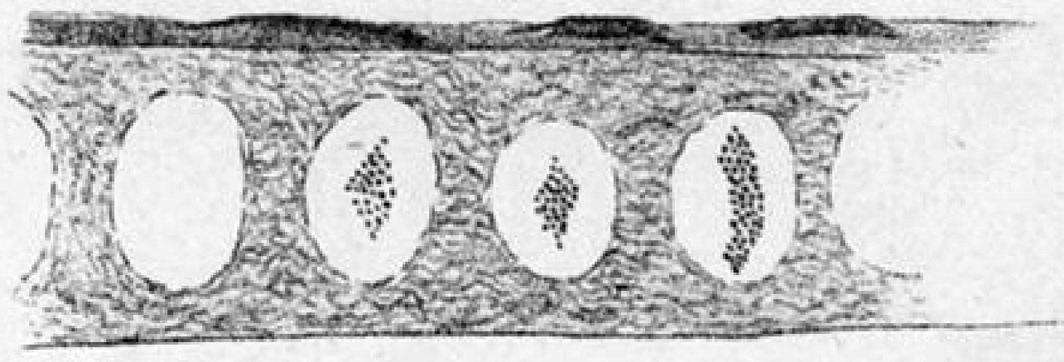

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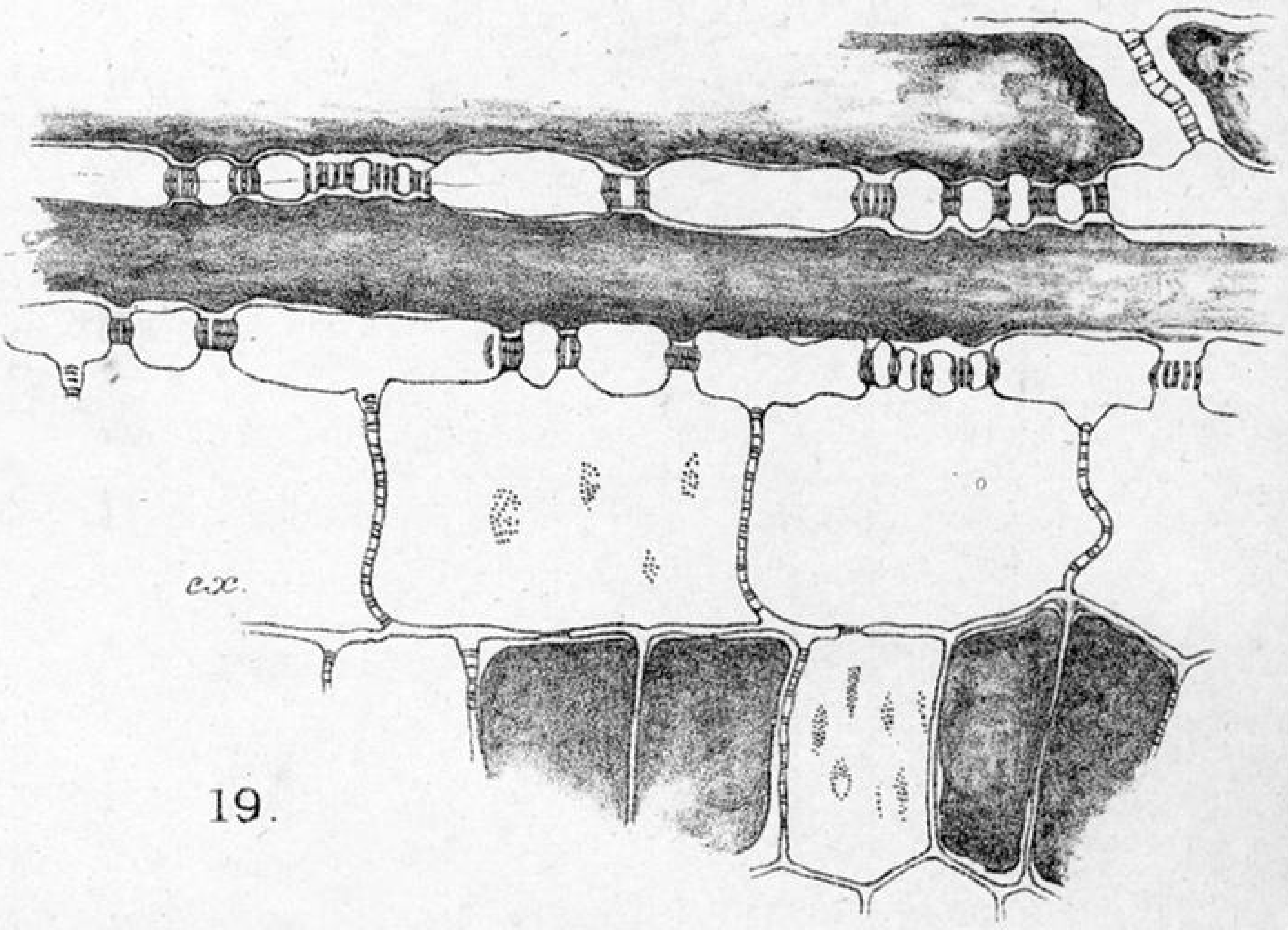

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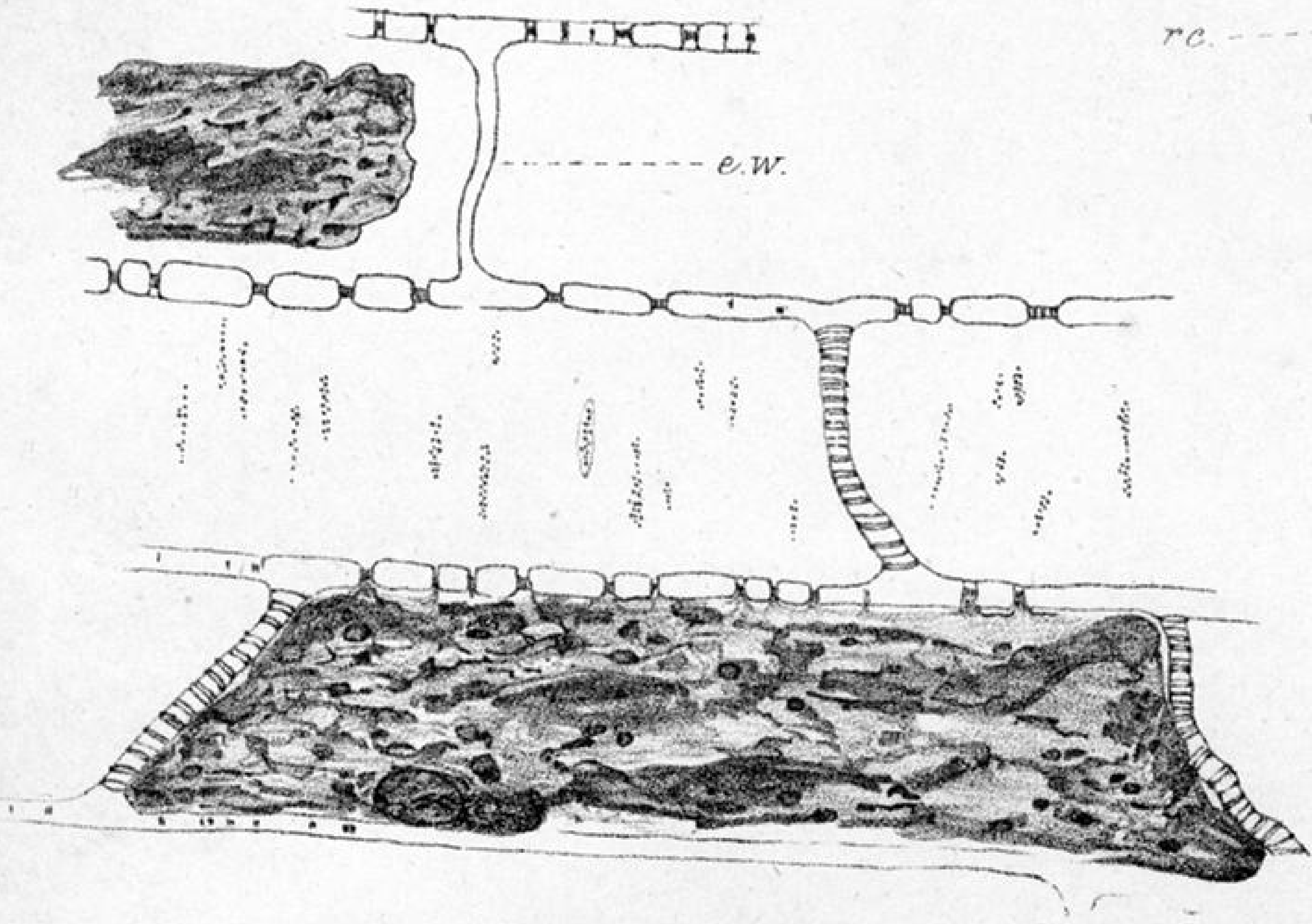

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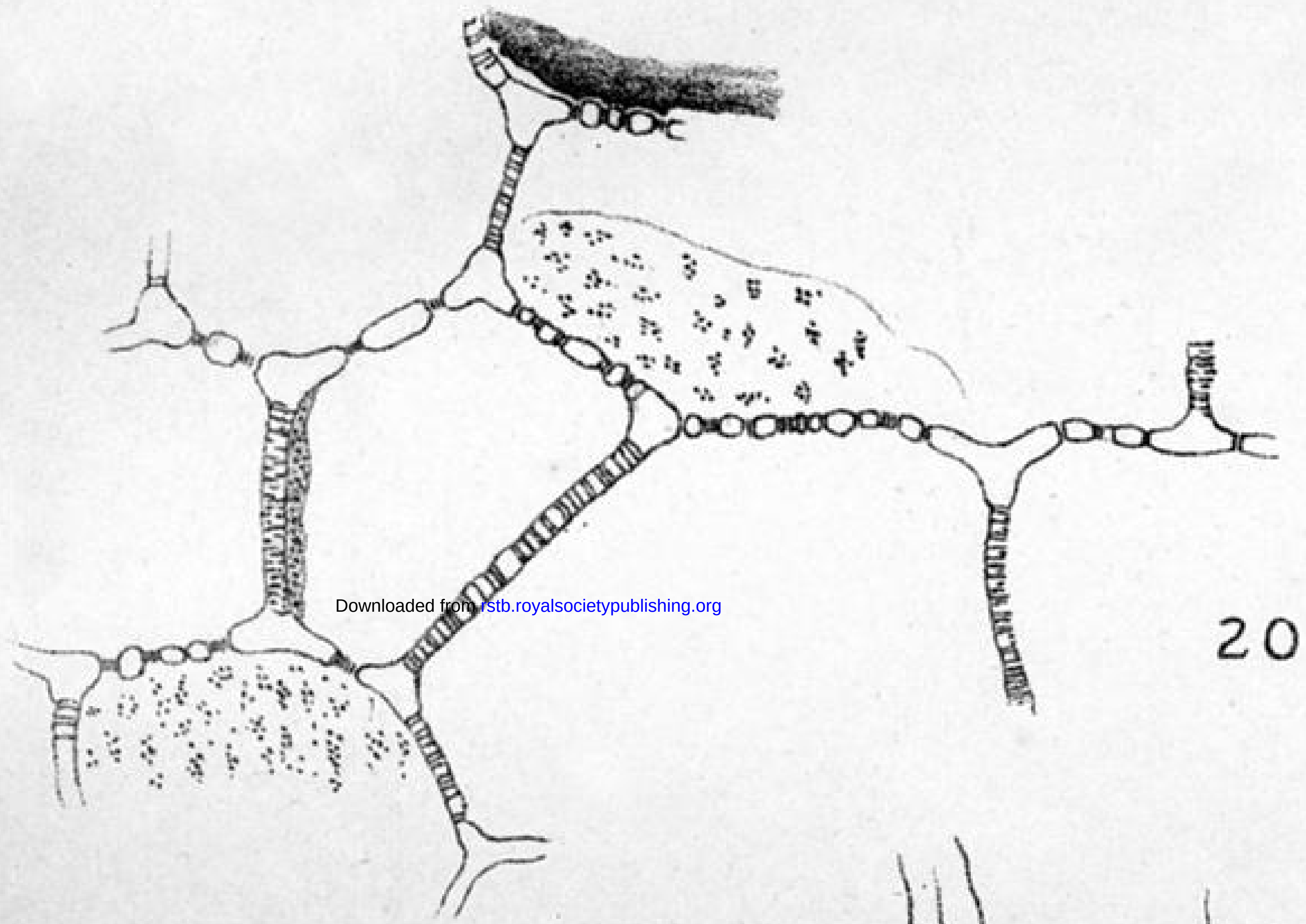

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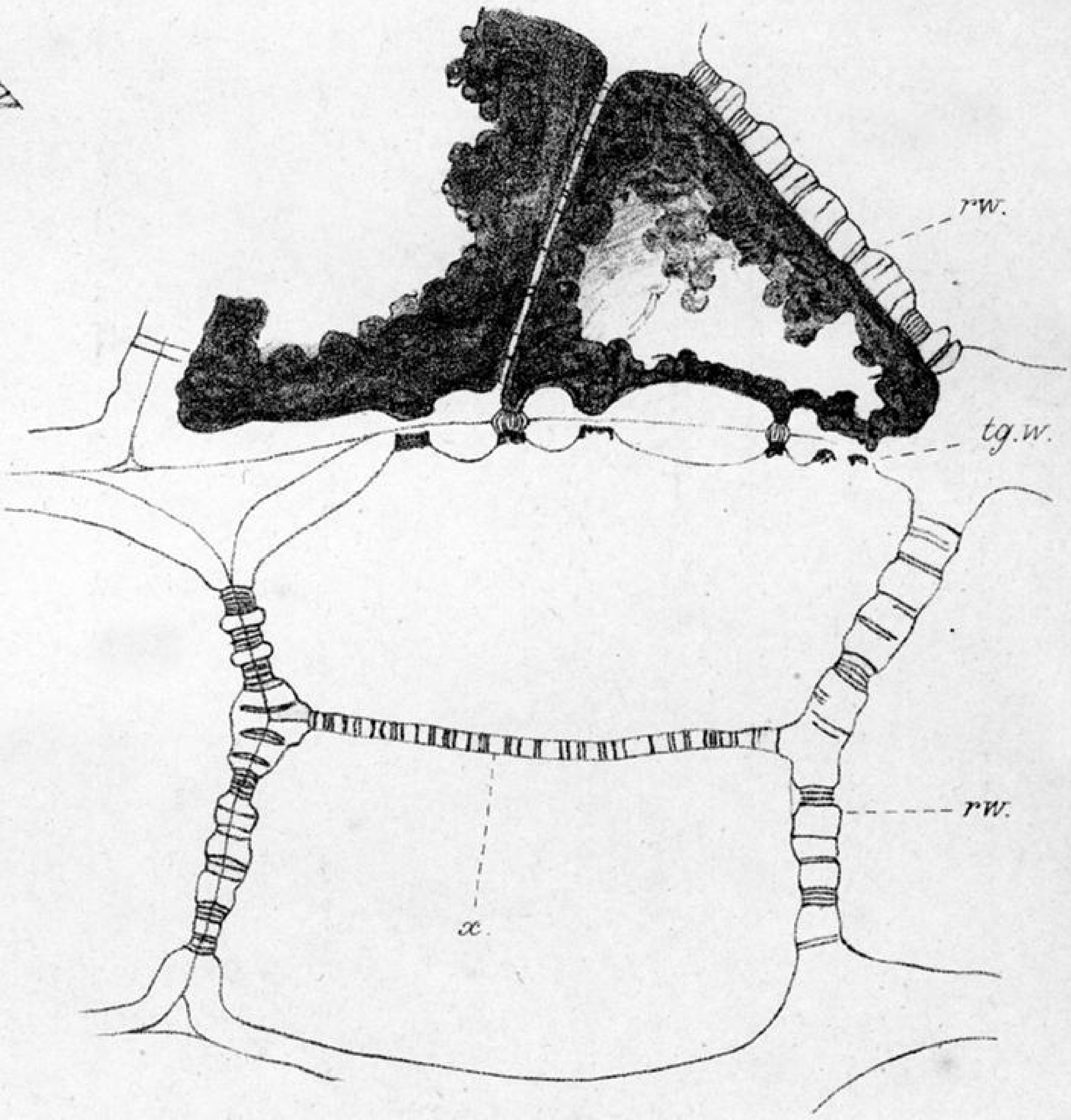

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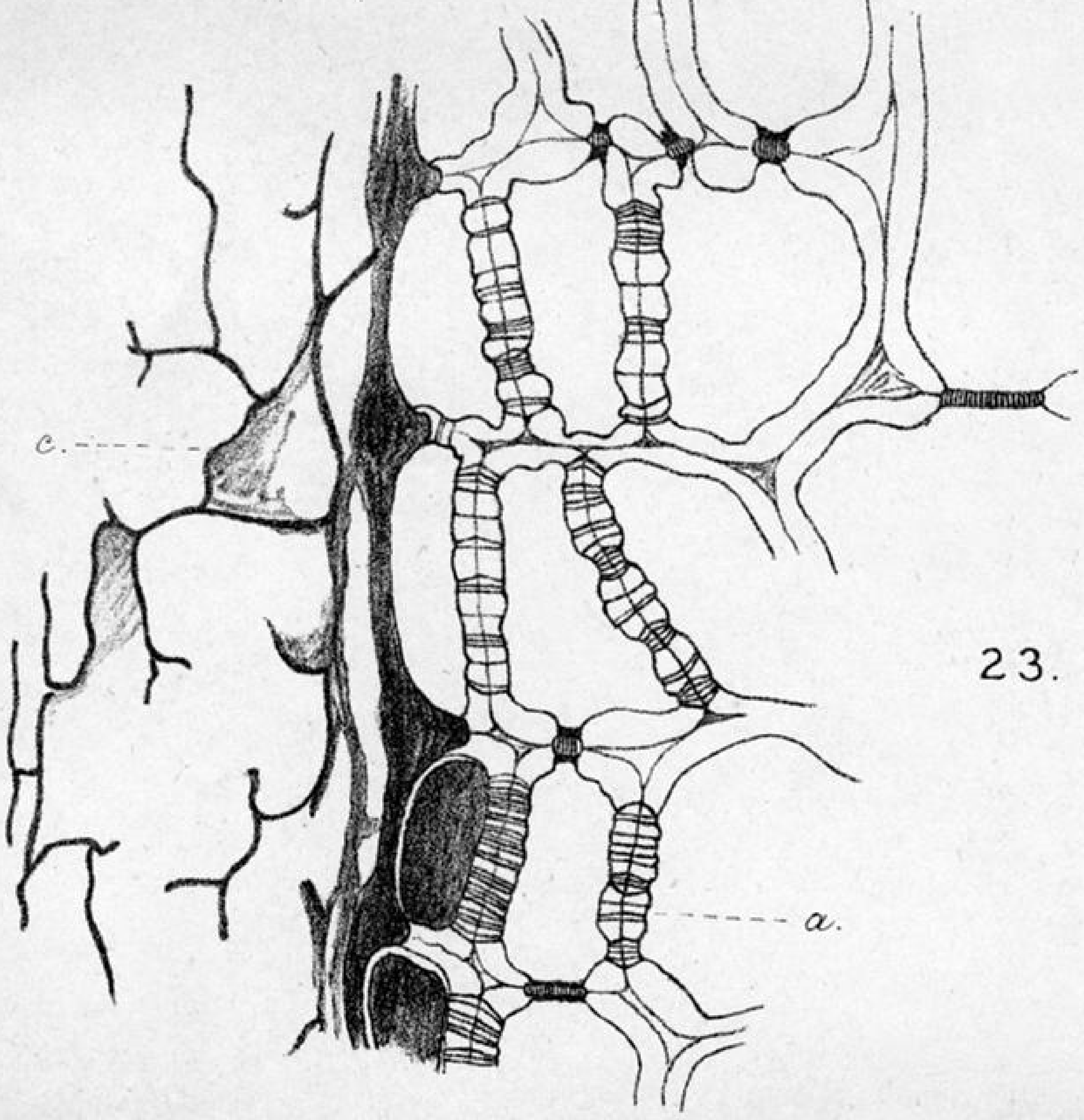

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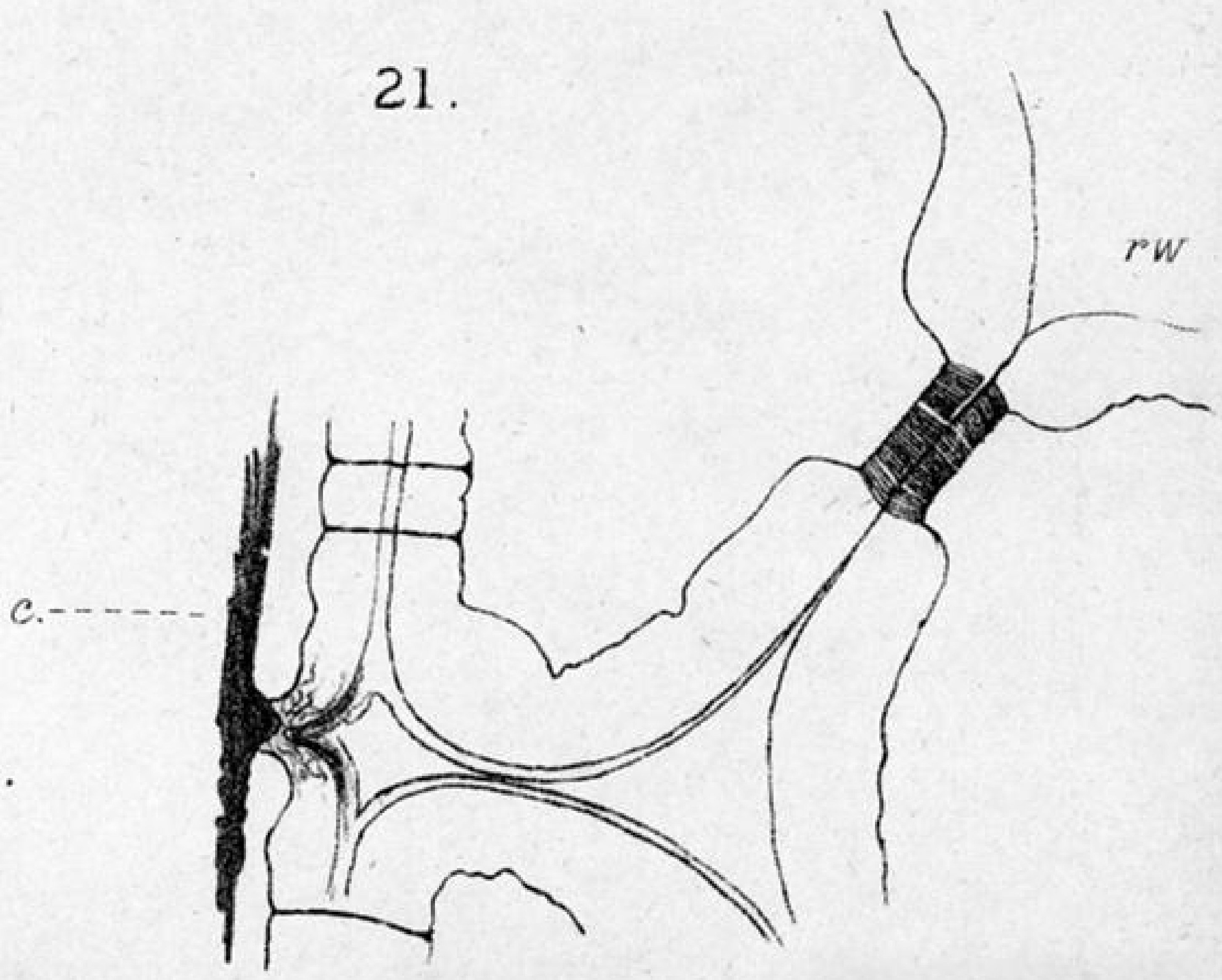

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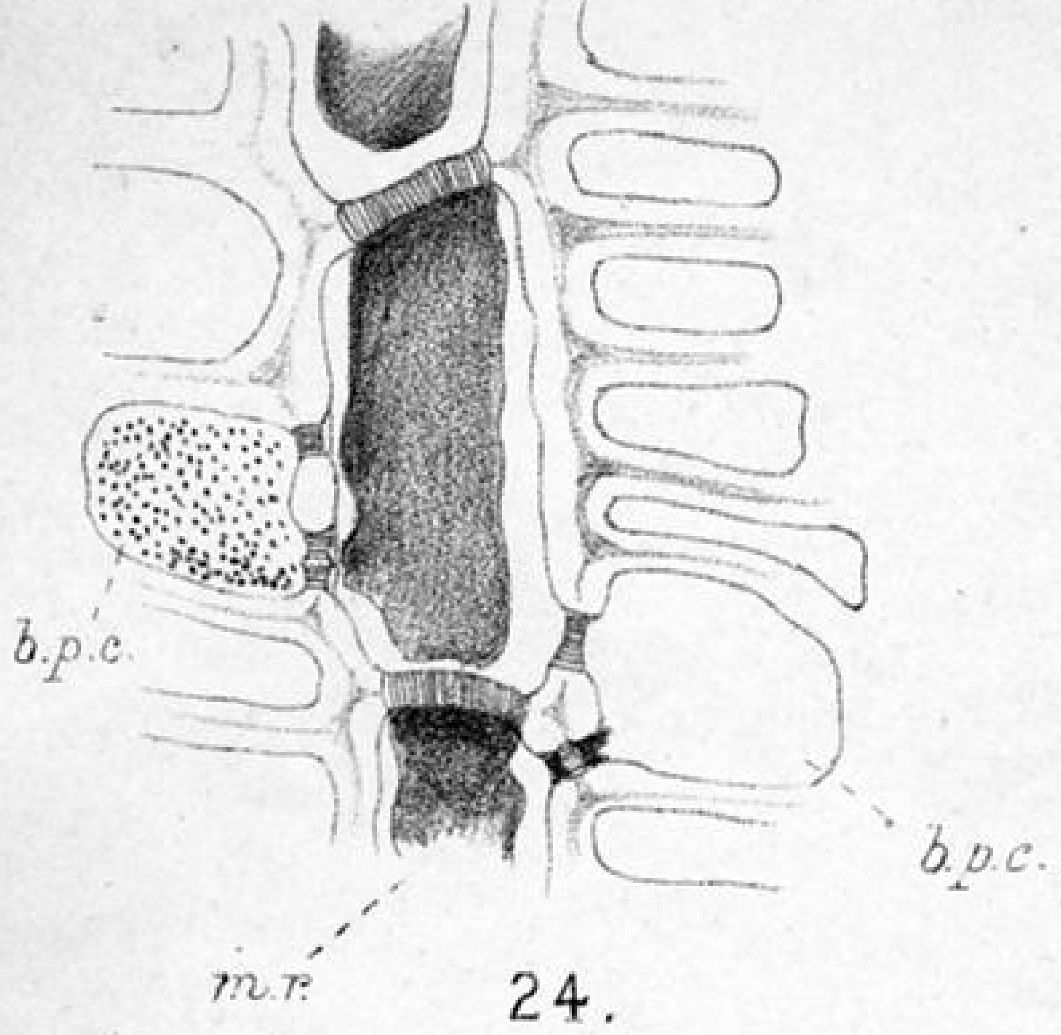

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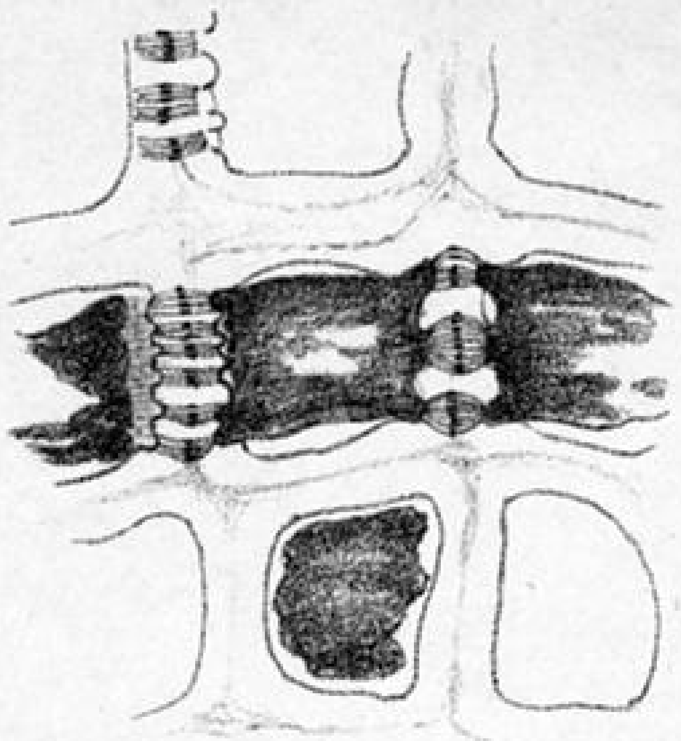

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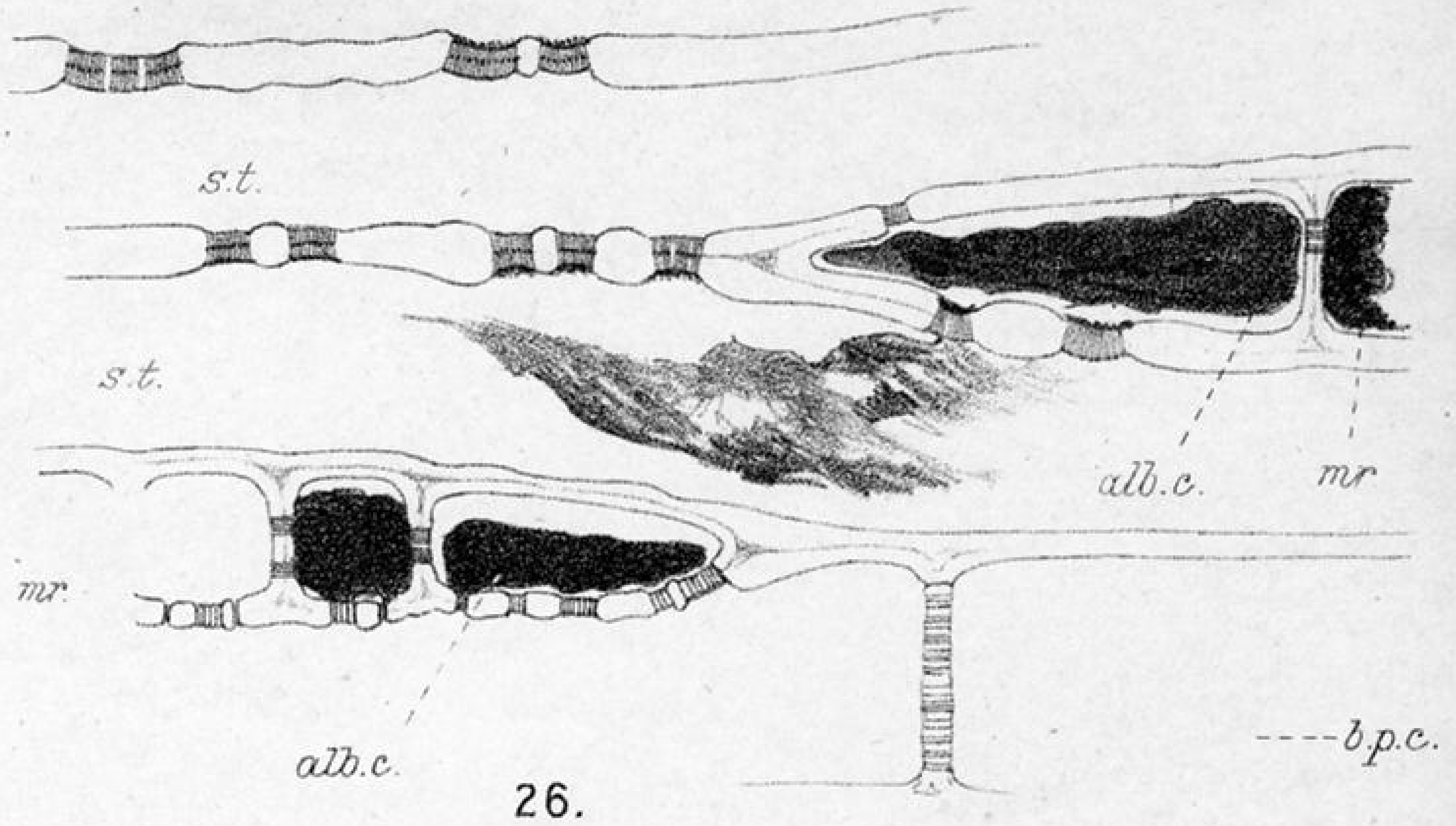

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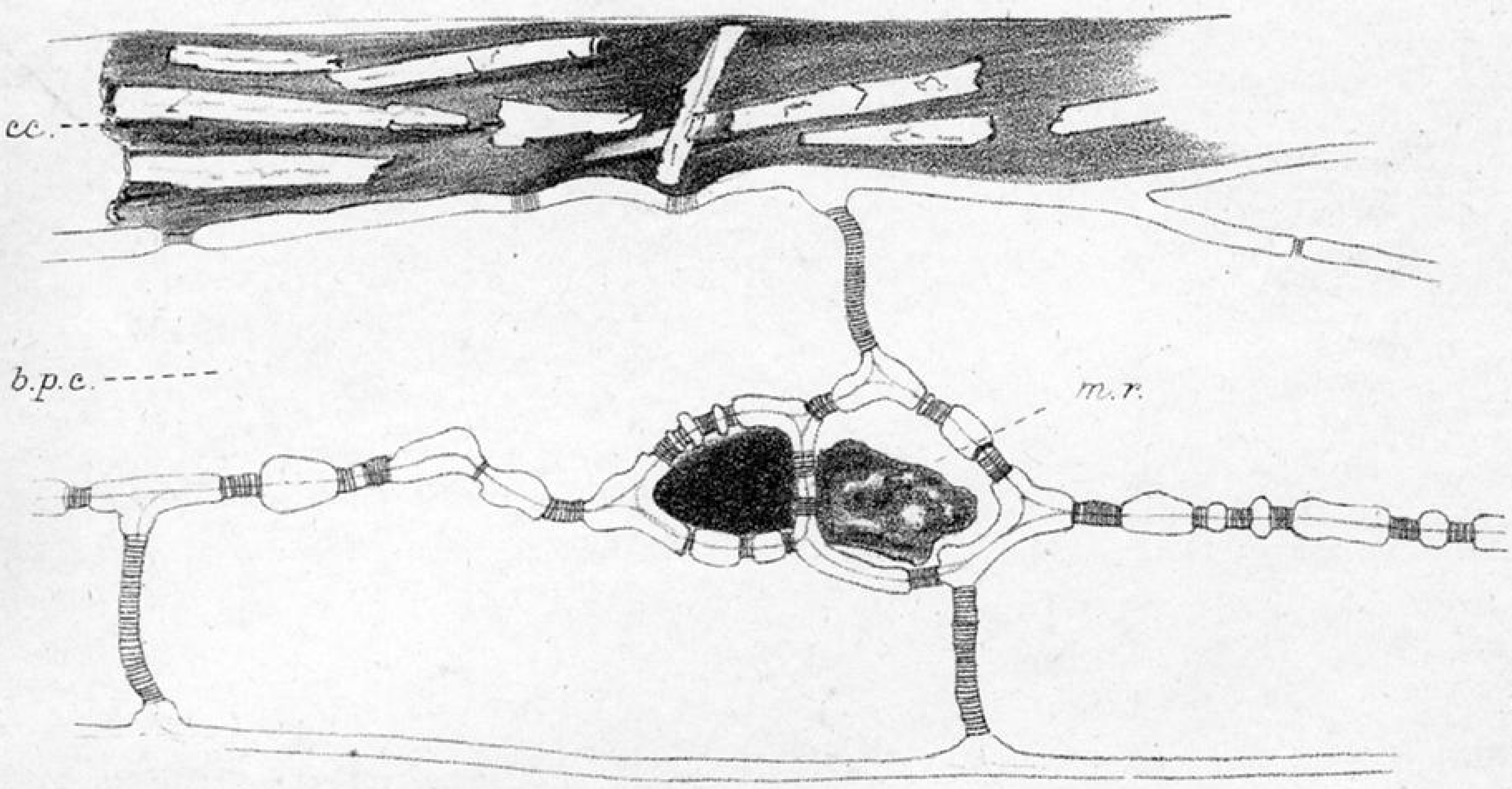

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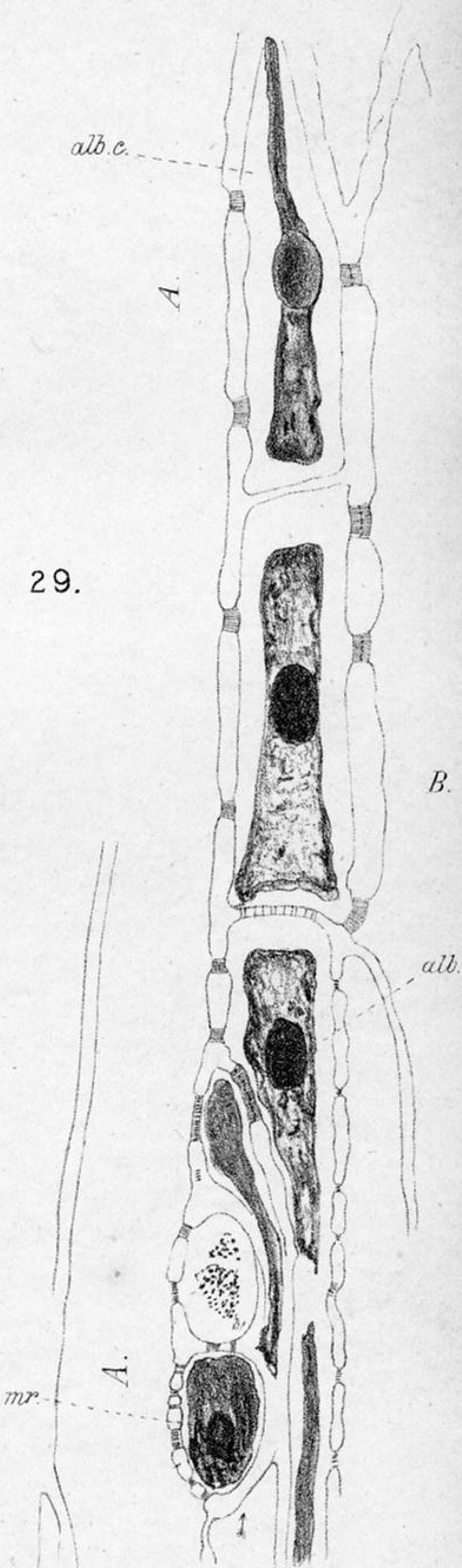

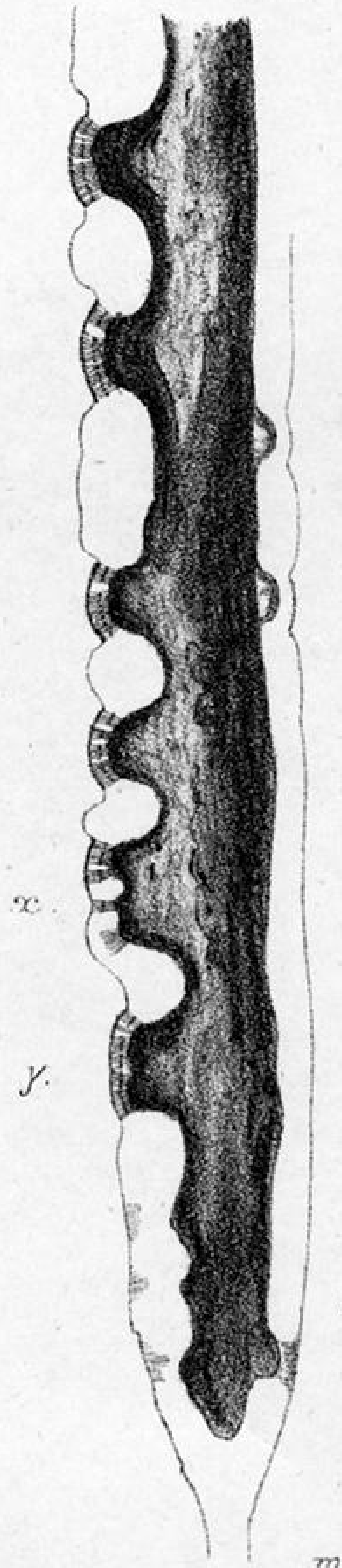

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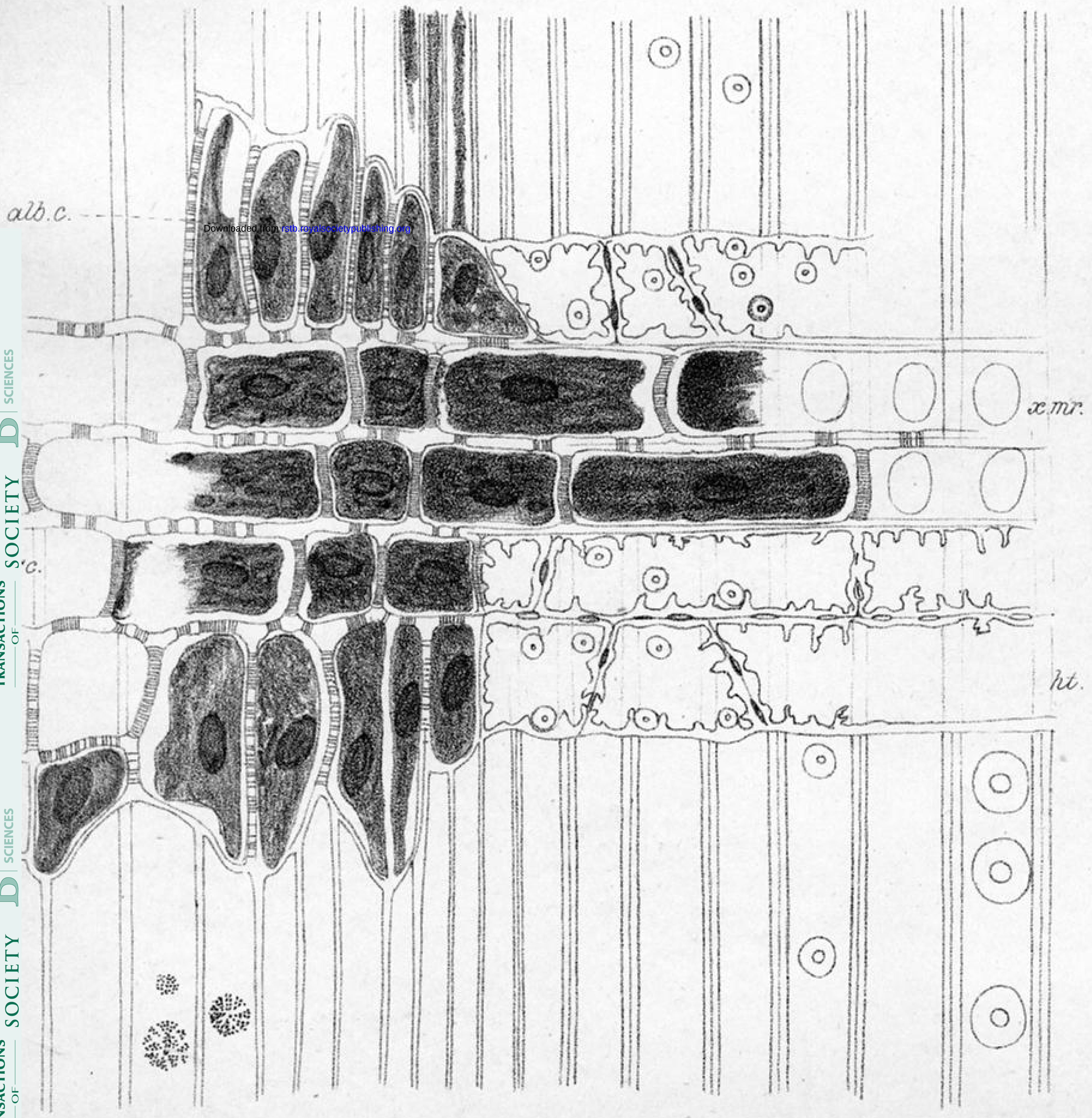

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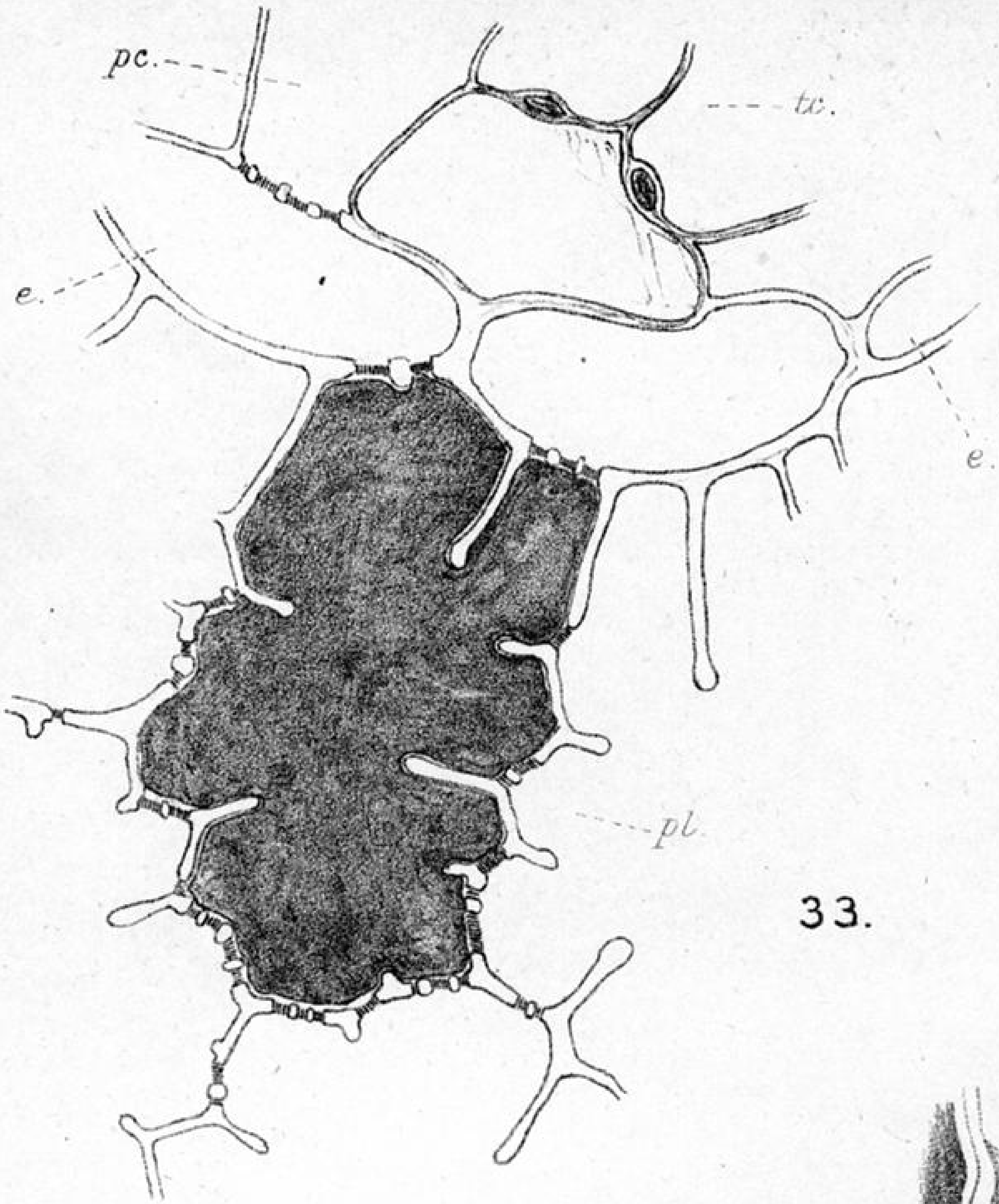

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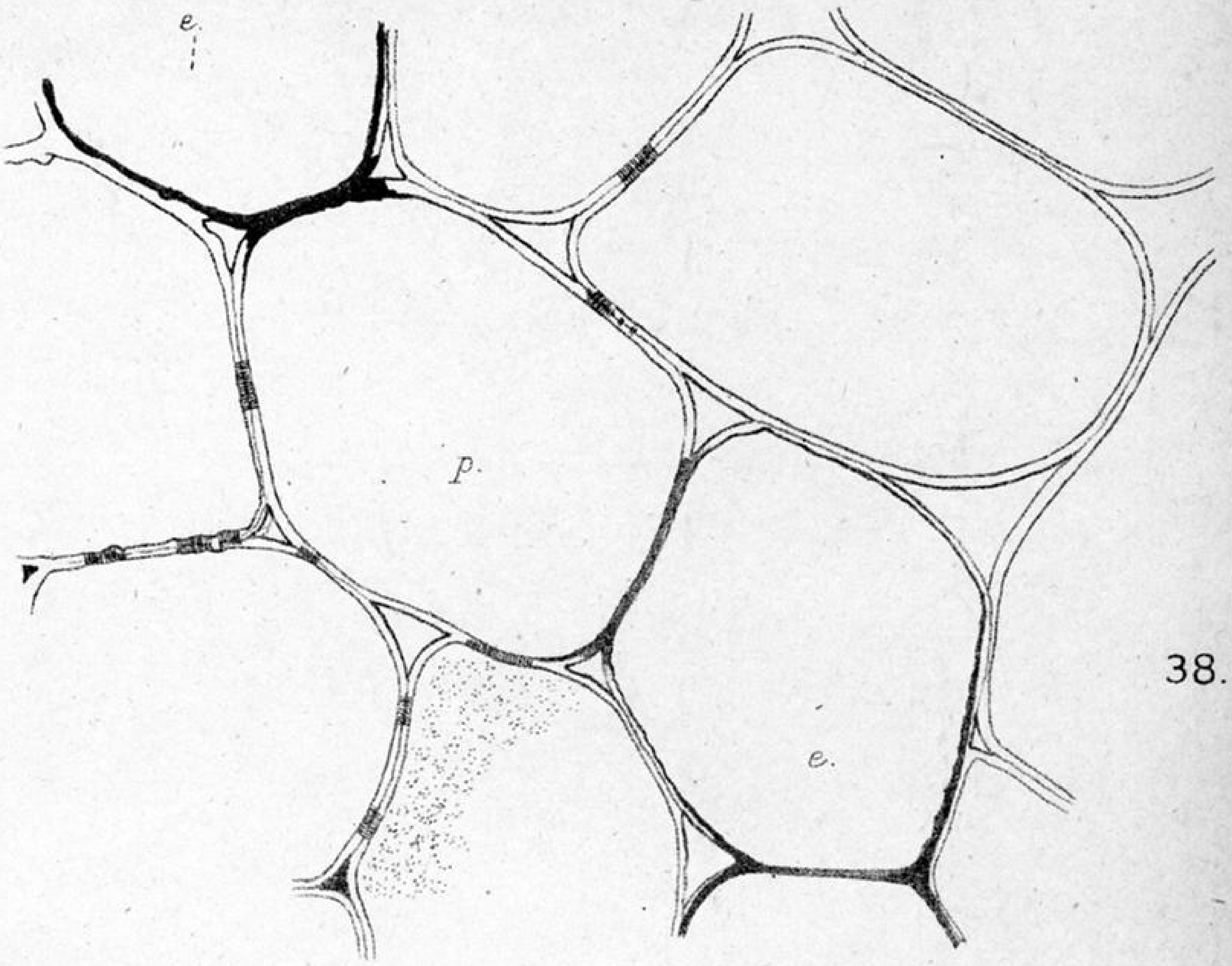

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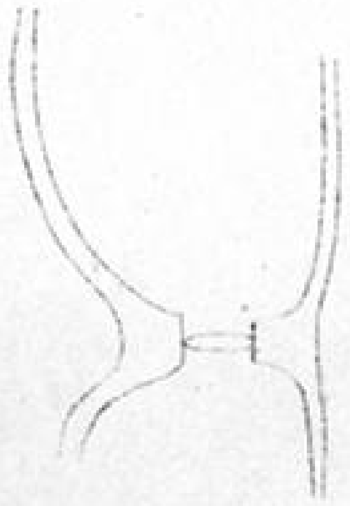

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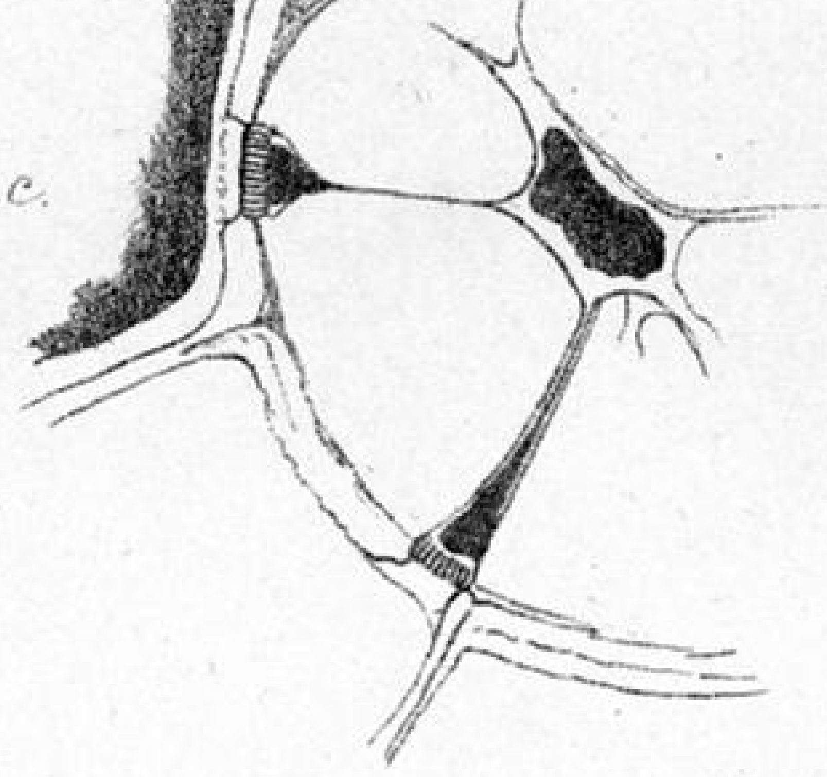

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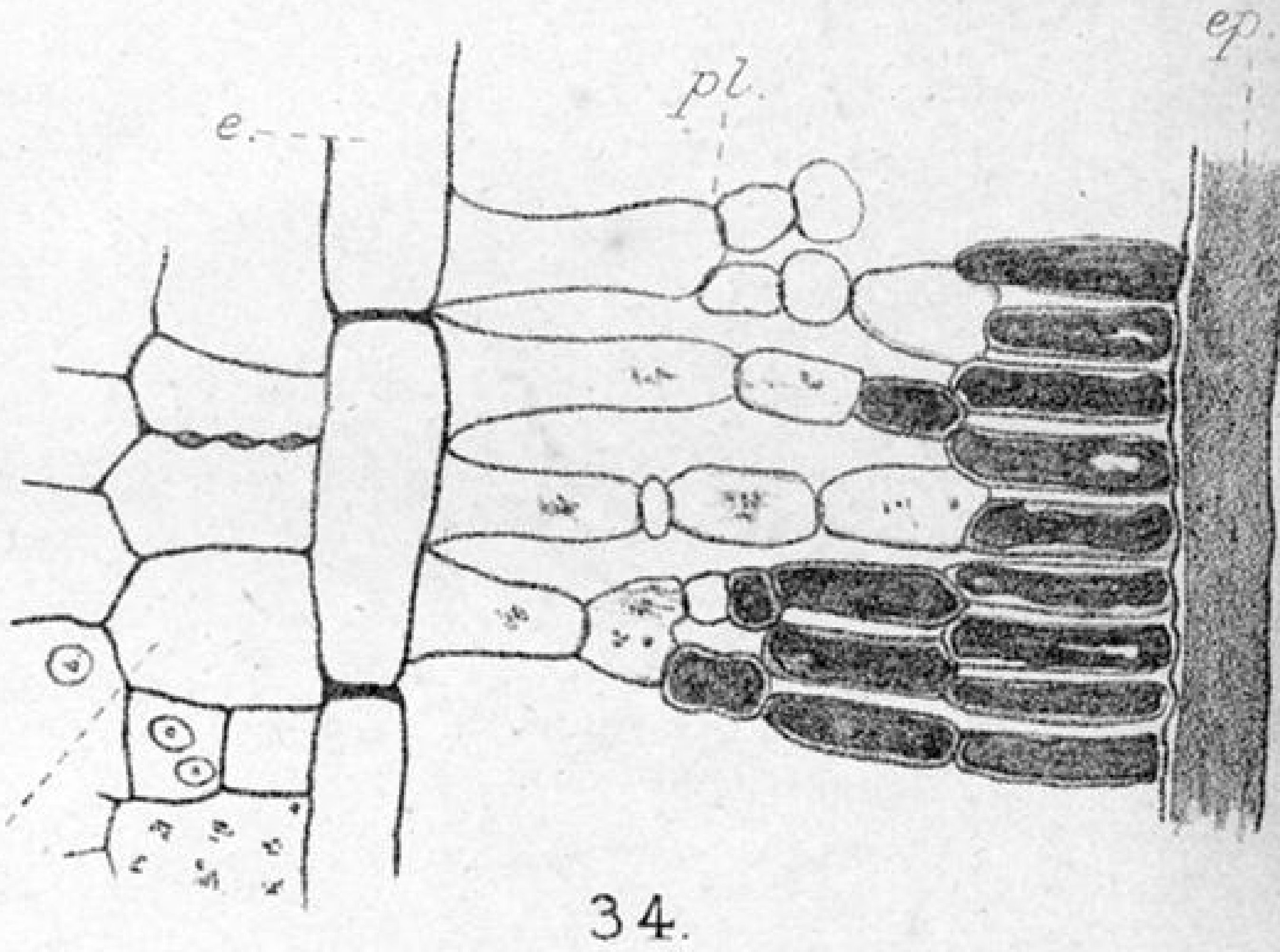

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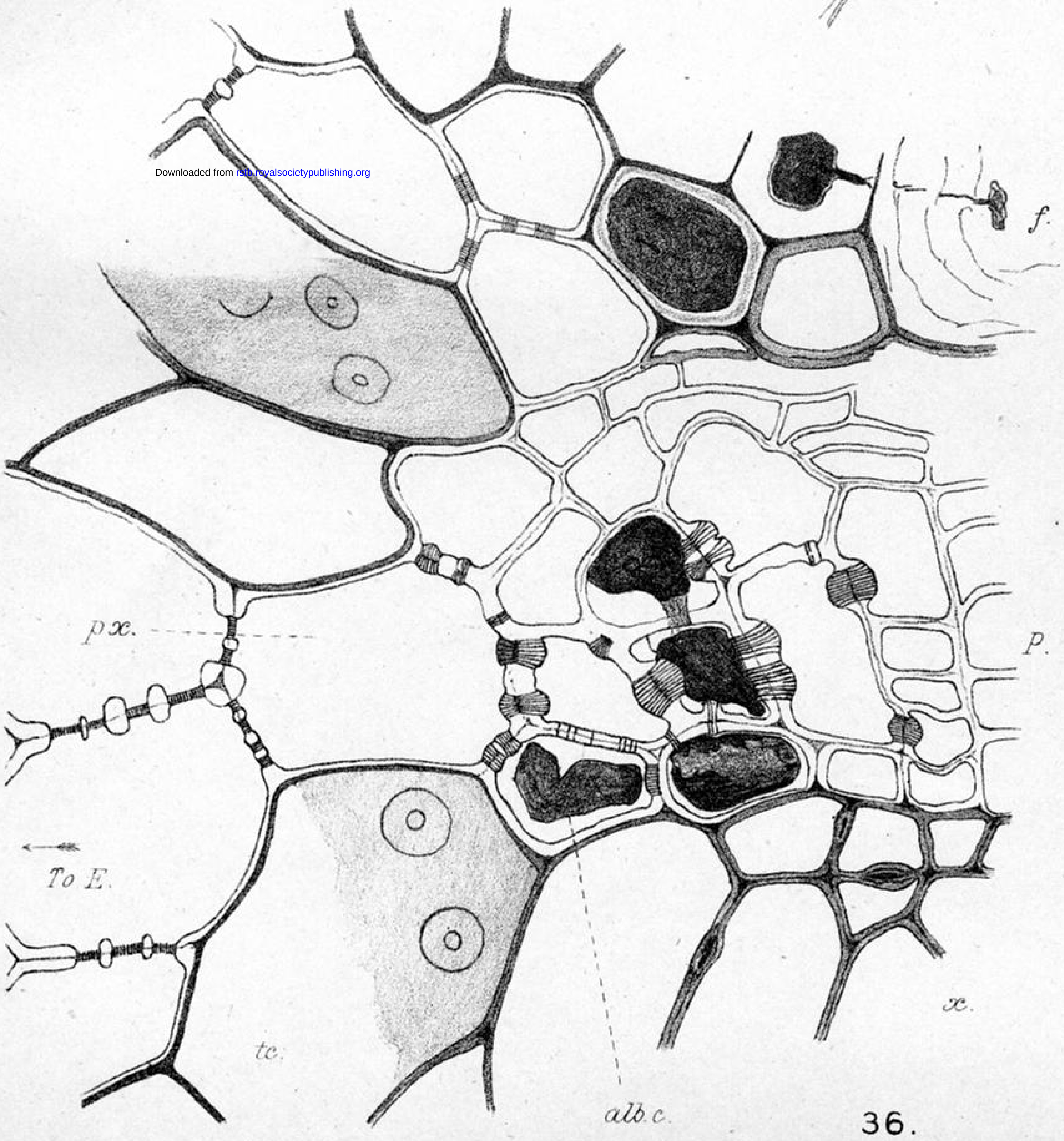

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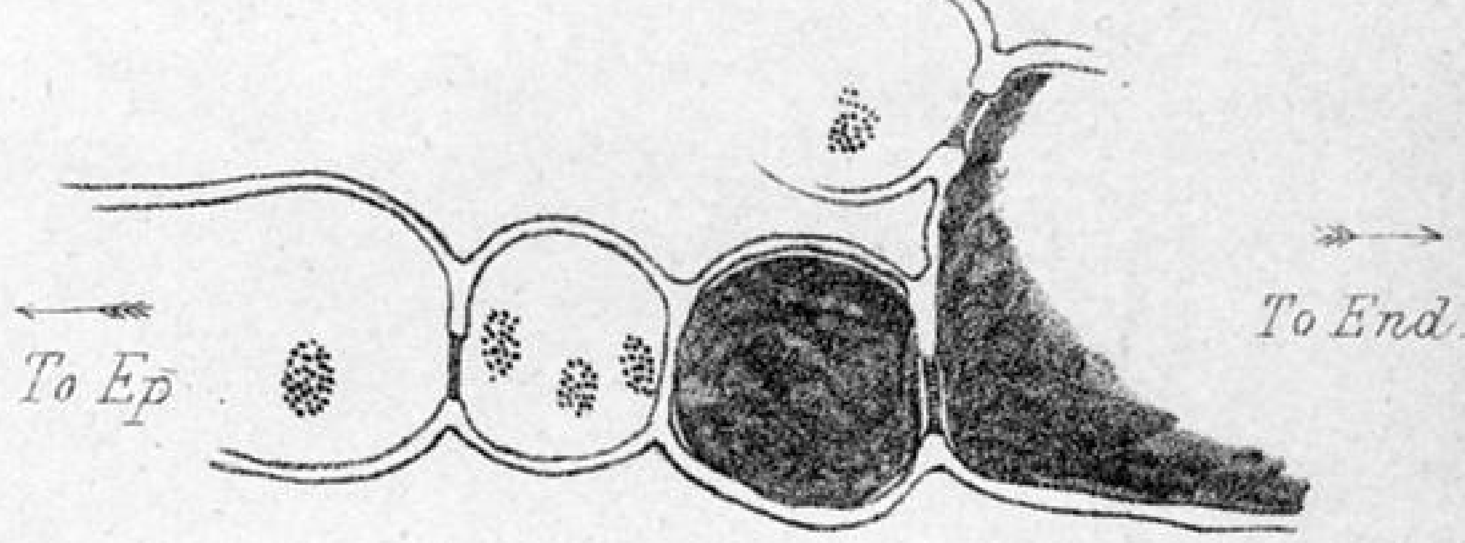

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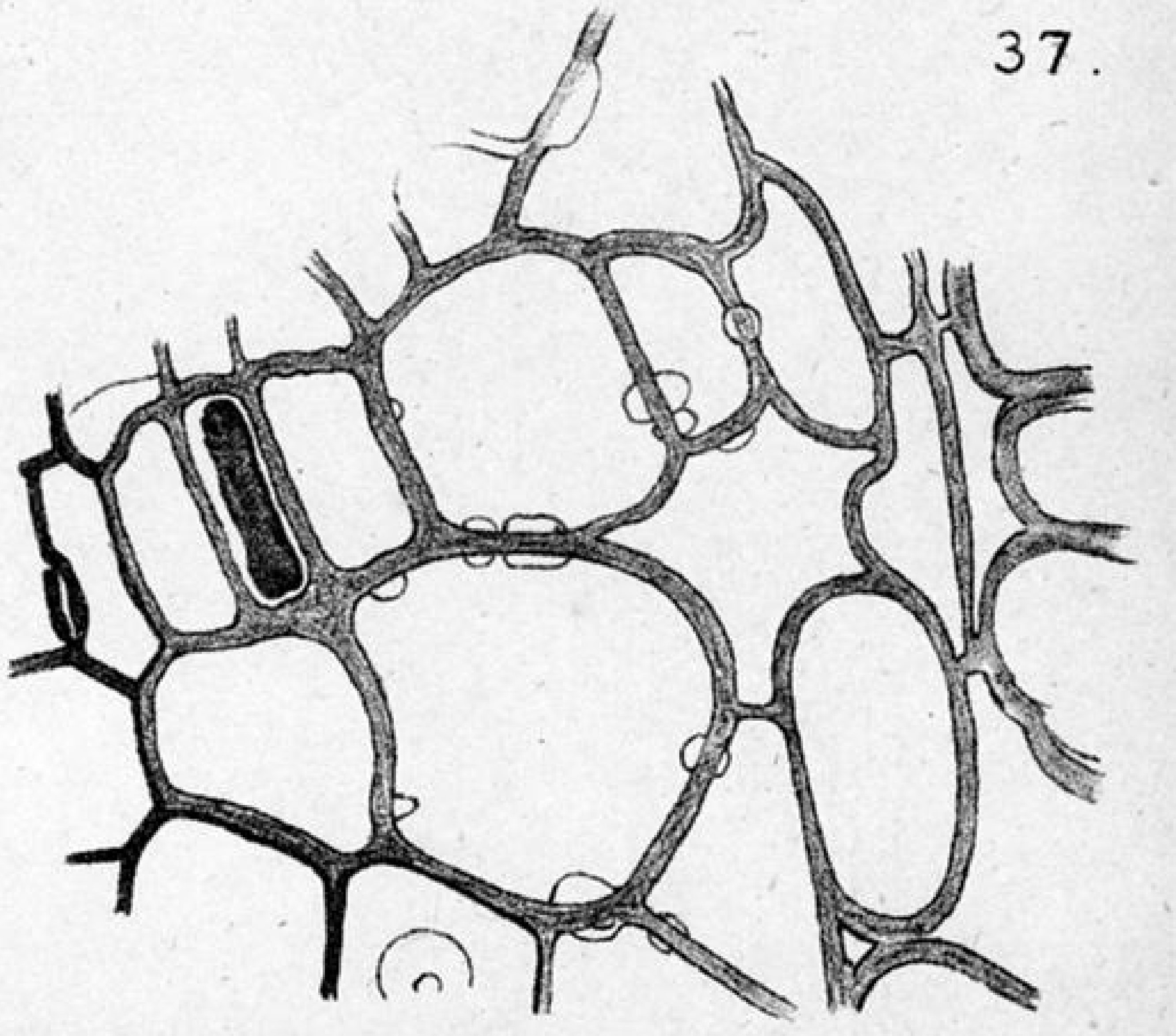

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