
On the Organisation of the Fossil Plants of the Coal-Measures. Part XVI

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V. *On the Organisation of the Fossil Plants of the Coal-Measures.*—Part XVI.
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[PLATES 5–8.]

DURING the last twenty years many single examples of vegetable forms from Carboniferous rocks have come into my possession, which were obviously different from any hitherto described. But I have carefully abstained from publishing such specimens until examples of each multiplied in my cabinet, enabling me to determine how far their apparently distinctive features were constant, and not merely individual, variations. Many such imperfectly known forms still occupy a drawer in my cabinet; but in the present Memoir I propose to describe several of which examples have accumulated so far as to enable me to speak with reasonable certainty as to their specific distinctiveness.

In several of my previous memoirs I have from time to time called attention to a curious development of a medulla in the centre of the axial vascular bundle, especially of the *Lepidodendra*. This was especially done in the Memoir, Part III., when describing the Burntisland *Lepidodendron*, to which, as was also the case with the Arran form (Part X.), I have not yet ventured to give a specific name.

In the case of the Burntisland plant I showed, in figs. 3, 4, 5, 8, and 11, a medulla, α , which, at first of very minute dimensions, gradually enlarged, *pari passu* with the increase not only in the diameter of, but also in the number of the vessels composing the non-exogenous vascular cylinder—the “*étui médullaire*” of BRONGNIART. In this example traces of primordial medullary cells, however minute and few in number, could be detected in the youngest twigs.

The Arran plant (Memoir, Part X.) presented different features. The very young leafy twigs, found in great numbers in the Laggan Bay deposit, had an axial vascular bundle, which consisted wholly of tracheids, in the interior of which no traces of cellular parenchyma could be found (*loc. cit.*, figs. 1 and 2), whilst at a more advanced stage of growth such a medulla began to make its appearance (*loc. cit.*, fig. 3), which ultimately attained to a considerable size (*loc. cit.*, figs. 6, *d*, and 6A, *d*). Though unsuccessful in my search for an example in which the earliest traces of such

medullary cells could be discovered, I had little hesitation in concluding that the small twigs devoid of medulla and the larger ones, in which such a medulla was very conspicuous, belonged to the same plant. This question of the development of a medulla in a manner so different from what is seen amongst living Exogens has long required to have more light thrown upon it; and I propose, in the present Memoir, to record some additional observations that I have made on the subject. But before doing so I would call attention to the existence of two distinct modes of ramification amongst these Carboniferous Lycopodiaceous plants. In one group, illustrated in Memoir Part III., Plate 43, figs. 19 and 20, and also in the *stems* of the Arran *Lepidodendron*, the vascular cylinder (*étui médullaire*) presents a dichotomous ramification, in which the cylinder divides into two virtually equal horseshoe-like halves. But in other instances only a small vascular segment separates from the cylinder. In my Memoir, Part II., p. 224, I showed that in *Halonial* segments only of the medullary vascular ring were detached to supply vascular bundles to the tubercles so characteristic of the genus, and which I showed (*loc. cit.*, pp. 224–5) were merely branches that had undergone an arrested development at an early stage of their growth. In the Memoir, Part XII., Plate 32, figs. 22, 23, 24, and 25, I showed that a similar mode of ramification existed in a Halonial (*i.e.*, fruiting) branch of the Arran *Lepidodendron*.

In the classic species of *Lepidodendron*, *L. Harcourtii*, I have not as yet succeeded in discovering any example of the first of the above modes of dichotomisation. But my young friend, Mr. LOMAX, of Radcliffe, brought me a fine branch of this plant in which the second type was conspicuous. This specimen gave us eleven transverse sections, which successively showed the progress of a bundle from its first separation from the medullary vascular cylinder to its existence as the vascular axis of a branch—Plate 5, fig. 1, represents a portion of the medullary vascular cylinder, as seen in the lowermost of the eleven sections. At *a* we have part of the large parenchymatous medulla. At *b, b* we see parts of the continuous ring of the medullary vascular cylinder. At *b'* we discover a segment of that cylinder becoming detached from the remainder at the points *b'', b''*. In fig. 2 we have the portions *a* and *b, b* of fig. 1, but the segment *b'* is now completely separated, as represented in fig. 3. The vascular portion is but little altered at *b', b'*, whilst a small portion of the medullary parenchyma, *a*, of fig. 1, coheres to the detached vessels at fig. 3, *a*. In fig. 5 we find the segment changing its form. Its two points *b', b'* are curving inwards towards one another, but traces of the medullary cells are still seen at *a*. In fig. 4 the convergence of the two points *b', b'* has advanced so far that they now virtually touch one another, whilst scarcely any traces remain of the medullary cells at *a*. They seem to have undergone absorption. In fig. 6, which now represents the transverse section of the vascular bundle as seen in a separating branch, the coalescence of the points *b', b'* of the previous figures is complete. The bundle has now attained the form of a symmetrical cylinder, wholly composed, apparently, of scalariform vessels. Having thus become the vascular bundle of an ordinary branch of a stem of which

a large cellular medulla is a conspicuous feature, such a medulla would, there can be little doubt, be developed in its interior, though no traces of cells can yet be detected in its central portion, where such an axial parenchyma should ultimately make its appearance.

Plate 6 and Plate 5, fig. 15, represent various stages of growth of a small species of *Lepidodendron*, from Halifax, of which I have now several examples, and to which I propose to give the name of *Lepidodendron mundum*. Its characteristic feature resides in its medullary vascular cylinder, *b*, which mainly consists, in young stems, of one, rather irregular, line of comparatively large and conspicuous scalariform vessels or tracheids, but which sometimes develops a second such series on the larger stems or branches. In both these cases this circle of conspicuous vessels is surrounded closely by a fringe composed of numerous, very much smaller, ones, from which the foliar bundles are solely derived.

Fig. 7 represents a transverse section of the youngest example of *L. mundum* I have yet obtained. In it the outer cortex, *c*, consists of a parenchyma, the diameters of the cells of which become smaller from within outwards, assuming, as they do so, the form of a coarse prosenchyma with somewhat thickened walls. The middle bark has disappeared from this, as also from all my other examples of this plant. At the centre, *b*, we have the vascular bundle, which is represented, still further enlarged, in fig. 8. It appears to consist wholly of a central mass of large tracheids, *b*, surrounded by a fringe of smaller ones, *b'*. I can detect no traces of cells amongst these tracheids.

In fig. 9 this solid axial cylinder has developed into a medullary vascular ring, *b, b'*, enclosing a few parenchymatous cells, *a*, forming a small but distinct medulla. In fig. 10, whilst the general conditions are similar to those of fig. 9, not only the tracheids of the vascular cylinder, *b, b'*, have become more numerous, but the medullary cells, *a*, have done the same. In this instance the cells, *a*, are crowded, thin-walled, and of irregular form, as if they had recently passed through a meristemic stage of multiplication. In fig. 11 this general enlargement and multiplication has not only gone still further, but the individual medullary cells have now assumed the hexagonal form of a very regular parenchyma. Fig. 12 represents a specimen in which these progressive developments of the medulla, *a*, and of the medullary vascular cylinder, *b, b'*, have attained to the maximum extension seen in any of the specimens in my cabinet. We also see in this specimen the well-preserved innermost cortex, *c*, which consists of a parenchyma the cells of which are uniformly of small size and shape, their mean diameters being about one-thousandth of an inch.

Fig. 13 represents a vertical section through the vasculo-medullary axis of a specimen of the same plant, the entire diameter of which, including its cortex, is about four-tenths of an inch. Here we have the medulla at *a* composed of cells with square or very slightly inclined transverse septa. The barred vessels* of the medullary

* The transverse bars of these vessels are connected vertically, as shown on Plate 5, figs. 14A and 14B, by delicate threads like those seen in the Arran plant (see Memoir X., fig. 4*).

vascular zone appear at *b*, whilst the inner cortex, *c*, of fig. 12 is now seen to consist of vertically elongated cells, amongst which those with rectangular and oblique septa are intermingled, whilst the thin-walled innermost ones, *c'*, present an obvious procambial aspect.

In fig. 14 we find the medullary vascular cylinder dividing in the regularly dichotomous manner seen among the larger forms of *Lepidodendra*. In fig. 15, on Plate 5, we have a section of my only example of this species in which the medullary vascular cylinder, *a, b*, is invested by a secondary, exogenously-developed zone, *d*.

The plant just described again illustrates the gradual development of a medulla within the interior of a vascular bundle where, in the youngest state of the bundle, no traces of cellular structure could be discovered, but the germs of which must necessarily have been furnished by the procambium from which, in the youngest twigs, the entire bundle originated. The probable philosophy of these facts may be considered after describing some additional undescribed types.

Figs. 16, 17, and 18 represent sections of a *Lepidodendron* from Halifax, for which I propose the name of *L. intermedium*, and which is remarkably distinct from any other form with which I am acquainted. Its vasculo-medullary axis, *a, b*, differs from all other known *Lepidodendra*, with one exception. The true medulla, *a*, consists of well-defined parenchymatous cells. The medullary vascular cylinder, *b*, is composed of numerous large barred tracheids. The external boundary of this cylinder is sharply and regularly defined, but its inner border is very irregular, some of its largest vessels being detached from it and isolated amongst even the most central cells of the medulla.* In addition to this characteristic feature, we have an exogenous zone, *d*, which is equally characteristic. The entire thickness of this zone, from its medullary to its cortical boundary, is only about the one-hundredth of an inch; yet many of its radial lines of tracheids consist of twenty-four distinct vessels. Measured separately, we find these tracheids ranging between the thirteen-hundredth and the twenty-six-hundredth of an inch in diameter. On examining these vessels under high powers, as they appear in tangential sections (fig. 17), we find them, *d'*, ascending and descending in extremely tortuous courses. They are here largely intermingled with cells, *d''*, *d''*, the diameters of which are equal to those of the vessels. These cells unmistakably correspond to those which constitute the medullary rays of the larger forms of *Lepidodendra*. (See 'Phil. Trans.,' 1872; Memoir, Part III., Tab. 42, fig. 13, *f*.) Fig. 18 is a vertical section made through the centre of the stem. At *a* we have the large vessels of the medullary vascular cylinder, intermingled irregularly at certain points with the medullary cells, as shown in fig. 16. At *d* we have the exogenous layer on one side of the central medulla and its vascular cylinder. In this zone we find the vessels of minute sizes, and again copiously intermingled with cells, many of which are arranged in radial mural lines like medullary

* In this respect the plant resembles *Lepidodendron selaginoides*; but it differs in the entire absence from its medulla of the barred medullary cells so characteristic of the latter type.

rays. At *e* we have the innermost zone of the cortex, as at fig. 16, *e*. The external cortex consists of a coarser parenchyma.

The next example to be described has a marked individuality. I propose giving to it the name of *Lepidodendron Spenceri*, after my friend Mr. J. SPENCER, of Halifax, who has so long been one of the most active of my several auxiliary collectors, to whom I have been so much indebted.

Fig. 19 is a transverse section of a stem or branch of this plant. The central structure, *a*, exhibits in this section no indication of medullary cells, but appears to be a solid rod of scalariform tracheids. It is surrounded at *e* by a narrow zone of the inner cortical parenchyma, the greater part of which has disappeared. At *f* is the middle cortex, characterised by an undulating outline, the outward prominences of which are frequently prolonged into points, *f'*. Fig. 20 represents one of these points further enlarged. In it, at *e*, we again have the zone of the inner cortex; at *f* is the middle cortex, and at *f'* we find the barred vessels of a foliar bundle passing outwards. The cells of which the middle cortex, *f*, is composed are not uniform in structure; dark, dense masses of thick-walled cells (fig. 19, *f''*) alternate with lighter groups with thinner cell-walls, *f'''*. In the centre of most of the darker groups of several of my specimens the tissue has become decayed, as at fig. 19, *f''*. This variation in the structure of the middle cortex appears to be a very characteristic feature of the species. None of my sections retain any traces of the outermost cortex and its foliar organs.

In fig. 21 we have a radial section of the above cortical zones; at *a* are two or three of the outermost vessels of the central bundle, giving off at *a'* a foliar bundle passing upwards and outwards through the middle cortex. This cortex chiefly consists of strongly-defined prosenchymatous cells. In fig. 22 we have a vertical section through the centre of the vascular axis, *a*, of fig. 19. We see some prosenchymatous but thin-walled cells belonging to the inner cortex at *e*, through which a foliar vascular bundle is again escaping at *a'*.

On turning to the section through the vascular axial tissue (fig. 22), we find some interesting features. Its exterior, *a*, consists of developed and strongly-defined barred tracheids; but the centre of this structure, *a''*, consists of thin-walled, unbarred, and much-elongated fusiform cells, whilst we have some very thin-walled, barred tracheids, but in which the bars are so thin as to be almost invisible. It is obvious that we have here a procambial string which is undergoing centripetal development into a vascular bundle, the more external tracheids, *a*, of which have undergone perfect lignification. Those indicated in fig. 22 by *a'''*, *a''''* are but partially lignified, whilst in the central part, *a''*, we have procambial elements which the process of lignification has not yet reached. This is the only specimen in which I have personally seen a Carboniferous example of a centripetally-developed vascular bundle. What appears to have been a somewhat similar one is referred to by M. RENAULT as occurring in his *Lepidodendron Rhodumnense*.*

* 'Cours de Botanique Fossile,' Deuxième année, p. 23.

The next species, which I propose to designate *Lepidodendron parvulum*, is the smallest of the Lepidodendroid family that I have hitherto met with. I have a considerable number of examples of it in my cabinet, but there is a remarkable similarity of shape, size, and structure throughout the entire series, the mean diameter of the transverse sections, including the leaves, being only about one-tenth of an inch.

Though so small, every example in my cabinet obviously possessed a cellular medulla, Plate 8, fig. 23, *a*. This was surrounded by a medullary vascular cylinder, *b*, from two to three tracheids in thickness, the tracheids being fairly uniform in size, though, as usual, the outermost are rather less than those occupying the inner margin of the ring, which they combine to form. The inner cortex has disappeared. The middle cortex (fig. 23, *c*) is always an unbroken circle of parenchymatous cells. Still more uniform in size and shape are the parenchymatous cells of the outermost cortex, *d*, as well as of the leaves. But between these two zones of the cortex, *c* and *d*, we have in most of my specimens the verticils of empty areas (figs. 23, *e*, and 24, *e*). These spaces are separated by the radial bands of cortical parenchyma (fig. 24, *e'*). The empty areolæ, *e*, were long unintelligible to me, but at length I obtained specimens in which, as in fig. 25, *e*, I found them to be normally occupied by a thin-walled parenchyma very distinct from that of which the remainder of the cortex, including the leaves, was composed. The latter is represented in fig. 26; the former in fig. 27. What the functions of these vertical bands, *e*, of specialised tissue may have been I can form no opinion. I have seen nothing like them in any other Lepidodendroid stem. The vascular bundle, *b*, of fig. 25, is subdividing in the usual Lepidodendroid manner when the branch is about to dichotomise. I have an ascending series of five sections, from the lowest, in which the vascular ring is unbroken, to the highest, in which each of its two halves has not only almost reconstructed its perfect cylinder, but is enclosed in a distinct cortex of its own, just about to separate into two distinct branches; each of these branches retains the features characteristic of the species. I have obtained the plant both from Oldham and from Moorside, in Lancashire.

A few remarks on the general relations of the objects described in the previous pages may not be out of place.

The *form* of ramification illustrated in figs. 1–6 is not wholly new. In my Memoir, Part II. ('Phil. Trans.,' 1872, p. 224), I demonstrated that the tubercles characteristic of the genus *Halonia* were merely branches the development of which had been arrested, and that, as in the case of the plant (figs. 1–6) of the present Memoir, the vascular bundle supplying such branches was given off from the medullary vascular cylinder, in a manner intermediate between a perfect dichotomy of that cylinder, representing ordinary ramifications, and the detachment of a few small vessels from its periphery, constituting the bundles supplying the leaves. In Memoir, Part XII. ('Phil. Trans.,' 1883, p. 459), I further showed that the Halonial tubercular

branches of my Arran *Lepidodendron* were supplied, as in fig. 1, by large segments cut off from the solid vascular bundle which, in the young branches of that plant, represents the medullary vascular cylinder of its older stem. I have also in my cabinet a section of the Burntisland *Lepidodendron* (cabinet number 502) which is giving off a similar branch. Various other specimens, of a like character, that have come under my notice, suggest the conclusion that the ordinary ramification of these *Lepidodendra* was dichotomous, as in fig. 25 of the present Memoir; but that, where a branch was of a special kind, characterised by an arrested development, then the mode of branching illustrated by figs. 1-5 was the normal one. It has long been certain that the scars of *Ulodendron* represent such arrested branches, which supported *Lepidostrobi*; and it is in the highest degree probable that the tubercles of *Halonia* are similar organs. A memoir by Mr. KIDSTON* clearly demonstrated that *Ulodendron* is not a *genus* of plants, but merely a *condition* of various *Lepidodendroid* genera; and the remark is equally applicable to the name *Halonia*, which, as is shown in Plate 34 of my Memoir, Part XII. ('Phil. Trans.,' Part. II., 1883), represents the extremities of an ordinary *Lepidodendroid* branch. A fine specimen of *Halonia regularis* in my cabinet shows that the ordinary branching of *Halonia* forms is dichotomous, as in fig. 14. It is therefore obvious that branches like figs. 1-5 represent some special ramification, distinct from the normal dichotomous one; and the only possible explanation that I can discover is that such arrested or subordinate branches were destined to support strobili.

It cannot now be doubted that the strobili of *Lepidodendron* were affixed to their sustaining branches in two ways. In one fine *Lepidostrobus* in my collection the base of the strobilus terminates the extremity of a *long*, slender pendulous twig. But in another very fine example, in the Museum of the Owens College, the large *Lepidostrobus* is planted laterally in an almost sessile manner upon a strong branch. In this instance the strobilus is evidently sustained by a short, arrested lateral twig, corresponding to one of the *Halonia* tubercles. The sections, figs. 1, 5, further establish another morphological fact, viz., that the young branches of a *Lepidodendron* may have a vascular bundle devoid of all visible traces of a cellular medulla, and yet such a medulla may be developed in its interior at a later stage of growth.

In some of my earlier memoirs I advanced the hypothesis that age produced other morphological changes, beyond mere growths, in these *Lepidodendroid* plants. To this M. RENAULT replied, speaking of *L. Harcourtii*, "On peut donc conclure que la différence de diamètre des rameaux de *Lepidodendron* n'apporte pas de changements dans la disposition générale des tissus qui les composent."[†]

My sections of *L. Harcourtii* demonstrate that such changes do occur; since, as the section, fig. 1, shows at *a*, the older and larger branches possess a very large medulla, which exists in like manner in all the older *Halonia* branches, which certainly

* "On the Relationships of *Ulodendron*," 'Ann. Mag. Nat. Hist.,' vol. 16, 1885.

† 'Cours de Botanique Fossile,' Deuxième année, p. 28.

continued to grow after the strobili had dropped off.* The illustration given above also tends to confirm statements made in my Memoir, Part X. ('Phil. Trans.,' 1880, p. 493), when describing the Arran *Lepidodendron*. I there gave my reasons for believing that, though no medulla was present in the centre of the vascular axis of any of the young twigs and branches of that branch, one had somehow or other been developed at a later stage of growth in those vascular bundles. Other conditions of these Arran specimens being considered, it now becomes an almost absolute certainty that such had been the case. The history of figs. 19, 20, and 21 of the present Memoir bears upon the same question, but little more can be said in reference to this latter plant until we obtain specimens of it in a more advanced state of growth. Though it and the Arran plant possess several features in common, I cannot identify them with sufficient definiteness to assign the same name to both. This, however, is of no consequence for the present, since I have not yet given any name to the Arran plant. Rather more important is the fact that M. RENAULT speaks of a stem having a solid vascular axis, like that of *Lepidodendron Spencersi*, to which stem he has given the name of *L. Rhodumnense*. The following description shows that it has some features in common with my plant:—La cavité centrale, due soit à un déchirement du tissu, soit à ce que le procambium n'a pas achevé sa lignification, est cylindrique, dans les échantillons non déformés, toujours de dimension extrêmement réduite, et ne présentant que des traces douteuses de tissu cellulaire.† Details in the structure of the cortex of *L. Rhodumnense* indicate a specific difference between it and my plant.

The *Lepidodendron intermedium*, figs. 16, 17, and 18, has a special interest when viewed in connection with the plant which I some time ago named *Lepidodendron fuliginosum*.‡ In my Memoir, Part XI., § in Plate 49, fig. 11, I represented a segment of a transverse section of the innermost cortex of this plant, in which a very rudimentary exogenous vascular zone is seen at *h*, and in p. 290 of the Memoir I called attention to the liability of these vascular elements to be diverted irregularly, and in an undulating manner, from their straight vertical course. Fig. 17 of the present Memoir, shows that though in the transverse section the vascular laminæ are arranged in regular radiating lines, as is also the case in the similar section of *L. fuliginosum* referred to above, vertical tangential sections of the same exogenous zone of *L. inter-*

* My meaning is not made sufficiently clear in this paragraph. In its transition from being a segment of a circle, as in fig. 3, to becoming a perfect cylinder, as in fig. 6, the vessels composing this bundle must have undergone precisely such changes of relative positions as M. RENAULT deems impossible. But the changes have not ended here. Supposing the bundle to have supplied an ordinary lateral branch, it must have become a hollow cylinder like that from which it sprang. If, on the other hand, it merely supplied an aborted Halonial tubercle which would be prolonged to form the axis of a Lepidostroboid fruit, it must have expanded in the axis of that fruit into a hollow cylinder, because all these strobili possess such hollow vascular cylinders, which enclose a true medulla.—September 3, 1889.

† 'Cours de Botanique Fossile,' Deuxième année, p. 23.

‡ 'Proceedings of the Royal Society,' vol. 42, p. 7.

§ 'Phil. Trans.,' 1881.

medium exhibit the same laminæ arranged, as in *L. fuliginosum*, in a very irregular, undulating manner. In both these cases this irregularity is due to the excessive development, amongst the vascular laminæ, of a cellular parenchyma. This feature, common to the two plants, is suggestive in both of a rudimentary type of exogenous growth; one, however, in which the *L. intermedium* has attained to a more advanced stage than *L. fuliginosum* has done. In the types in which the exogenous zone has reached a yet higher condition the number of the disturbing cells has been very much reduced, such only remaining as could be utilised as muriform medullary rays. How far a yet lower Lepidodendroid state has existed, in which no form of exogenous growth was developed at any period of life, cannot yet be determined. Thus far, however, we have obtained no specimen of *L. Harcourtii* which possesses such a zone, though I have a stem of that plant which is $3\frac{1}{2}$ inches in diameter. Nevertheless, that still larger stems may yet be discovered, showing exogenous growths of xylem, is suggested by the Arran plant, of which I have sections fully 3 inches in diameter, in which no such growth has yet made its appearance; whilst other stems of very much larger dimensions have the exogenous cylinder fully an inch in thickness between medulla and cortex. It now becomes more than probable that at one stage or another of their development all the Carboniferous Lepidodendroid stems grew exogenously. In some cases, as in fig. 15 of the present Memoir, such a growth took place when the medullary vascular cylinder of a branch was not more than the one-fortieth of an inch in diameter, whilst in others, as in the Arran plant represented in Plate 14, fig. 5, of my Tenth Memoir, the exogenous growth, though present, had made very small progress when the medullary vascular cylinder was fully an inch and a half in diameter.

The various instances in which I have now been able to trace the development of a true medulla in the Lepidodendra throws, I think, some light upon the physiological character of that development, as well as upon its homologies amongst living plants. All botanists are aware, though many geologists may not be, that the medulla of an ordinary exogenous stem makes its appearance in a very different manner from that seen in the Lepidodendra. The tip of a growing twig consists of a mass of what is termed "primitive tissue," viz., of undifferentiated parenchymatous cells. Almost, though not quite, simultaneously, a ring of vascular bundles is formed, which separates the lower portion of that primitive tissue into an inner mass, the medulla, or pith, and an outer ring of cortex. The medulla thus formed, though of small size, is merely a downward prolongation of the mass of apical cells, the two being absolutely continuous. As we trace this medulla downwards into the lower part of a shoot of the first year we find that the medulla increases in size up to a certain point, the distance of which point from the growing tip varies in different species of plants. As we thus descend we find that the increase in size is due to an increase partly in the number of the cells and partly in the diameter of the individual cells. Still lower down the

diameter of the medulla either remains constant or even diminishes, so that in many old stems but feeble traces of it can be discovered.*

This process is a very different one from what we see in figs. 7–12 of the present Memoir. In fig. 7 the growth of the twig in length and diameter has not only made considerable progress, but its tissues have developed into a definite central vascular

* In illustration of this point I select a few examples from a number of measurements which I have made from transverse sections of growing stems, the measurements being recorded in decimal parts of an inch.

The plant.	Transverse diameter at apex of medulla.		Mean diameter of the medullary cells.	Diameter at successive points lower down the stem measured from apex of medulla.			
	Of branch.	Of medulla.		Distance.	Stem.	Medulla.	Medullary cells.
<i>Æschylus Hippocastaneum</i>	.085	.04	.0007				
" "	6 inches	.25	.175	.0014
" "	18 "	.45	.175	.002
<i>Tydaea</i>	.1	.04	.0009				
"	$\frac{1}{4}$ inch	.11	.05	.0019
"	$\frac{1}{2}$ "	.125	.175	.0019
"	21 inches	.25	.2	.005
"	28 "	.22	.25	.006
<i>Geranium</i>	.06	.05	.0014				
"	1 inch	.225	.105	.0035
"	4 inches	.275	.225	.0057
"	Old stem	.4	.2	.0035
Elder	.050	.03	.0014				
"	4 inches	.17	.12	.0043
"	14 "	.25	.15	.0043
"	2 feet	.6	.35	.0057
"	3 "	.55	.25	.0057

These measurements show us that, approximately, whilst

In *Æschylus* the medulla enlarges transversely from .04 to .75,

" the medullary cells enlarge from .0007 to .002.

In *Tydaea* the medulla enlarges transversely from .04 to .25,

" the cells enlarge from .0009 to .006.

In *Geranium* the medulla enlarges transversely from .05 to .2,

" the cells enlarge from .0014 to .0057.

In Elder the medulla enlarges transversely from .03 to .25,

" the cells enlarge from .001 to .0057.

We are thus led to the approximate conclusion that—

In *Æschylus* three-fourths of the transverse enlargement of the medulla is due to the expansion of the primitive medullary cells.

In *Tydaea* all the transverse enlargement of the medulla is due to expansion of those primitive cells.

In *Geranium* all the transverse enlargement is due to the expansion of the primitive cells.

In Elder three-fourths of the transverse enlargement is due to the expansion of the primitive cells, and not to an increase in their number.

bundle, invested by at least two distinct zones, the outermost of which bore leaves before any traces of a medulla could be discovered. Thus we discover at the outset a difference between the history of the medulla of a *Lepidodendron* and that of an Elm or an Elder tree. Tracing yet further the development of the Lepidodendroid type we find that in it the medulla first appears as one or two individual cells formed in the centre of a bundle of tracheids or vessels; once existing, however produced, these cells multiply rapidly by the ordinary meristemic process of fission. So far as my specimens throw light upon the latter process, it exhibits some peculiarities. The meristemic internal subdivision of these cells was not going on continuously, but interruptedly; at certain periods the whole of the fully-developed cells of the medulla simultaneously underwent such a division. Fig. 26A represents a cluster of cells from the medulla of a branch of *Lepidodendron Harcourtii* undergoing this meristemic multiplication. Some of these *matured* cells are subdividing into four or five of the younger generation. At this stage the latter are all thin-walled, small in size, and irregular in form; but all these conditions gradually become changed. The walls become more strongly defined; the area of each cell enlarges from two to two-and-a-half times its original size; and its unsymmetrical form develops into that of the regular pentagon or hexagon seen in the primary, or *mother*, cells of fig. 26.

But the effect of these changes is not limited to that produced upon the medulla. They reach the vascular bundle within which the increase in the number of the medullary cells is taking place. The first result of the internal tension occasioned by these cellular expansions is to develop the solid mass of vessels into an annular ring, *b*, of increasing diameter. Fig. 8 becomes progressively converted into what is seen in figs. 9, 10, 11, and 12. But this vascular ring, *b*, not only increases in diameter, but the vessels composing it increase in number, and change their relative individual positions as they do so. At later periods this process of meristemic division and subsequent expansion of all the new cells appears to have been repeated from time to time, until the medulla and its surrounding medullary vascular ring attain to their ultimate magnitudes—a condition which was probably coincident with the first appearance of the more external exogenous zone. I was at one time inclined to think that some of the young medullary cells assumed a procambial form, and were converted into new vessels; and even now I am not sure that this is not so in some instances. But it appears to me now that, in such examples as figs. 7–14, the new vessels must be produced on the cortical side of the medullary vascular cylinder—*i.e.*, centrifugally rather than centripetally. However this may be, the enlargement of this cylinder is evidently effected mainly, if not wholly, through the internal tension occasioned by the subsequent multiplications and expansions of the medullary cells—a condition that has no existence amongst the exogenously-grown trees now living.

But a partially parallel state of things does exist amongst some living plants. In his learned work on the ‘Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns,’ the late Dr. A. DE BARY observes: “In many Ferns the

original axile bundle widens out, as the stem grows stronger, into a tube, which is for the most part closed all round, and has only at each node, below the insertion of the leaf, a relatively small slit, or *foliar gap*, through which the medullary parenchyma is connected with the cortex, and from the margin of which one or several bundles pass into the leaf.”* I think there can be little question but that this widening out of an axile bundle which, as the same author observes, “extends itself, and forms a tube, which surrounds a parenchymatous cylinder of pith” (DE BARY, *loc. cit.*, p. 283), presents substantially an analogous condition to what is so general amongst the Carboniferous Lycopods. At the same time, though the two cases are identical in their general features, they present differences. I have not yet found any Fern in which a solid central bundle develops a medulla within its own component vessels. The medulla is existent *ab initio*, surrounded by a circle of such vessels. Thus, in *Aspidium filix mas* this medulla has a diameter of about a tenth of an inch close to the growing apex of the stem, and at its utmost development it rarely attains to more than four times that diameter; even then the interspaces between the bundles composing the entire vascular cylinder are very large. This is very different as to details from some examples found amongst the Lepidodendra, where a medulla developed from some invisible cell-germ has expanded to more than an inch in diameter.

Plate 8, fig. 28, represents a transverse section of a *Rachiopteris*, of which I have several sections. At the first glance its central vascular bundle, cut through transversely, has a Zygopteroid aspect, but it differs in the fact that, whilst its side *a* consists of a line of large vessels, its opposite side *b* is composed of very small ones: at the two points *c*, *c'* the bundle consists of a number of the small vessels resembling those at *b*, but here forming an irregular mass surrounding a vacant space at each end of the central portion, *a*, *b*; at *d* a cluster of these small vessels is detached in Zygopteroid fashion, as if going to supply some peripheral organ. The outer cortex is composed of an uniform cellular tissue. I propose the name of *Rachiopteris irregularis* for this very distinct organism, which is from Halifax.

* English Translation, p. 284.

Supplementary Observations.

Strong objections have been offered to the supposition contained in the foregoing paper that any translation of position in the elements constituting any *permanent* tissue was possible. Since the paper was written I have devoted much time to this matter, which has an important bearing upon the chief subject dealt with in the present Memoir. The further I carry my enquiries into the question of the origin and growth of the medulla, and the contemporaneous expansion of the investing vascular medullary cylinder (the "étui médullaire" of BRONGNIART), the more clear the evidence becomes that in these primæval vascular Cryptogams we are brought face to face with important histological and physiological phenomena to which no exact parallels are to be found amongst living plants. Yet these phenomena must be as capable of explanation as the many similar ones to which the present race of philosophic botanists have given so much attention; and, as the phenomena in question must have an important bearing upon the problem of evolution, they demand a similar amount of careful study.

Though, as already observed, living plants present no exact parallels to the conditions which I have discovered amongst the Carboniferous Cryptogams, we can scarcely suppose that those conditions are the results of vital agencies of which no traces have descended to living plants. Some further important conclusions arrived at by the late Professor DE BARY seem to me to have a practical bearing upon the subject. Speaking of the origin of intercellular spaces, he says, "These arise in two ways in the original masses of cells, which, at least when in the state of meristem, are always in uninterrupted connexion. First, by separation of *permanent** tissue elements, as the result of their unequal surface-growth in different directions, the original common walls splitting, while the common limiting layer, which was originally present is—perhaps always—dissolved. Secondly, by disorganisation, dissolving, or in many cases rupture of certain *transitory* cells, or groups of cells, which are surrounded by permanent tissues. We may call the first mode of origin *schizogenetic*, the second *lysigenetic*" ("Comparative Anatomy of the Vegetative Organs of the Phanerogams and Ferns," p. 200).

In the above passages DE BARY had chiefly in view the formation of cavities destined to be occupied by gums, resins, and various other *unorganised* secretions; whereas, in the case of our fossil plants, though we have to deal with similarly enlarged cavities, these latter are destined to be occupied by an *organised* cellular parenchyma; but these differences in their ultimate purpose do not materially affect the way in which the newly-formed and expanding cavities are brought into existence. The essential points established by DE BARY are: first, that vertically elongated, more or less cylindrical canals can be developed even in *permanent* tissues where such hollow spaces had no previous existence; and, secondly, that such cavities may be

* The *italics* are Professor DE BARY'S.

formed alike by the one or the other of the two processes, which he respectively names *schizogenetic* and *lysigenetic*. So far as I can see at present, we must choose between these two processes in seeking an explanation of the development of the medullary area and the coincident annular expansion of the vasculo-medullary cylinder, so characteristic of all the Carboniferous Lepidodendroid plants.

In the preceding Memoir I have once more shown (figs. 1–6) that a stem or branch, the transverse section of which reveals a large and conspicuous parenchymatous medulla surrounded by a tracheidal, vasculo-medullary cylinder, frequently can, and possibly always does, give off to a much younger and smaller twig a *solid* axial bundle, in the interior of which no traces of a medulla can be seen. I have also again demonstrated (figs. 7–15) that a very young twig, destined in the future to enlarge into a branch, but in which the axial bundle of tracheids or vessels (fig. 8) is solid, not a hollow cylinder, and in which no traces of parenchyma can be detected, undergoes changes as it grows older and larger; the axial vascular bundle becomes more and more hollow, whilst, in its expanding interior, a cellular medulla, at first very small, and consisting of but a few cells (fig. 9), becomes gradually larger (figs. 10, 11, 12), and its component cells more numerous, as explained in the Memoir. These are indisputable *facts*, whatever may be the explanation of them. In seeking such an explanation, I repeat, we are shut up to the two processes described by DE BARY, to account for the expansion of the solid axial vascular bundle into a hollow cylinder. Either the youngest, first formed tracheids were *pushed asunder* by the centrifugal pressure of the growing and multiplying cells of the young medulla developing in their midst (a *schizogenetic* process), or they were *absorbed (lysigenetically)* under the influence of the same pressure. In the first case, all the relations of contact and propinquity between the primary vessels or tracheids composing the bundle must have been subjected to a continued succession of changes; because not only had the *primary* vessels, &c., to enclose a larger area than previously, but they had to allow the intercalation of a succession of newer additional vessels supplied from the investing meristemic cortex. This latter necessity is demonstrated by the fact that, as the vascular ring increased in diameter, enclosing at the same time a growing medulla, the actual number of its component vessels likewise increased. My present conviction is that the schizogenetic hypothesis is most in harmony with the known facts; but, should further investigations fail to support this conclusion, which I scarcely conceive to be possible, we must then fall back upon the second hypothesis. In doing this we must conclude that *all* the vessels or tracheids seen in fig. 8 were doomed to undergo absorption, and thus make room for the young medulla of fig. 9, and that, in like manner, the successive vascular rings of figs. 10–12 had but a temporary existence; the only permanent vessels being those of fig. 15, *b*, after the formation of which the development of the exogenous zone, *d*, always appears to have arrested the further expansion alike of the medulla and of its investing vascular cylinder in these Lepidodendroid plants.* The objection, in the present case, to this

* A note on p. 466 of my Memoir XII. on this subject is, I fear, an erroneous one.

lysigenetic hypothesis is strong and definite. We never find that the tracheids forming the inner border of the ring *b*, in specimens like figs. 10–13, have their walls torn or disorganised, which must have been the case had these inner tracheids been subject to a continuous destructive action.

Professor HUGO DE VRIES, of Amsterdam, who at my request has given some little attention to this subject, has suggested to me the question—Are such sections as I have represented in figs. 7–15 really examples of branches of the same plant in various stages of development? About this I have no doubt whatever. The twig in these arborescent exogenous Lycopods, as in modern exogenous trees, is but the young state or precursor of the future branch. It is a material point, bearing upon this part of the subject, that the above arguments are not based upon some isolated example of these Lepidodendroid plants. My specimens show that the conditions to which I am once more calling attention are not isolated or rare. *They are characteristic of the entire Lepidodendroid family, whether arborescent or otherwise.* Throughout the entire group we know that the large dichotomous branches did not shoot into existence as such. They were all once slender twigs, and I am convinced that such series of sections as abound in my cabinet, corresponding to those now represented in my figures 7–15, are illustrations of twigs and branches of the same plant in successive stages of their growth.

I should also like to remark on the objection that in this and some of the preceding Memoirs I am in danger of establishing new *species* without sufficiently defining them. In fact, the establishment of *species* of Coal-plants in the strict sense of the word has not been my object. The difficulties in the way of doing this are, in my judgment, insuperable. In the earlier of this series of Memoirs I made no attempt to attach specific names to the objects which I described. I mainly sought to throw new light upon the morphology and histology of the Carboniferous plants. I soon found that, whilst one type of structure was common to the entire group of Lepidodendroid and Sigillarian plants, this type was subject to numerous remarkable modifications as regarded the details alike of structure and of growth. It became necessary, by some symbol, to facilitate reference to each of these modifications. There was no room for doubting that where such details were conspicuously *different* I was dealing with forms that were specifically distinct. But the converse was not necessarily true. It was quite possible, though incapable of demonstration, that identical modifications of vegetative structures might exist in plants in which the reproductive organs might have shown specific distinctions, as is so commonly the case amongst living Lycopodia and Selaginellæ. BRONGNIART, however, had already followed the example set by WITHAM of employing the Linnean binomial nomenclature under similar circumstances, in his descriptions of *Lepidodendron Harcourtii*, of *Sigillaria elegans*, and of *Sigillaria spinulosa*; and after some consideration I deemed it best to follow so distinguished a precedent. At the same time, I wish it to be distinctly understood that my specific names are intended to represent modifications of types of organisation rather than specific forms.—THE BOTANICAL LABORATORIES, OWENS COLLEGE, *July 31, 1889.*

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Fig. 1.

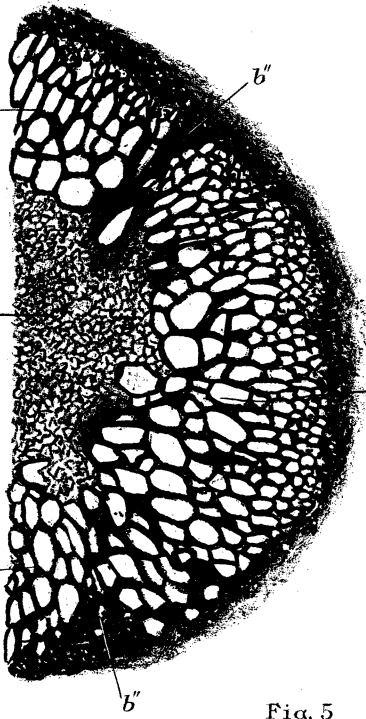


Fig. 2.



Fig. 3.

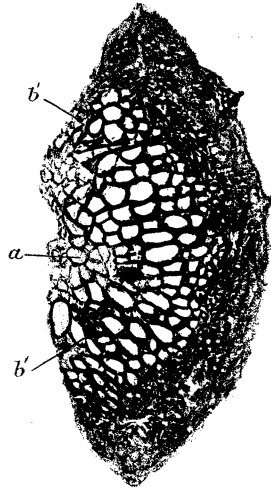


Fig. 4.

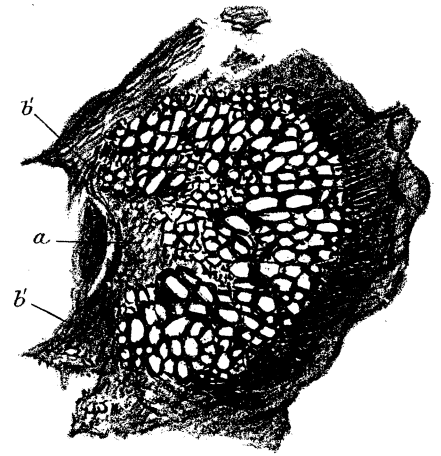


Fig. 5.

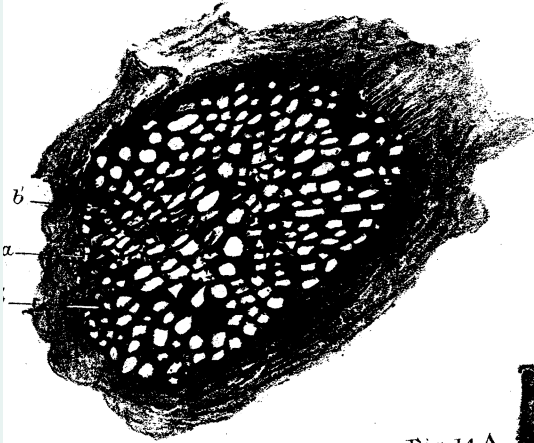


Fig. 6.

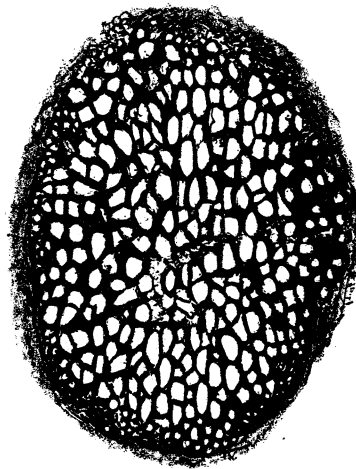


Fig. 14 B.

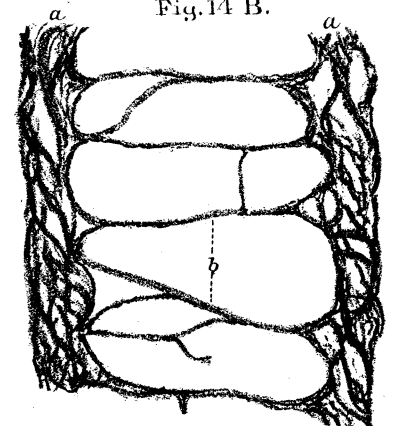


Fig. 14 A.

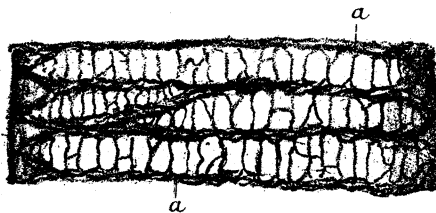


Fig. 26 A.

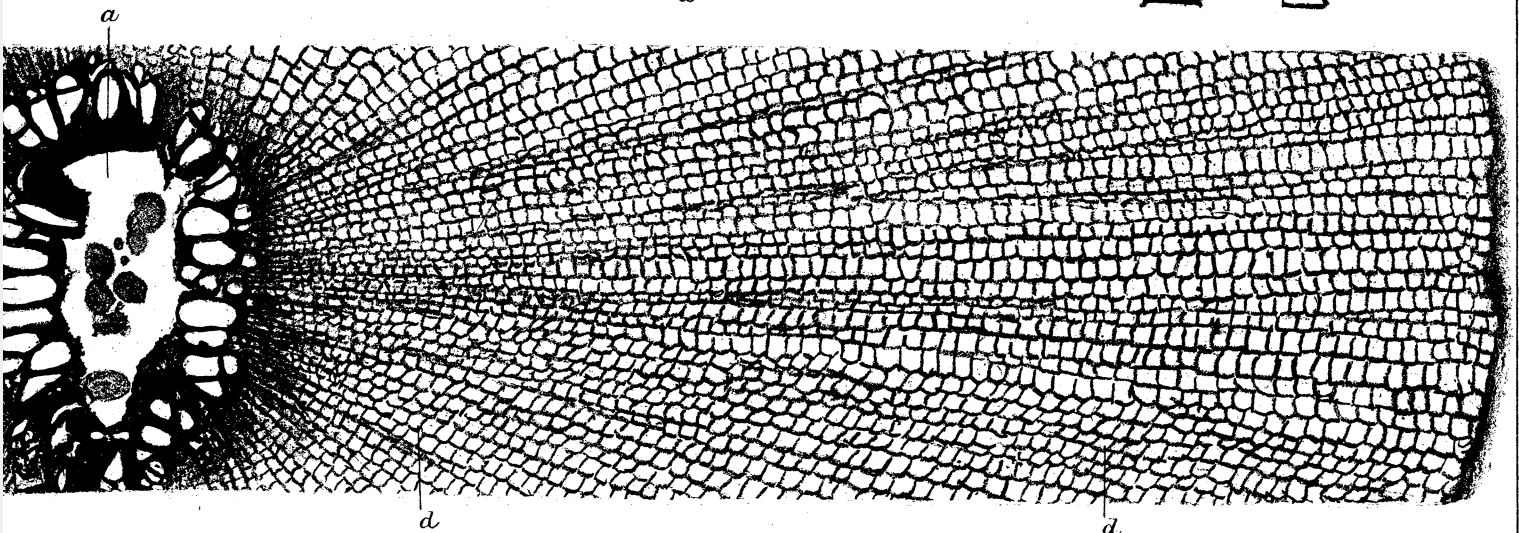
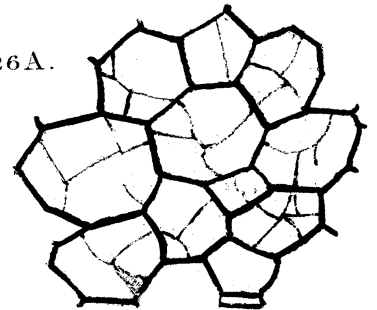


Fig. 15.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF BIOLOGICAL SCIENCES

Fig. 7.

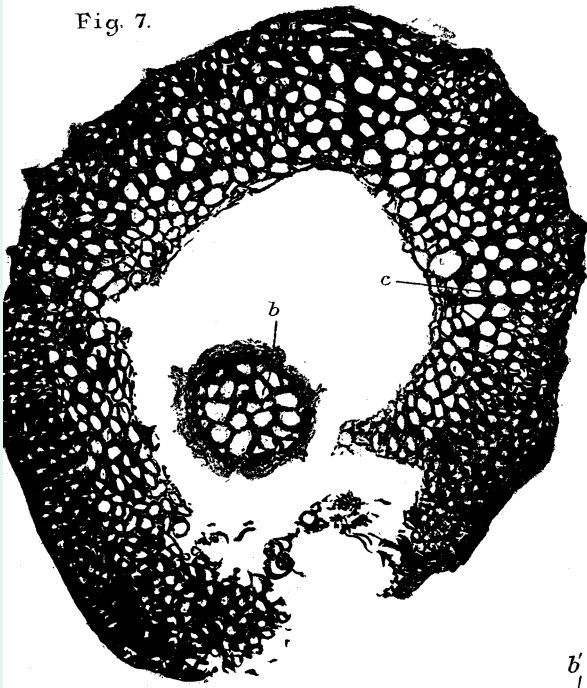


Fig. 13.

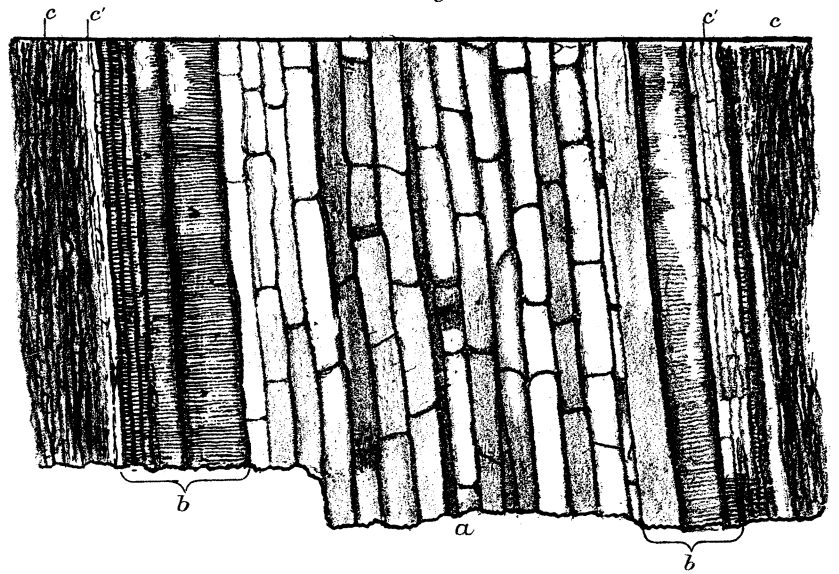


Fig. 12.

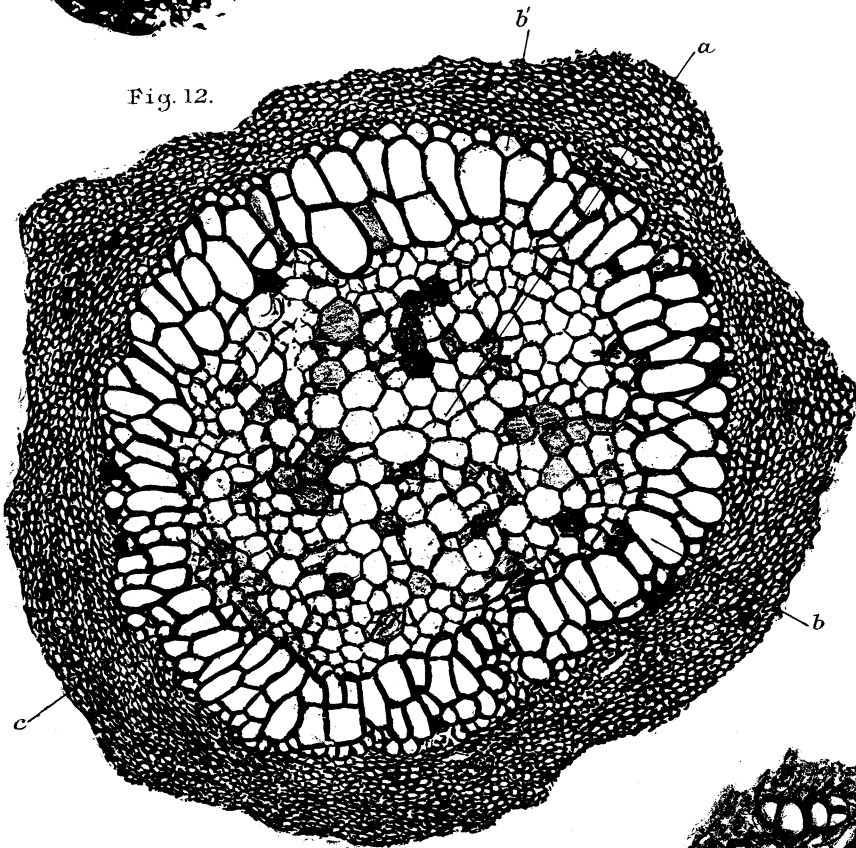


Fig. 14.

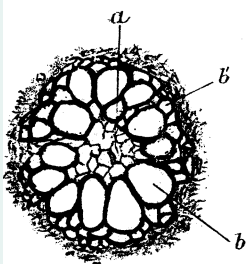
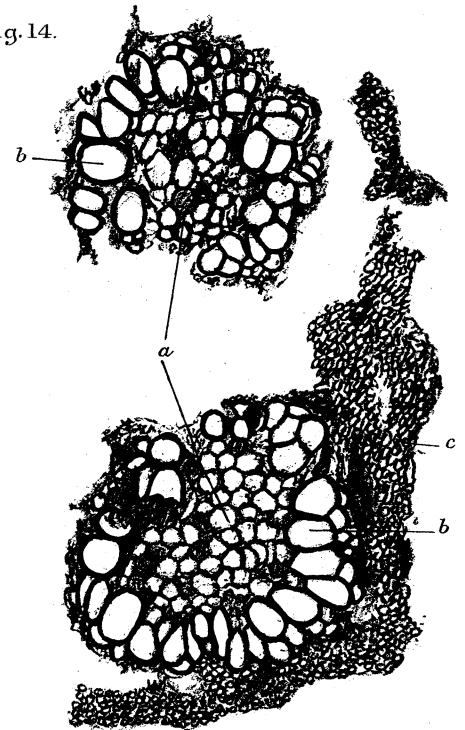


Fig. 9.

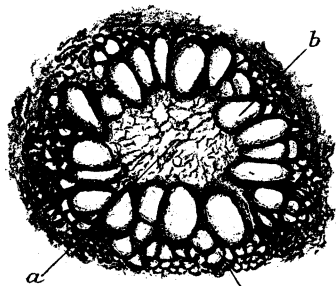


Fig. 10.

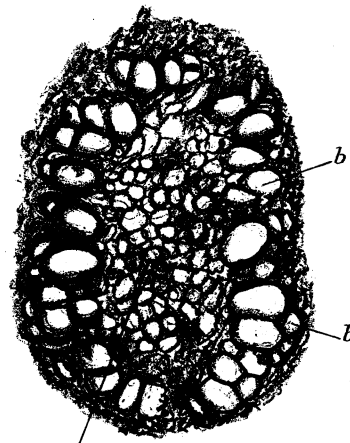


Fig. 11.

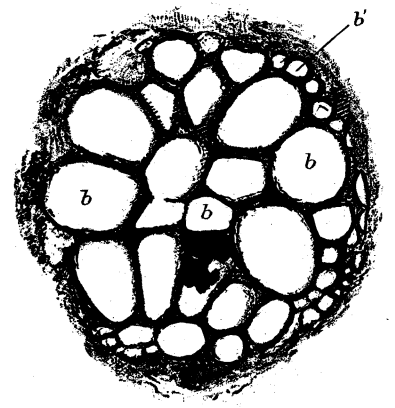


Fig. 8.

PHILosophical TRANSACTIONS OF THE ROYAL SOCIETY OF BIOLOGICAL SCIENCES

Fig. 17.

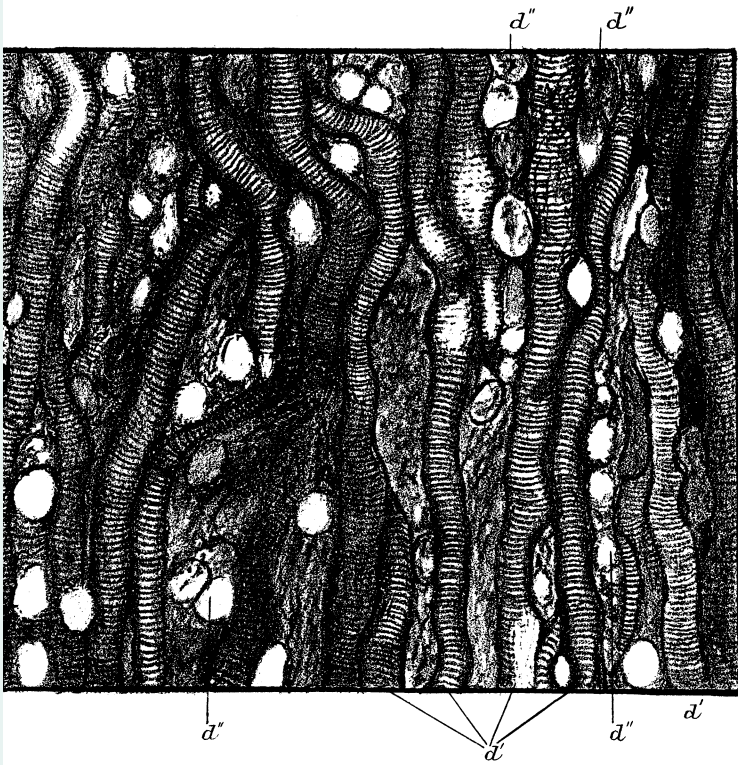


Fig. 22.

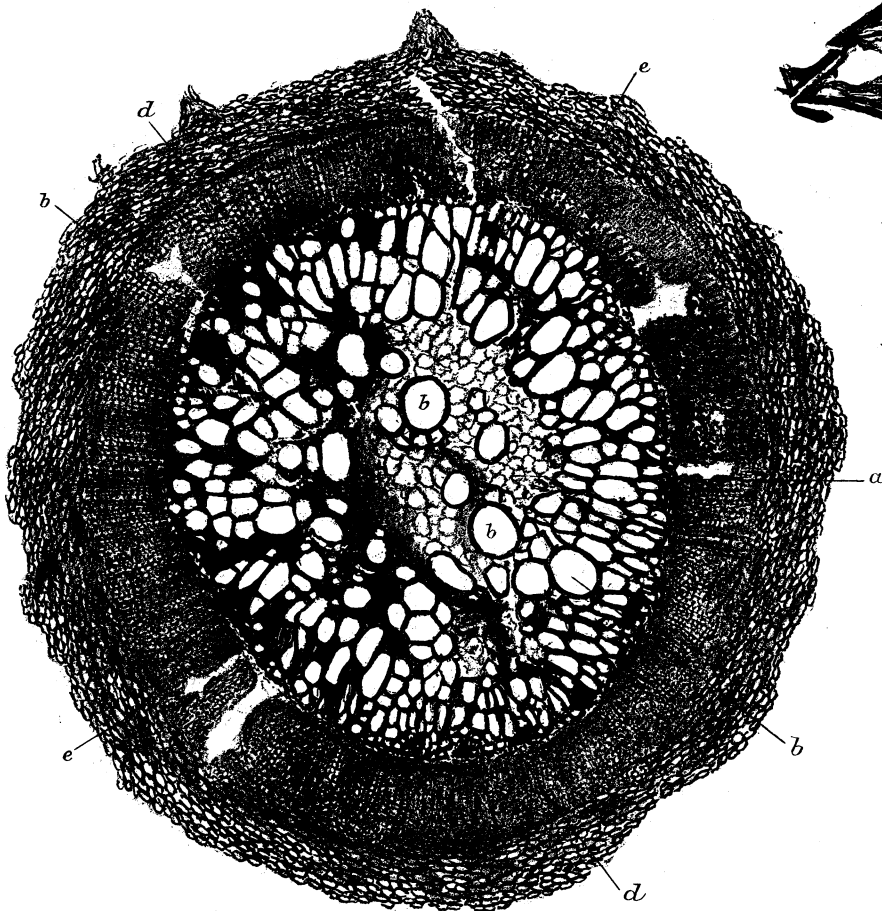
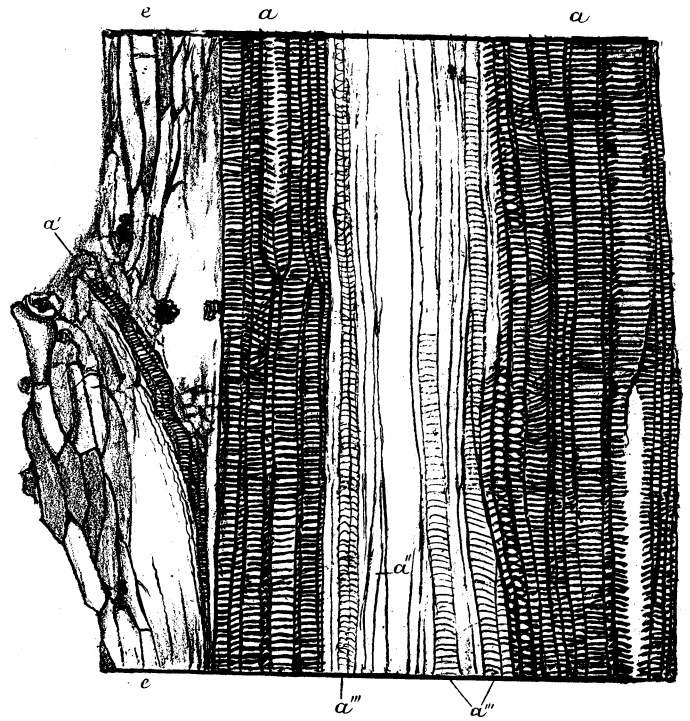


Fig. 16.



Fig. 20.

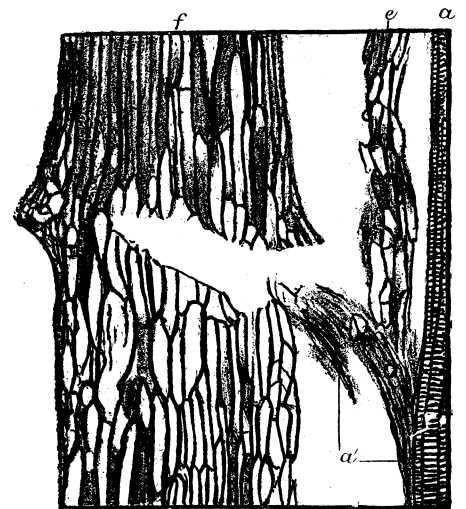


Fig. 21.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY OF BIOLOGICAL SCIENCES

Fig. 19.

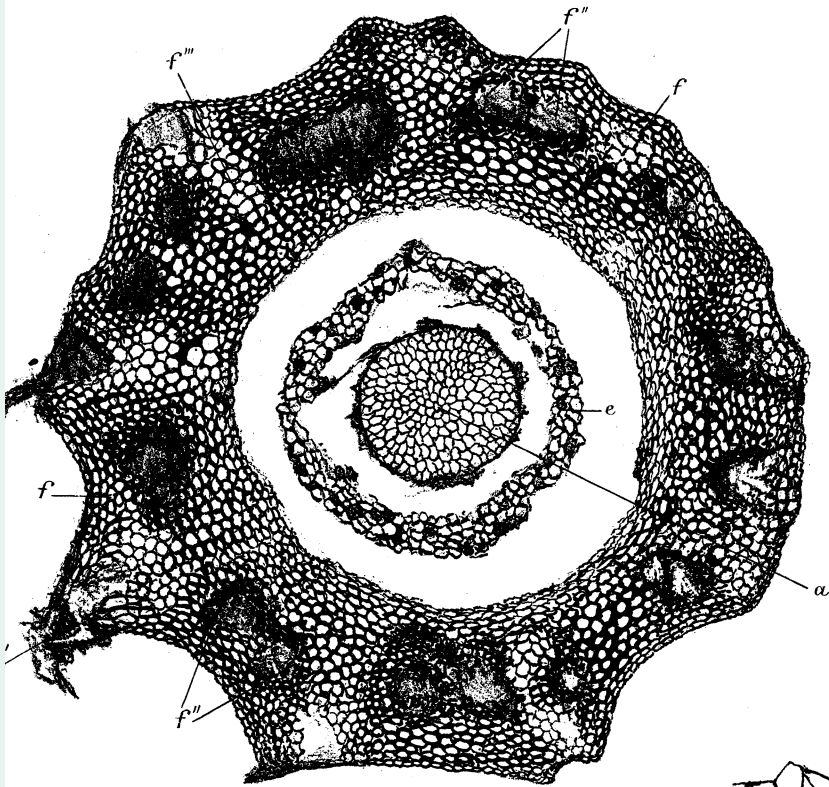


Fig. 23.

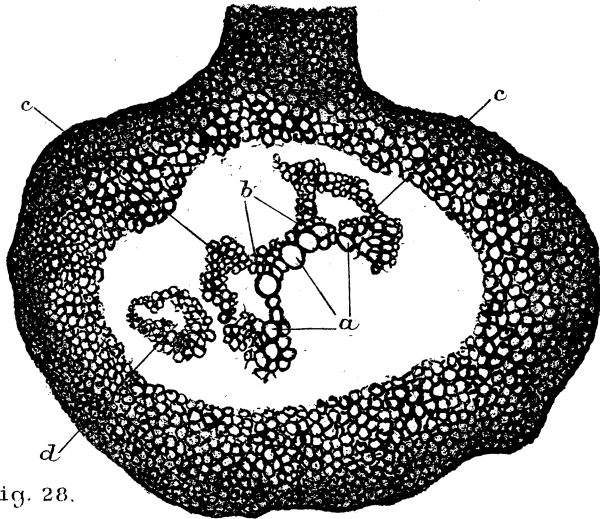
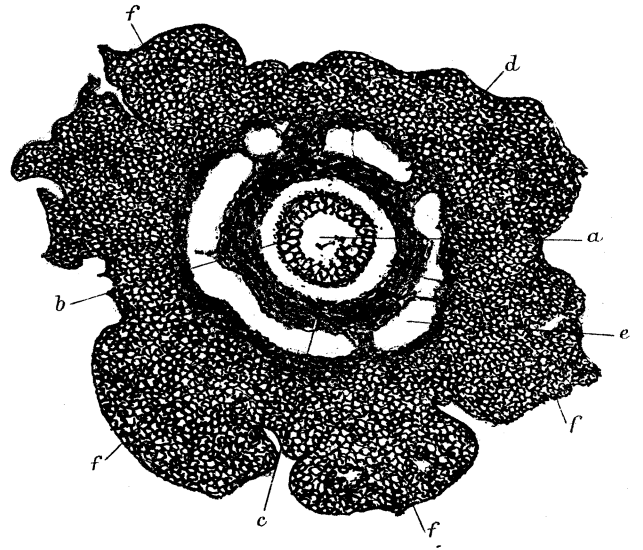


Fig. 28.

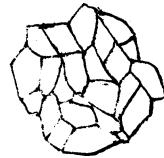


Fig. 27.



Fig. 26.

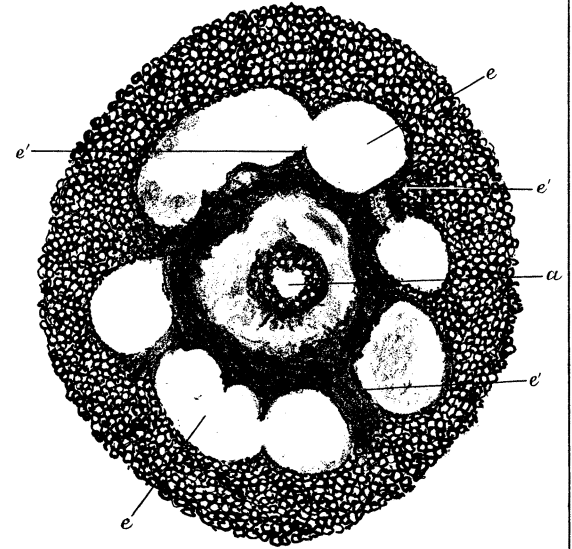


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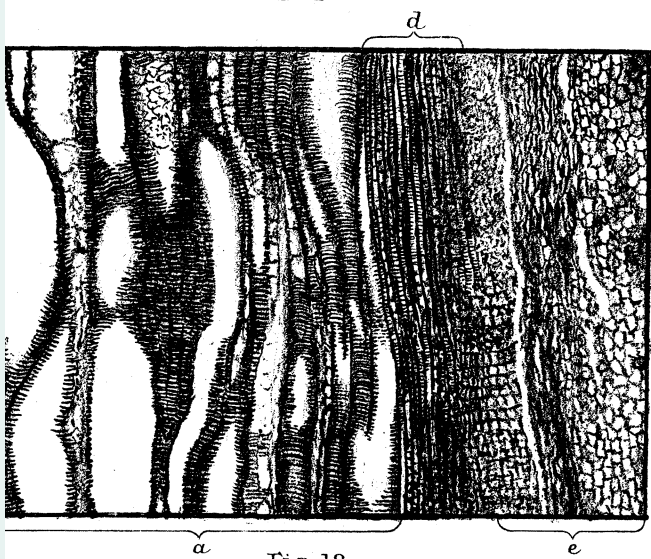


Fig. 18.

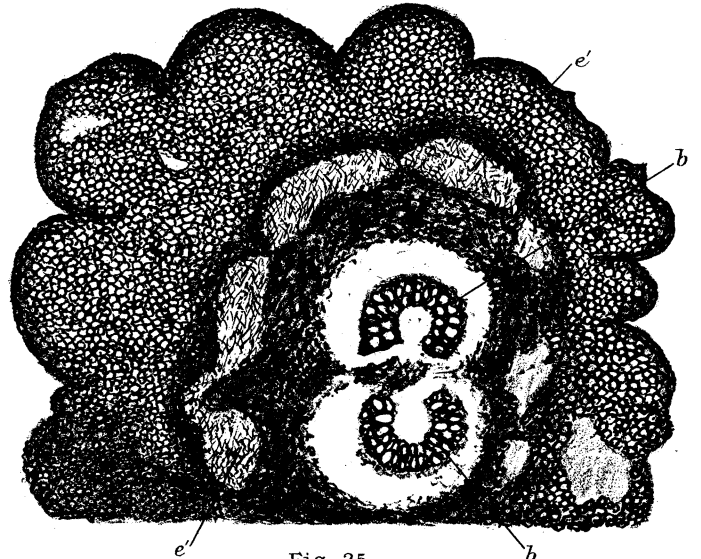


Fig. 25.

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Fig. 1.

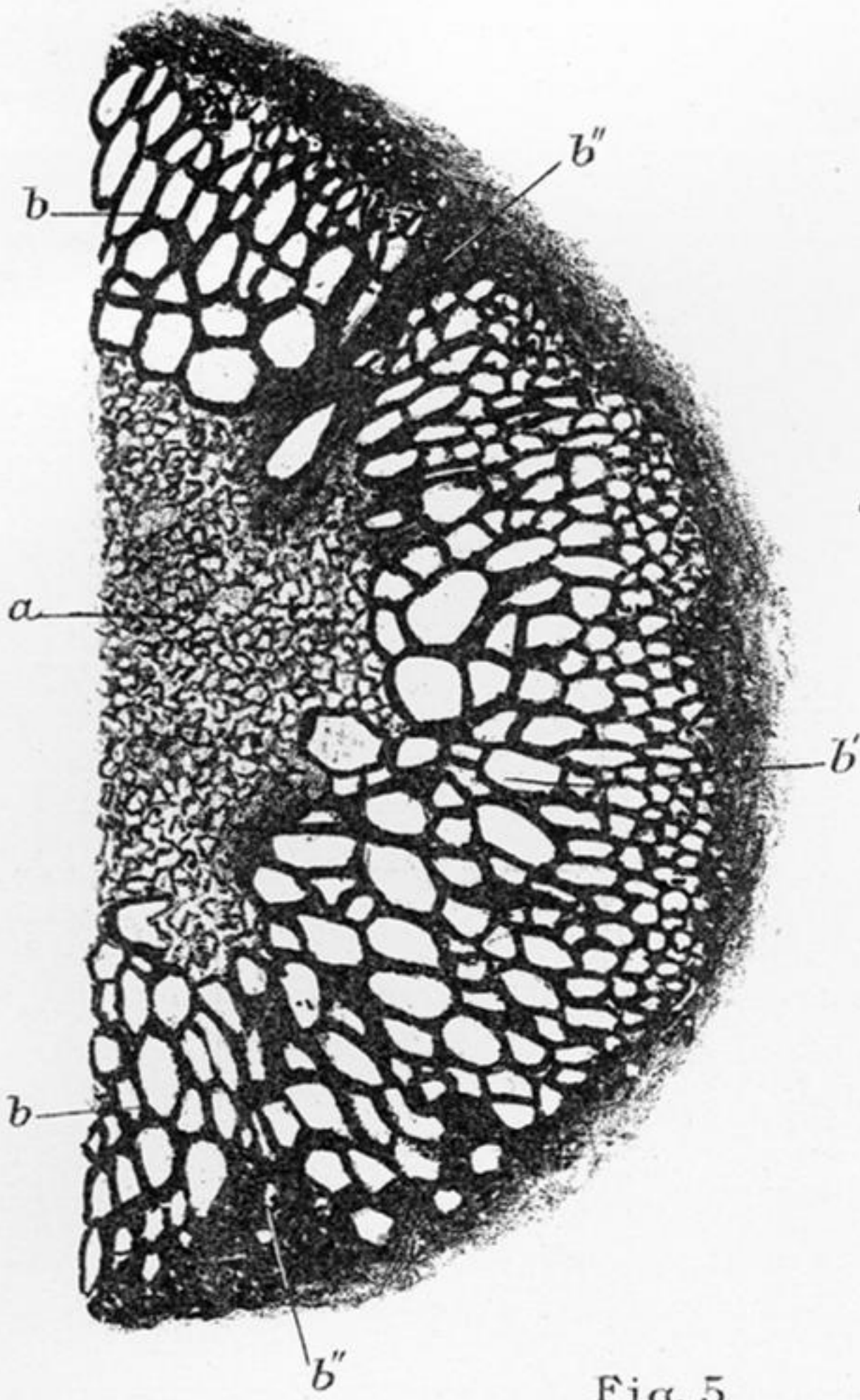


Fig. 2.

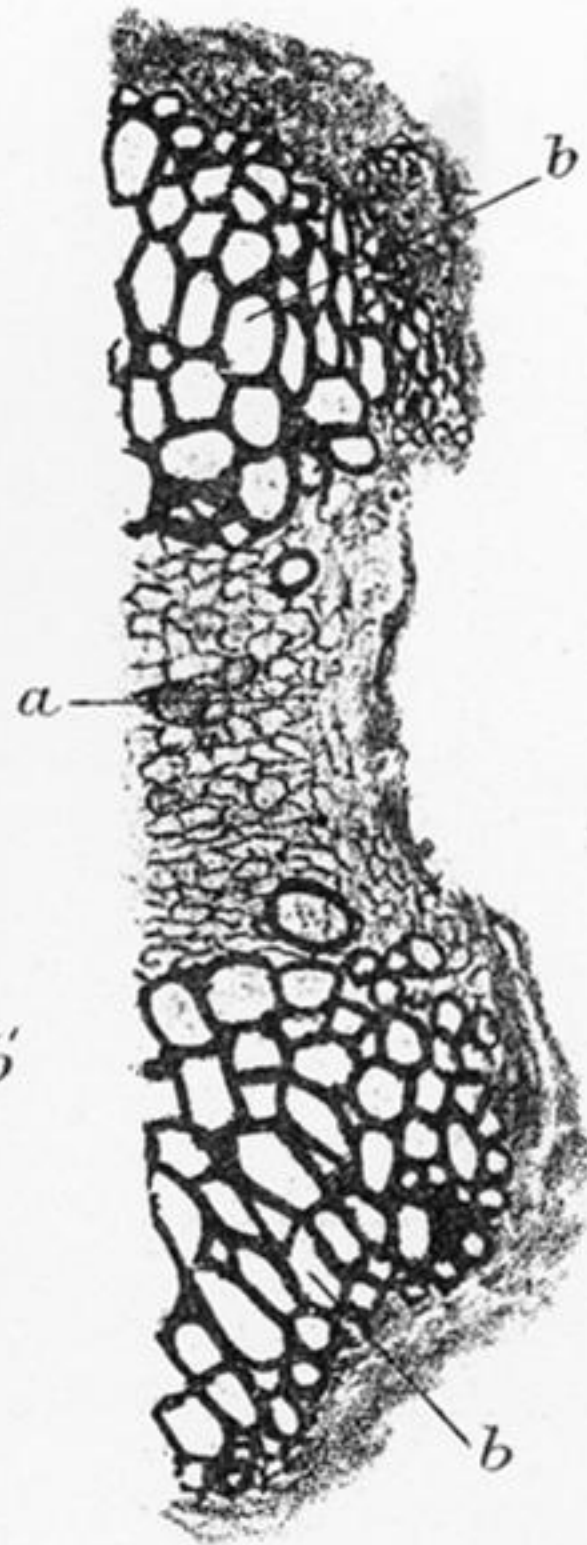


Fig. 3.

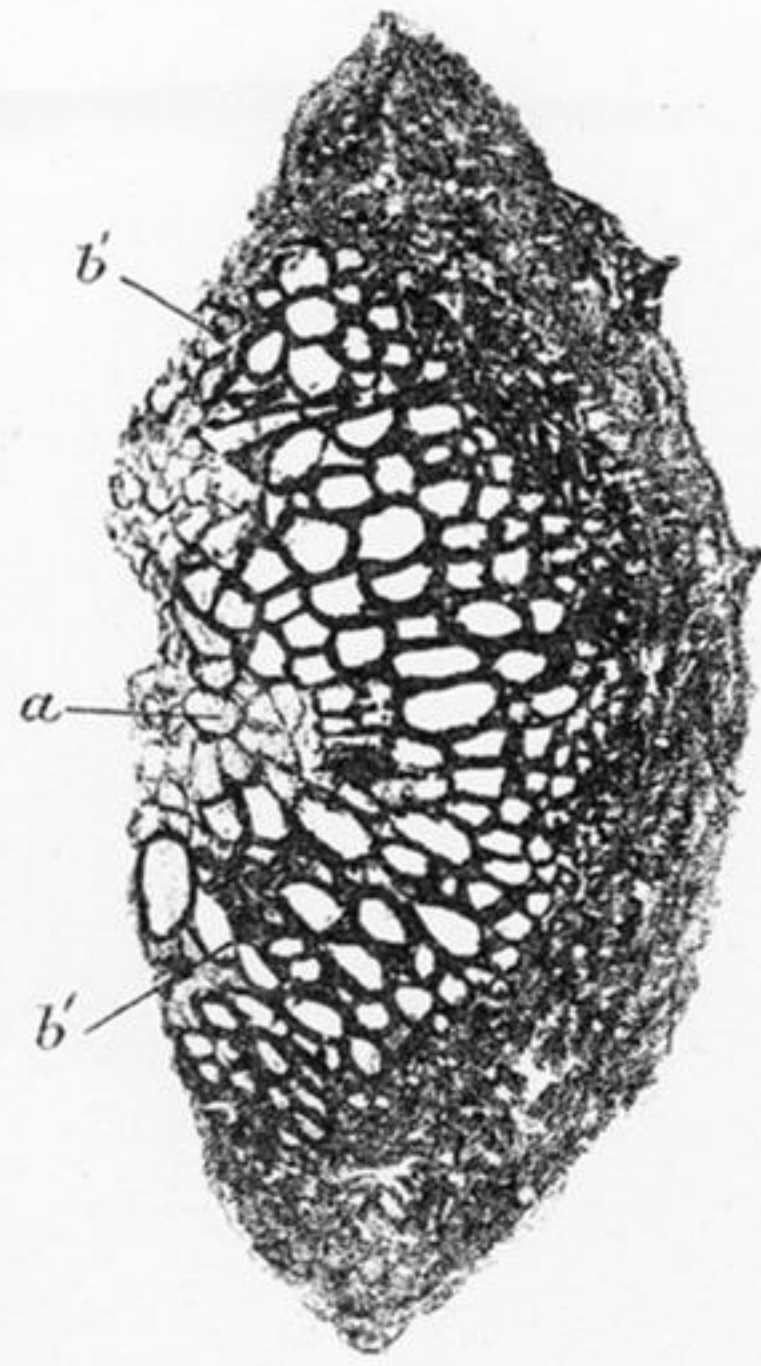


Fig. 4.

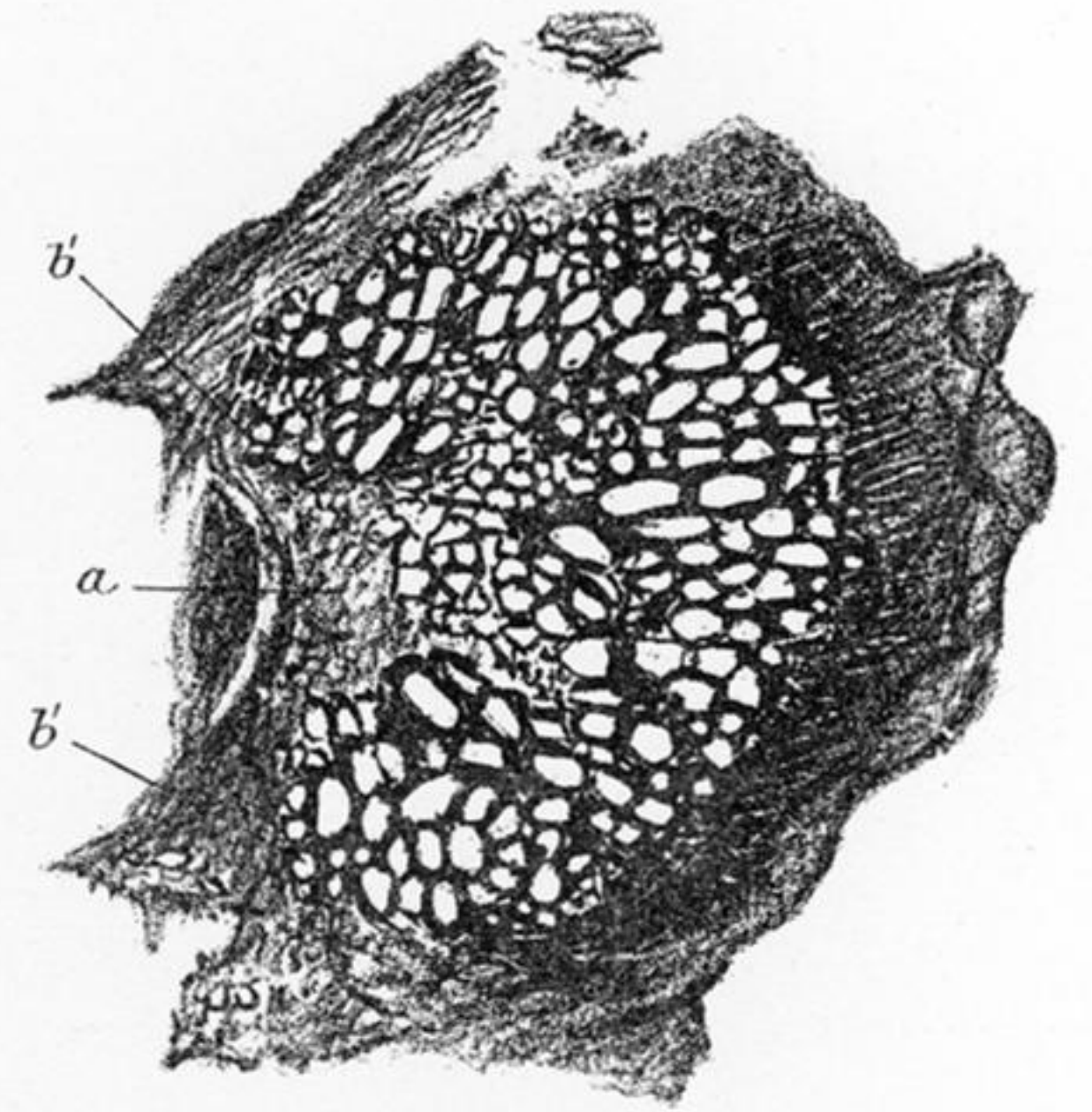


Fig. 5.



Fig. 6.

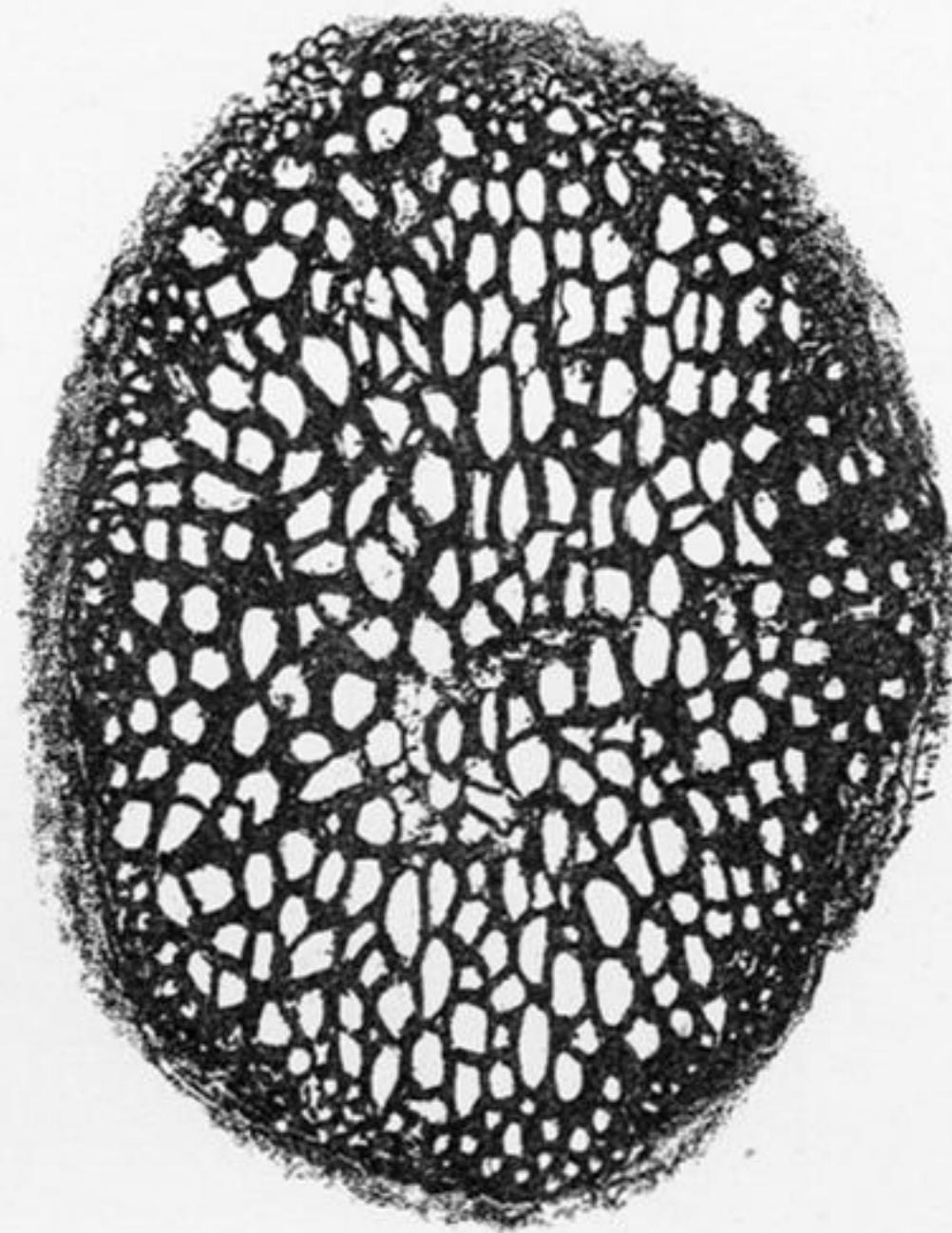


Fig. 14 B.

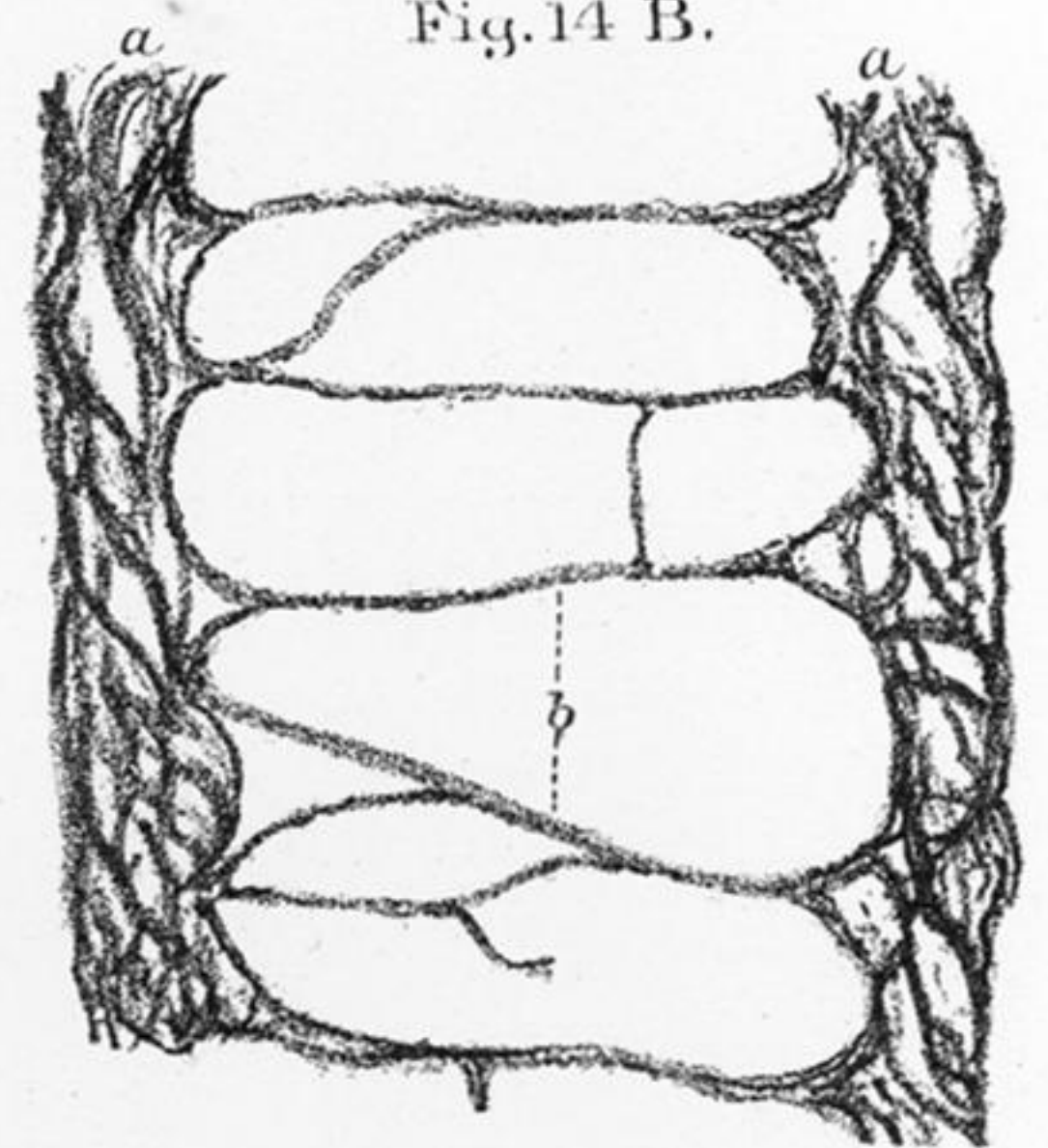


Fig. 14 A.

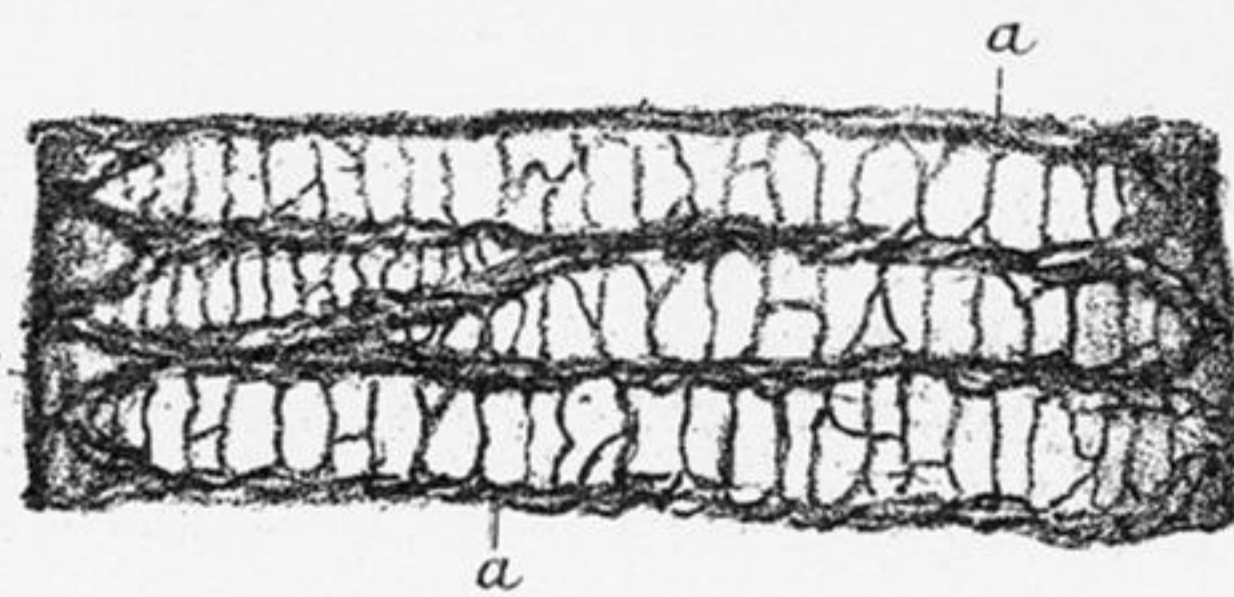


Fig. 26 A.

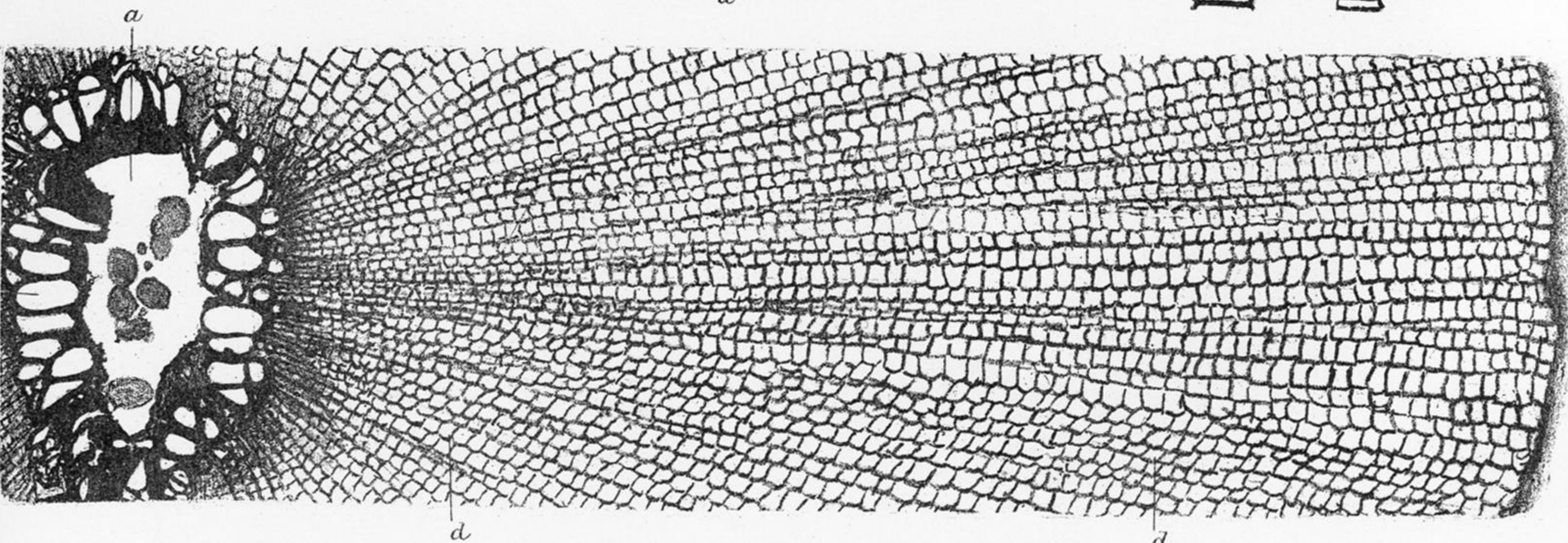
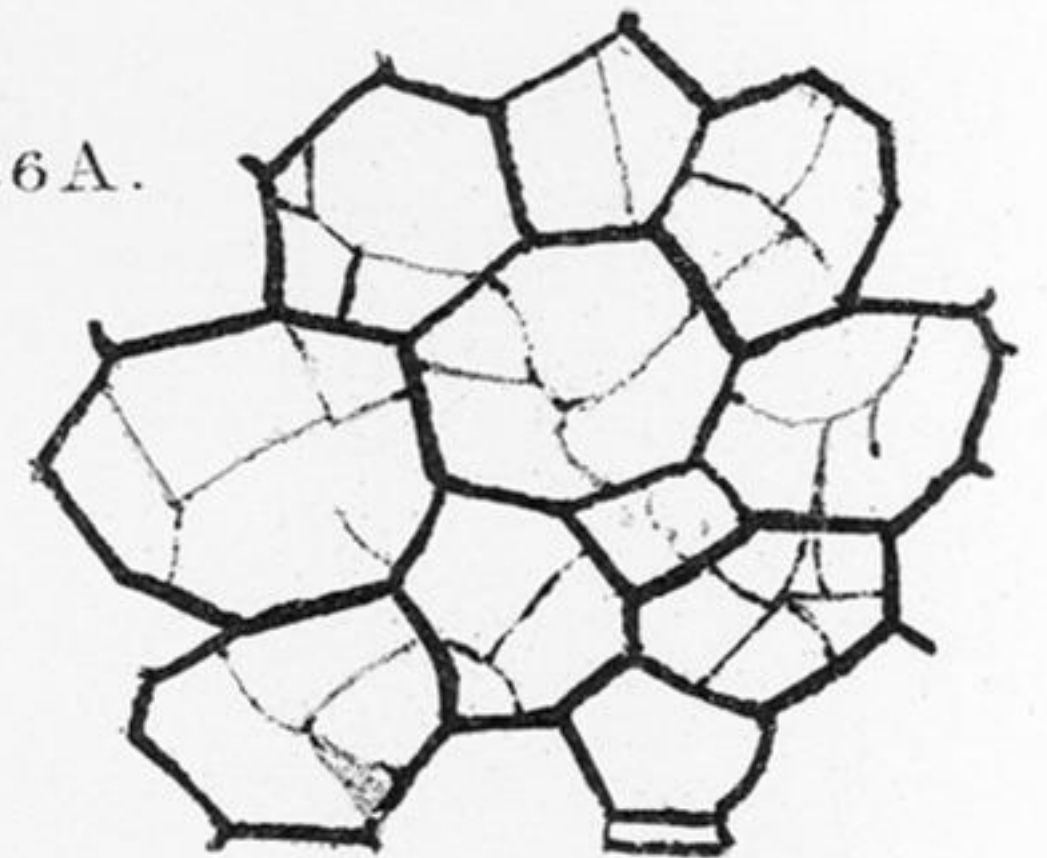


Fig. 15.

Fig. 7.

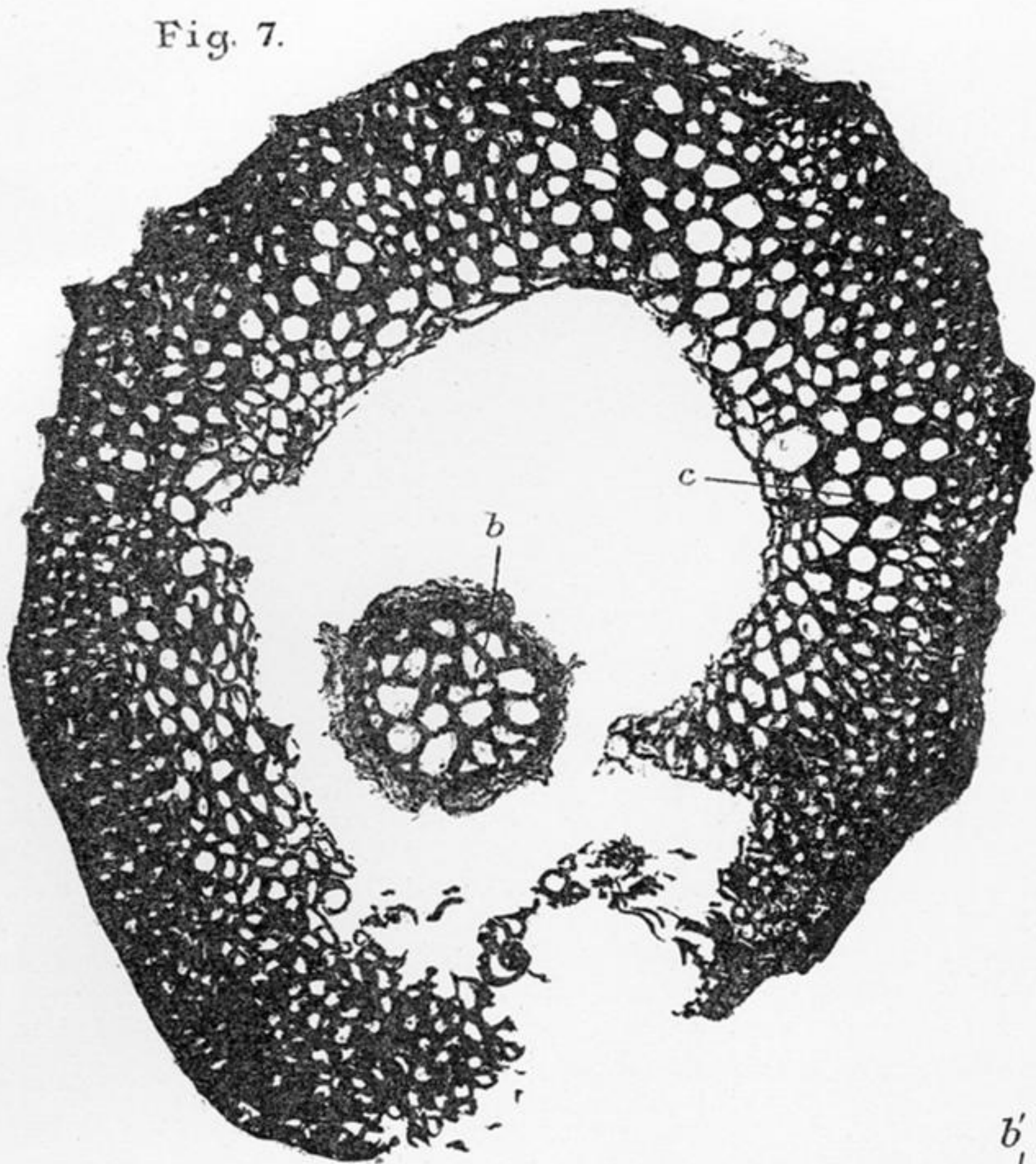


Fig. 13.

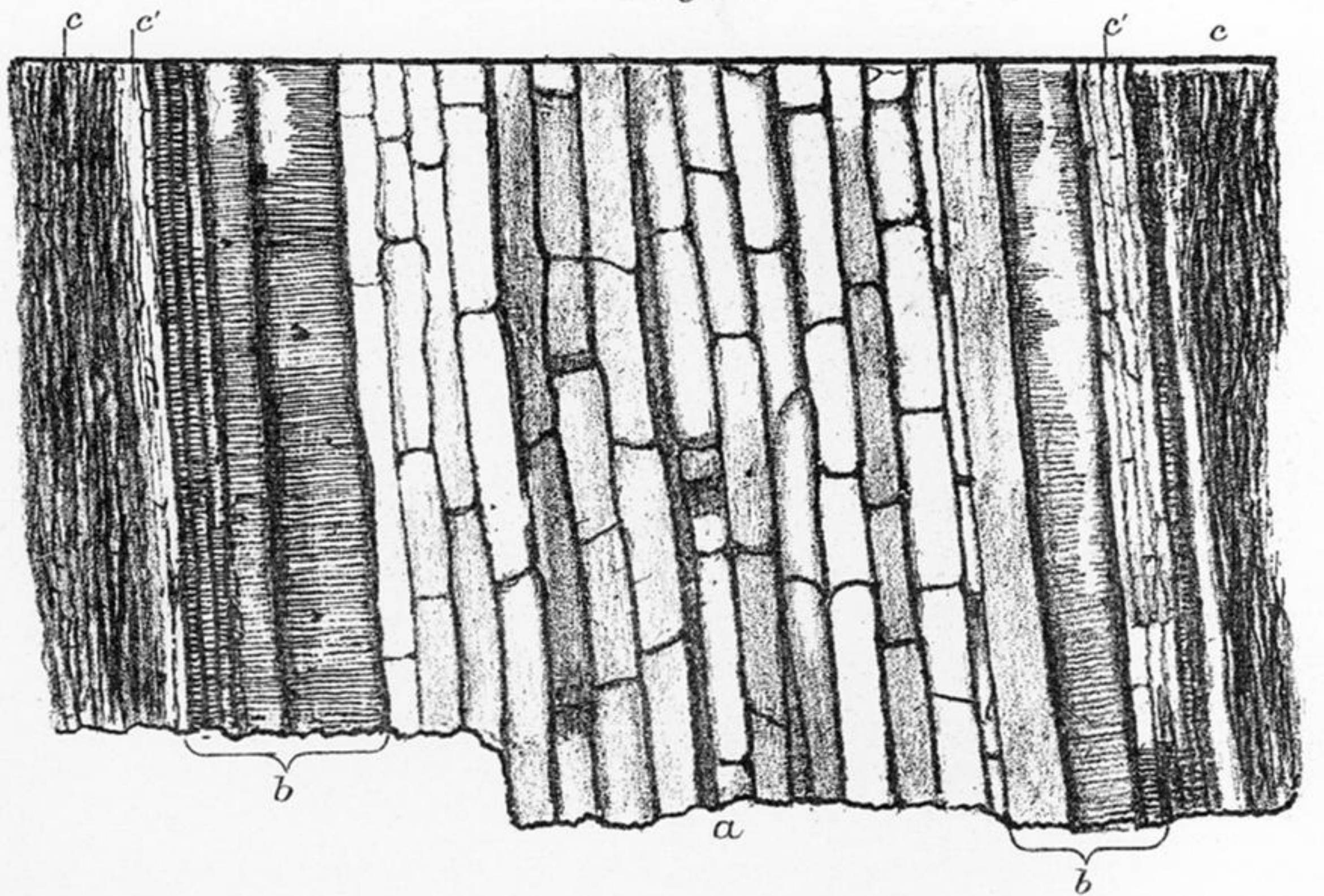


Fig. 12.

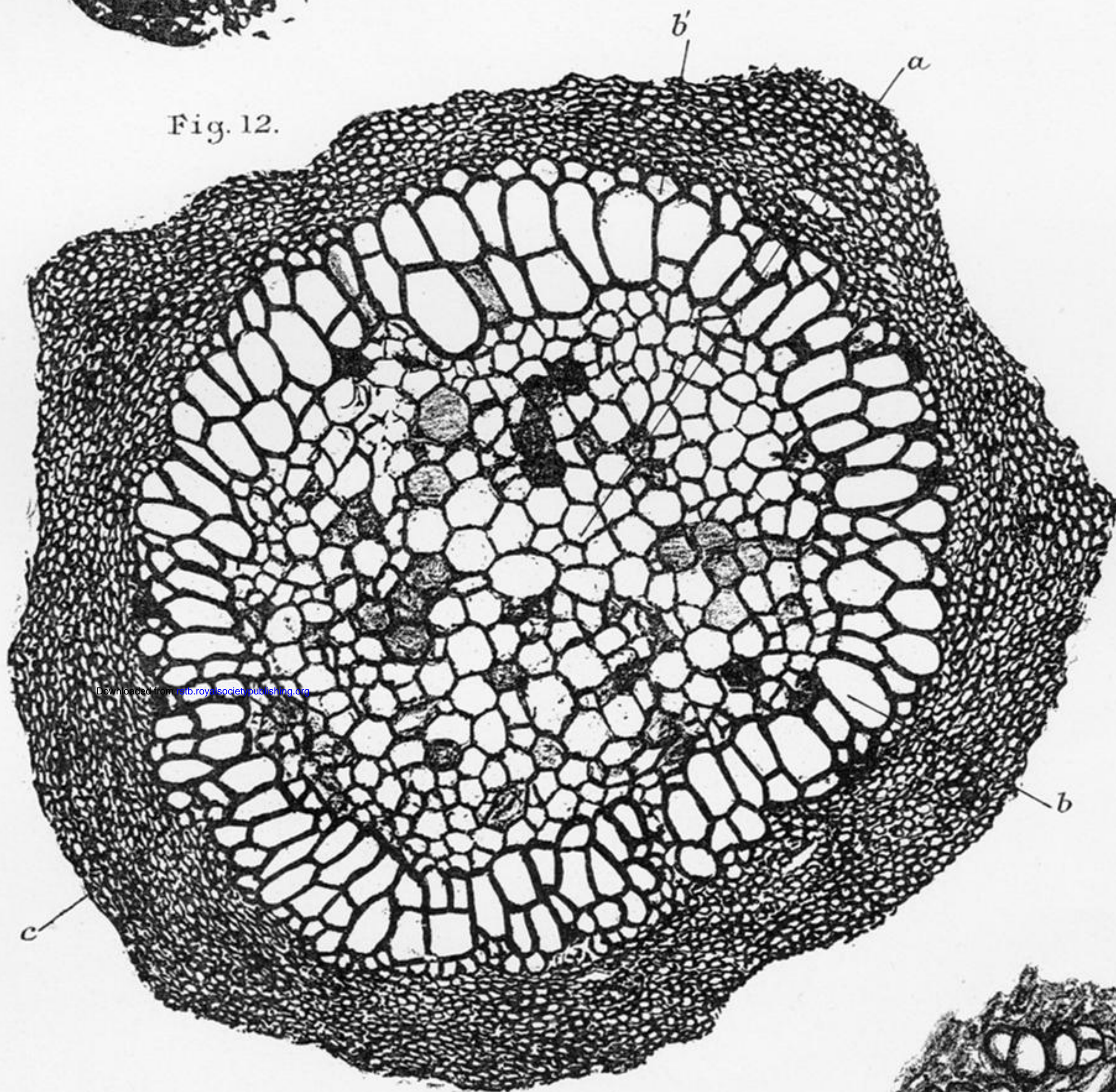


Fig. 14.

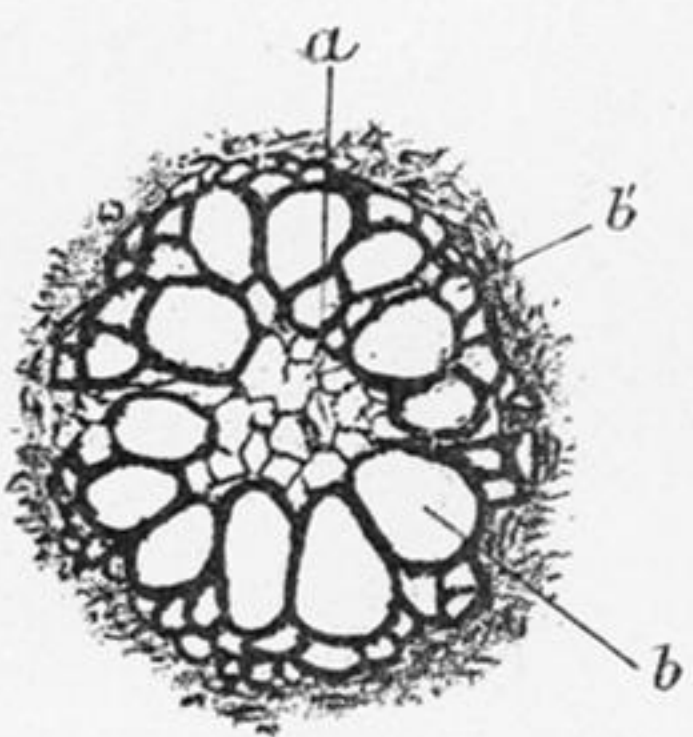
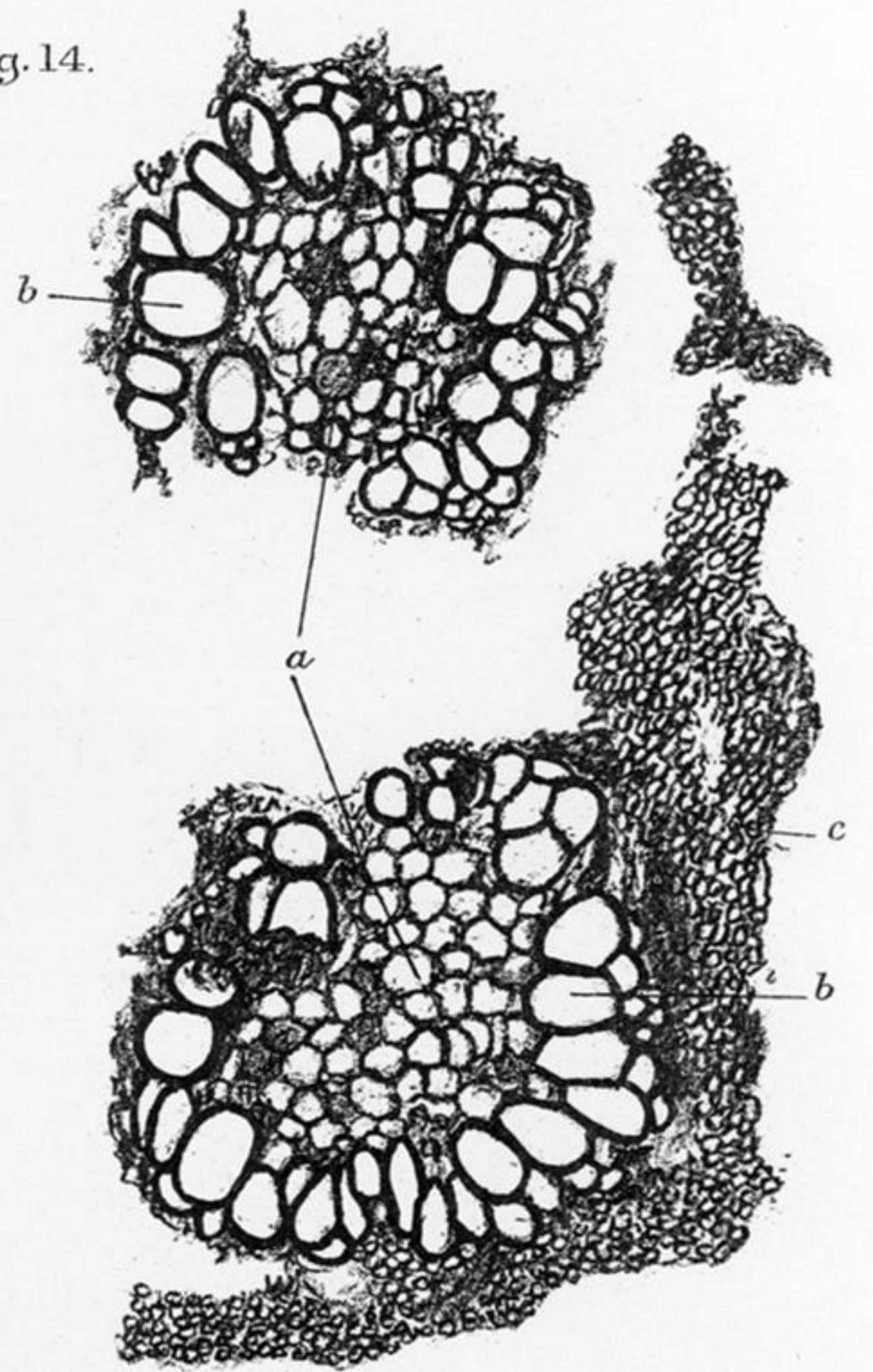


Fig. 9.

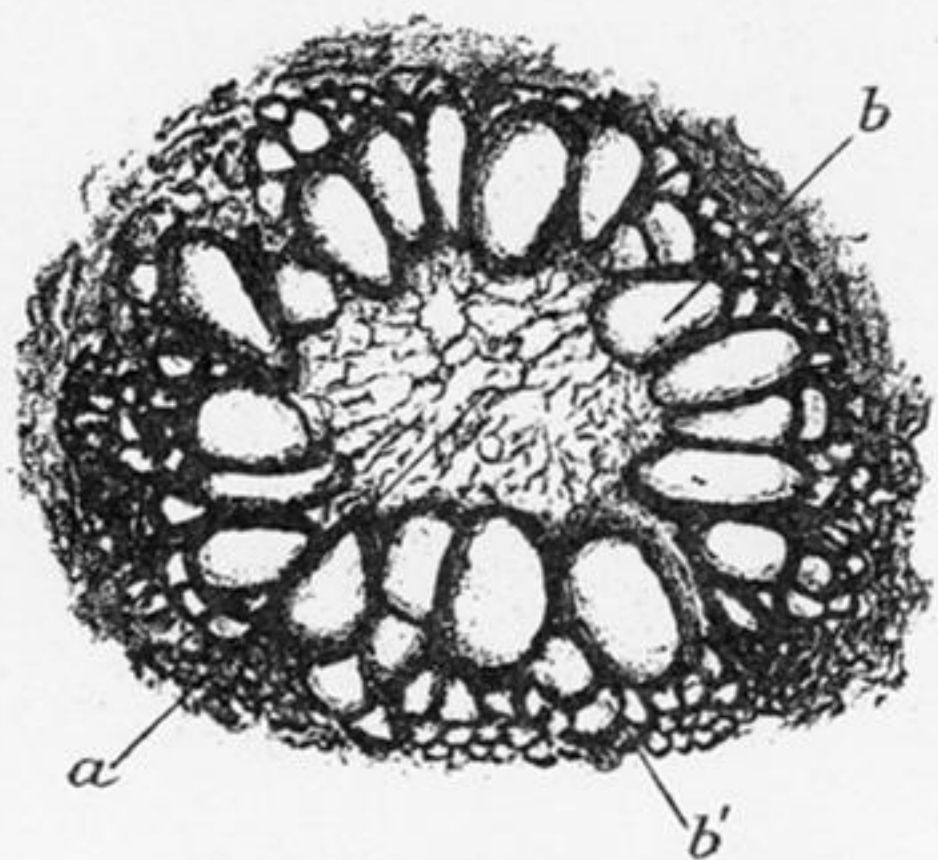


Fig. 10.

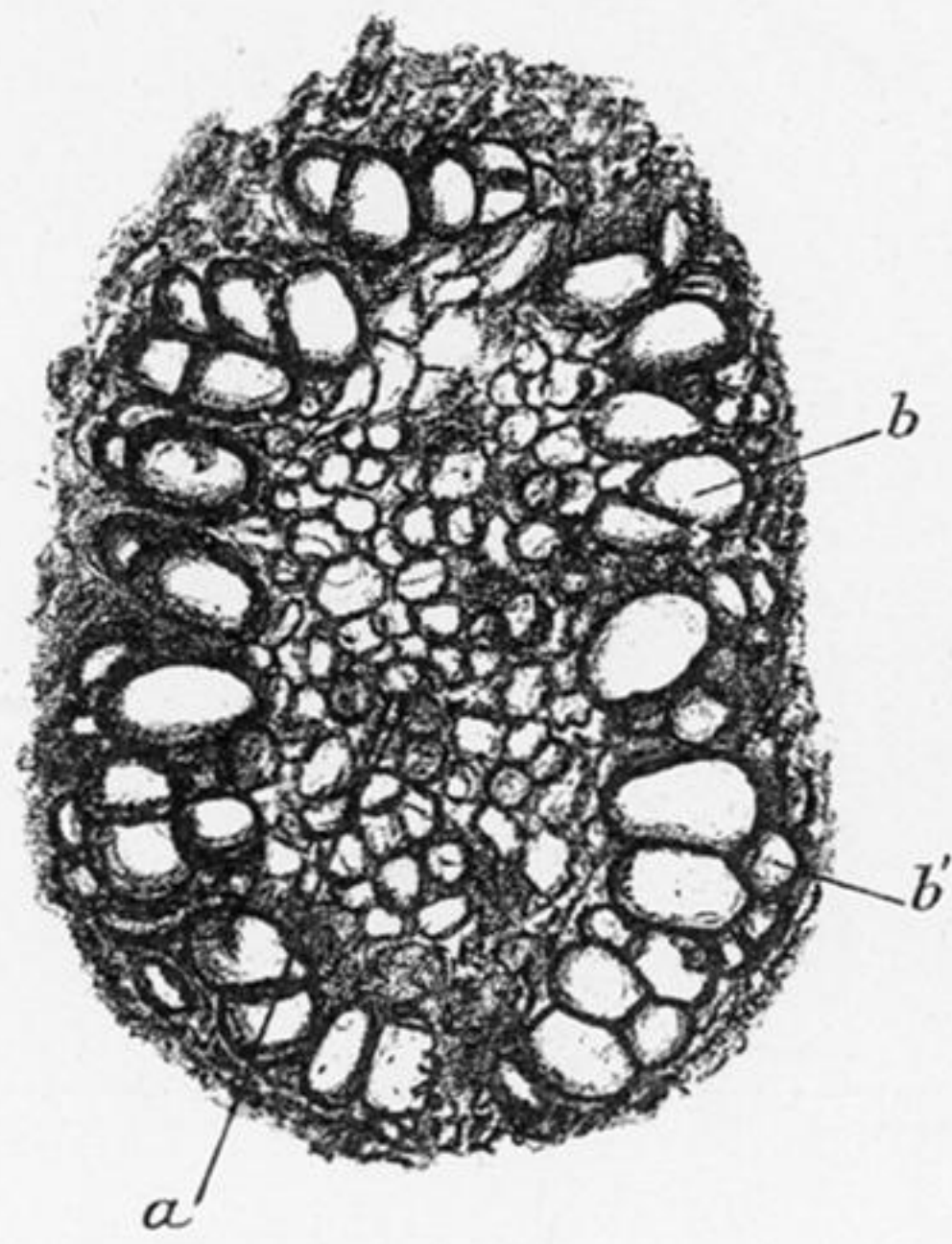


Fig. 11.

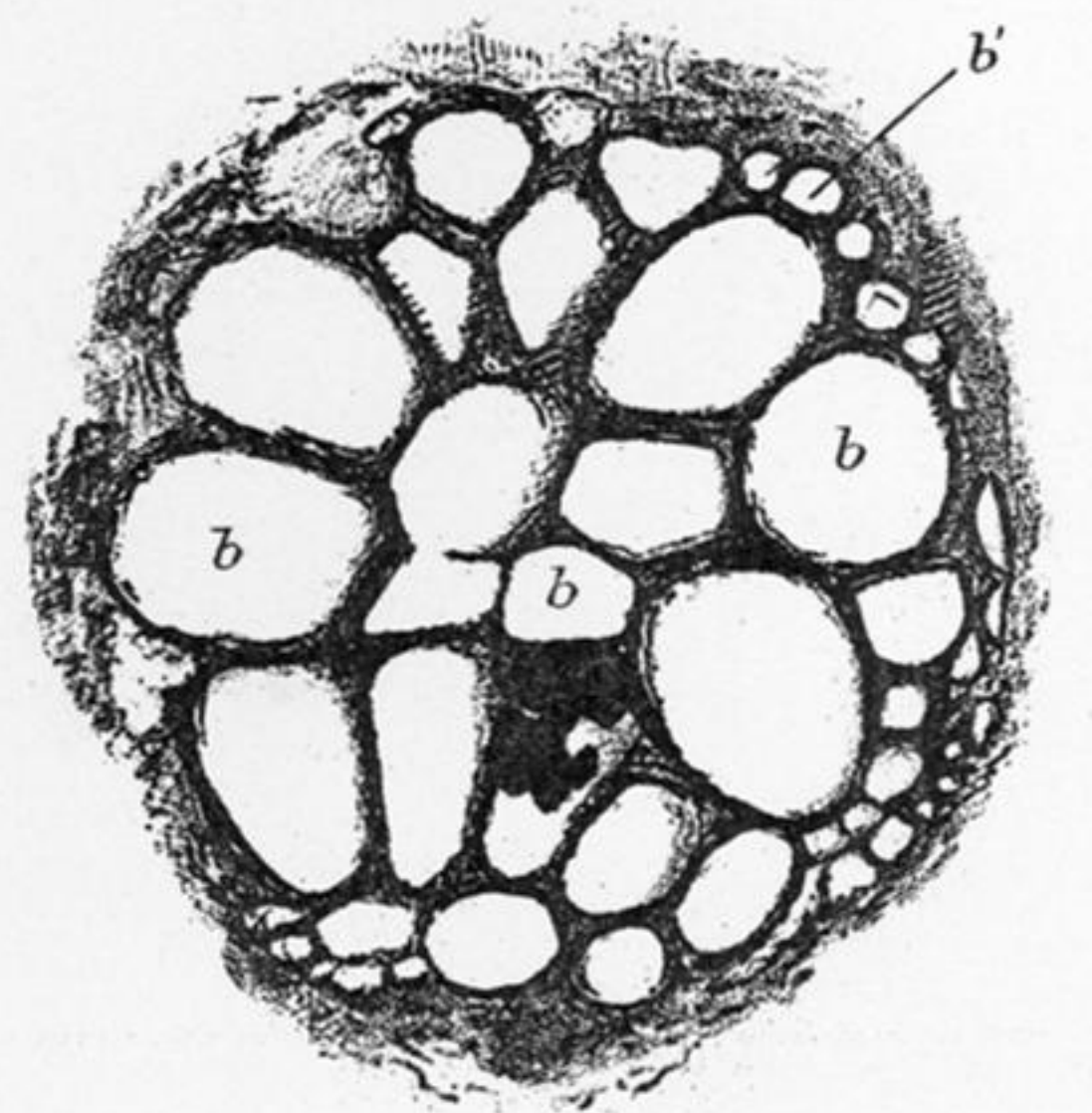


Fig. 8.

Fig. 17.

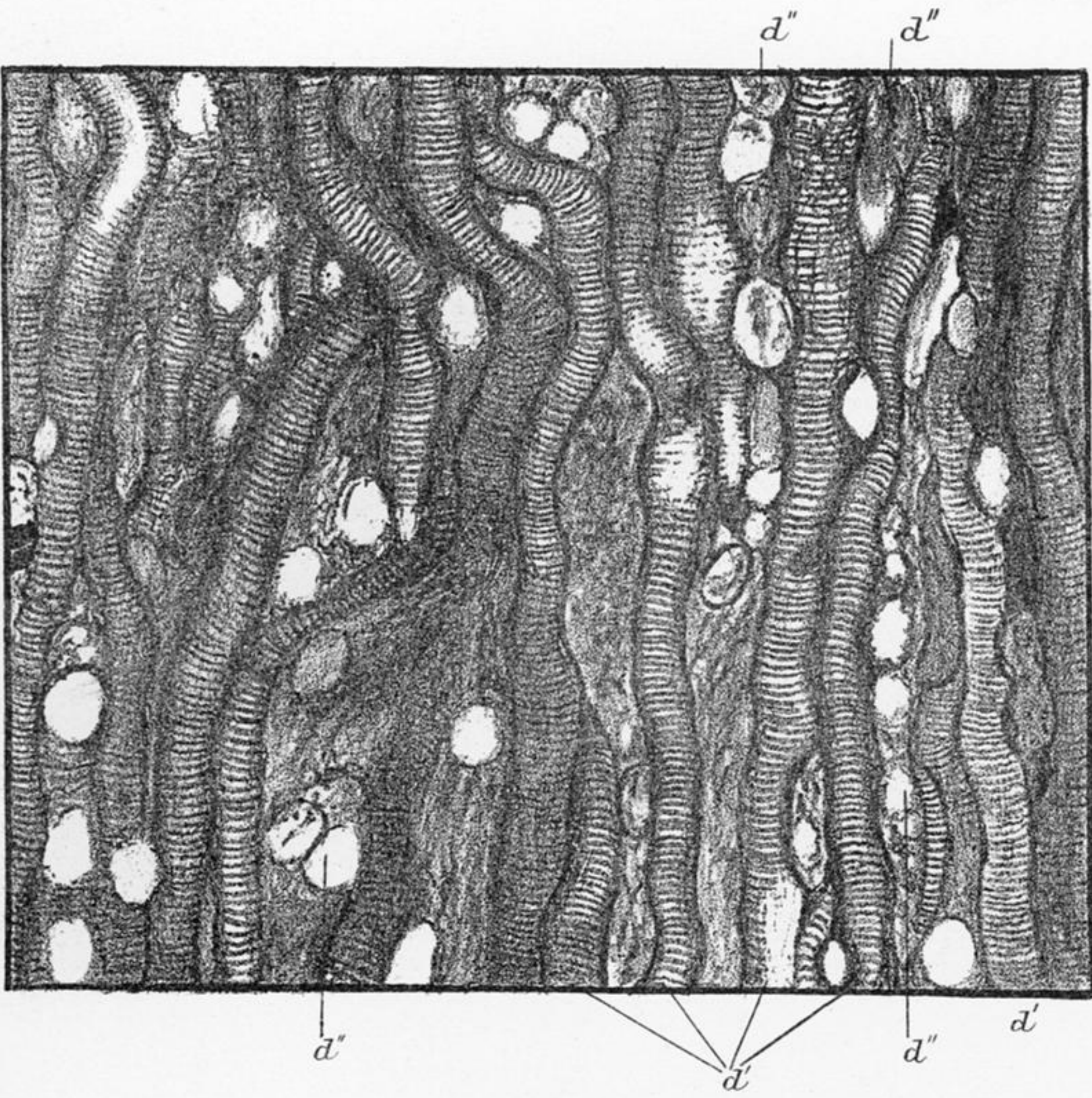


Fig. 22.

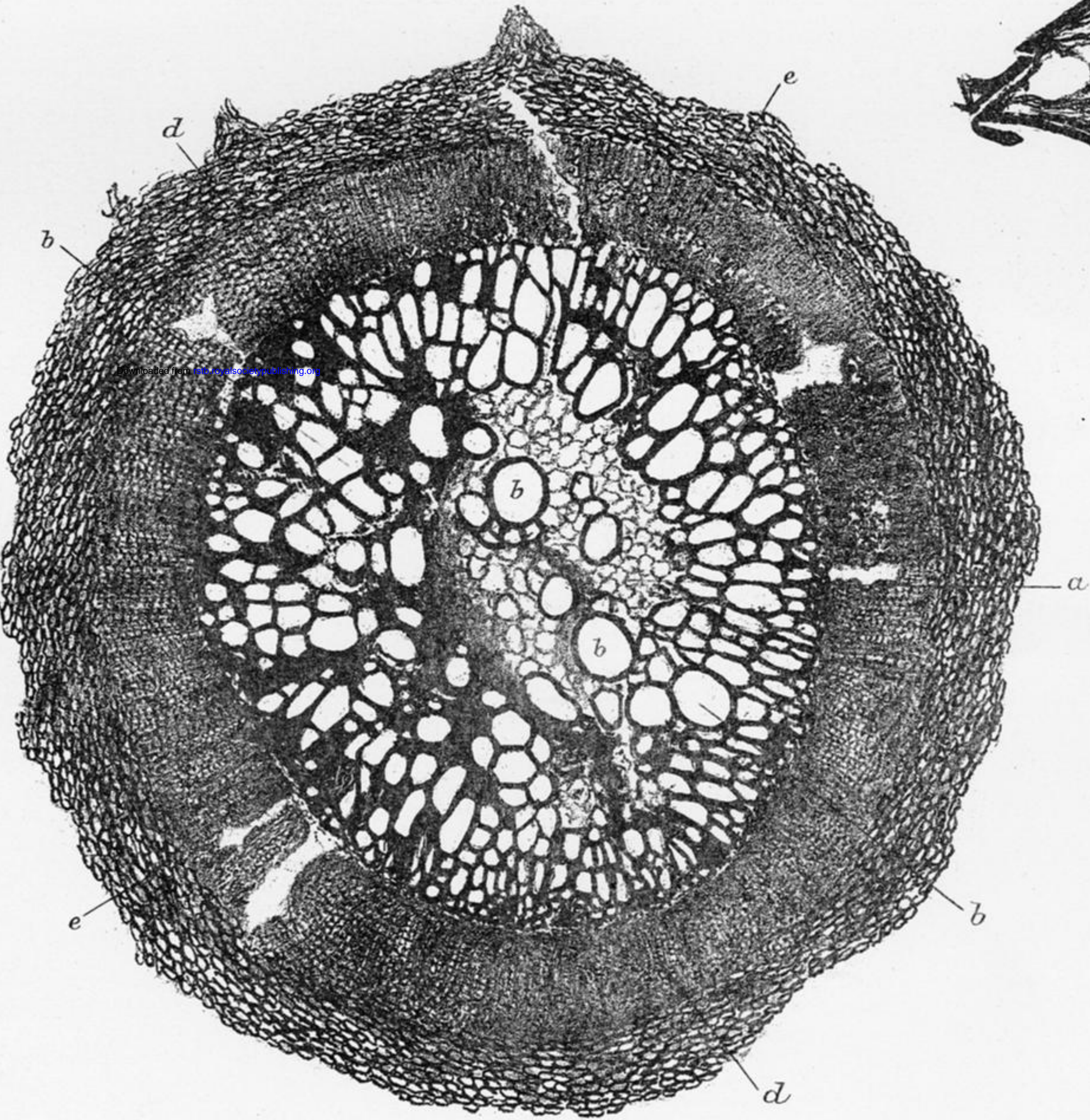
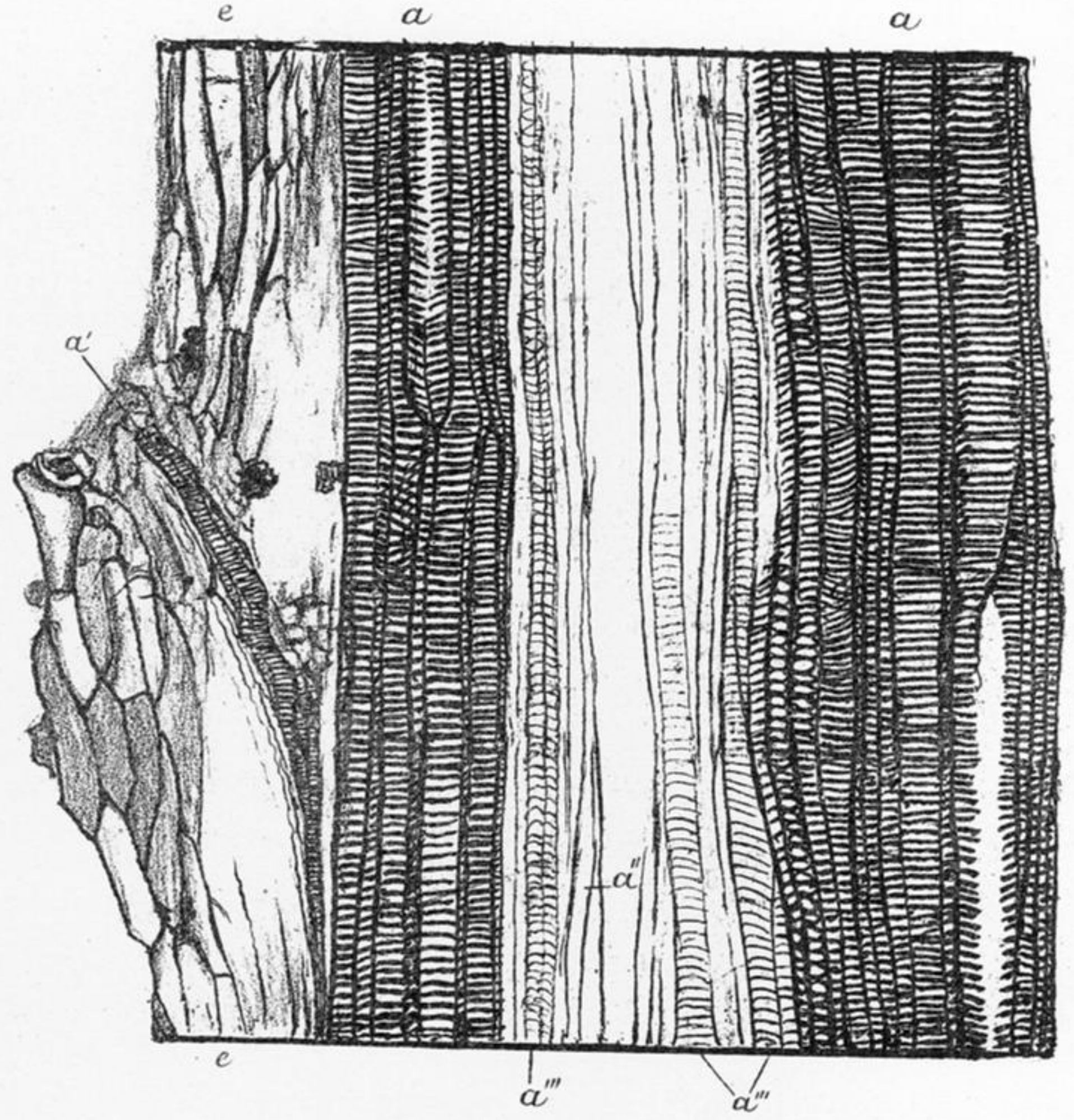


Fig. 16.

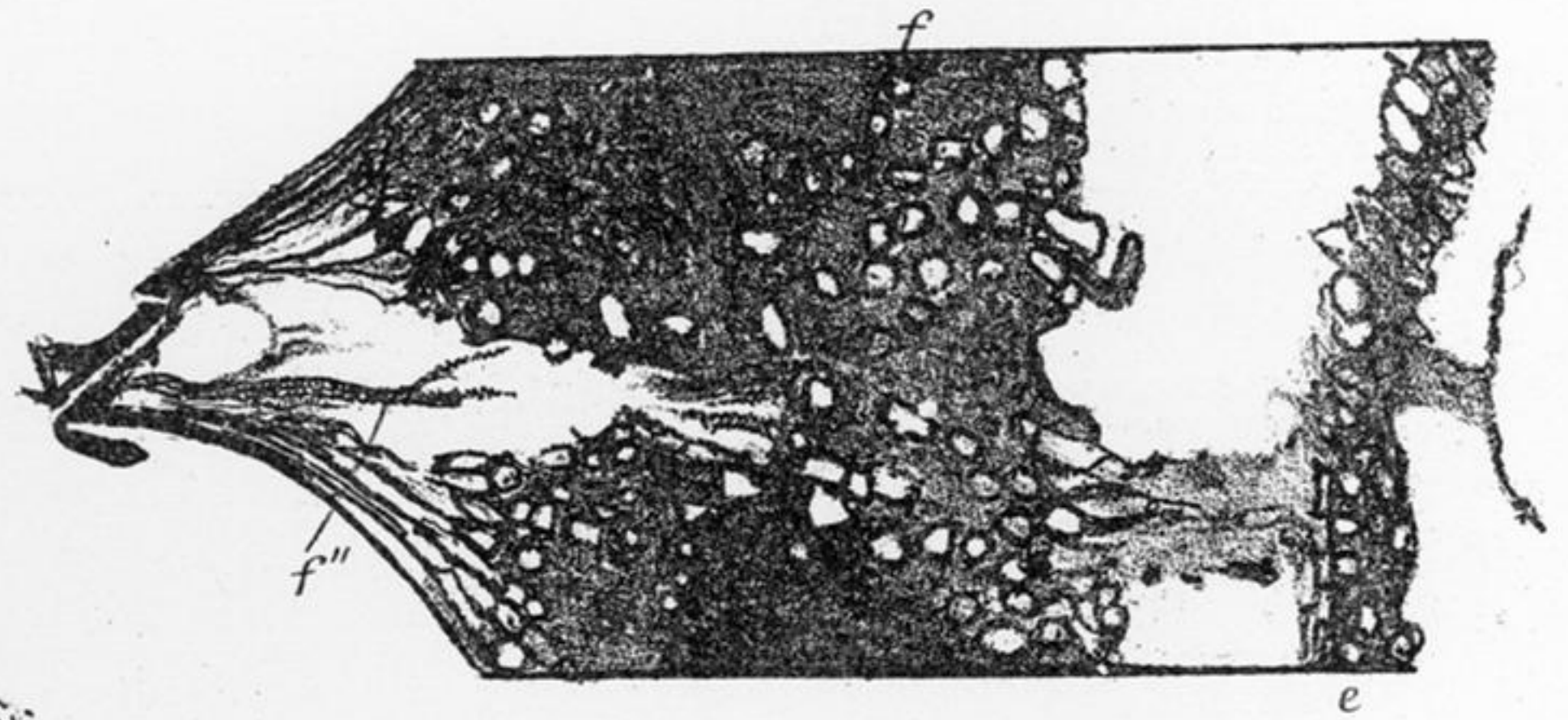


Fig. 20

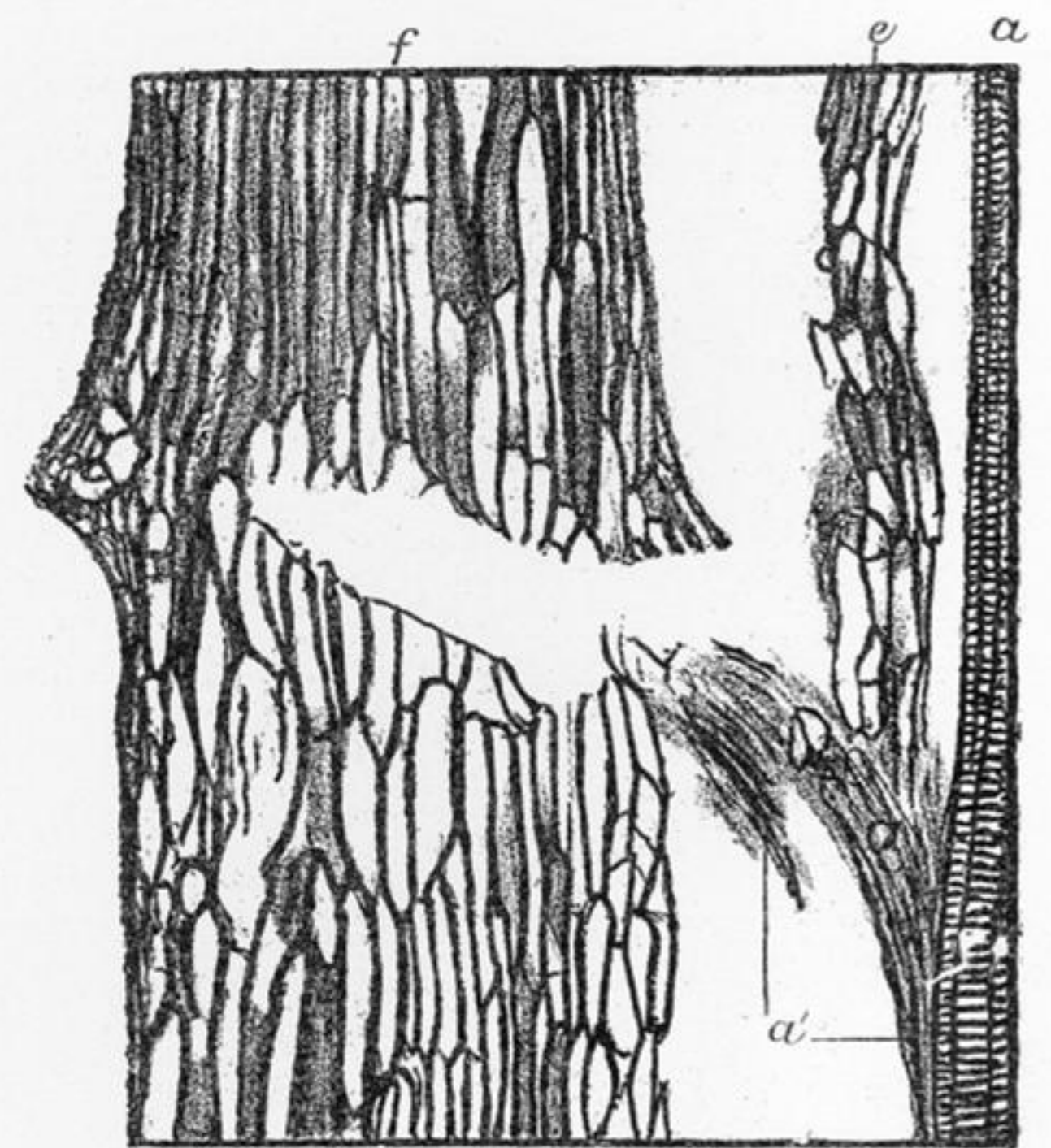


Fig. 21.

Fig. 19.

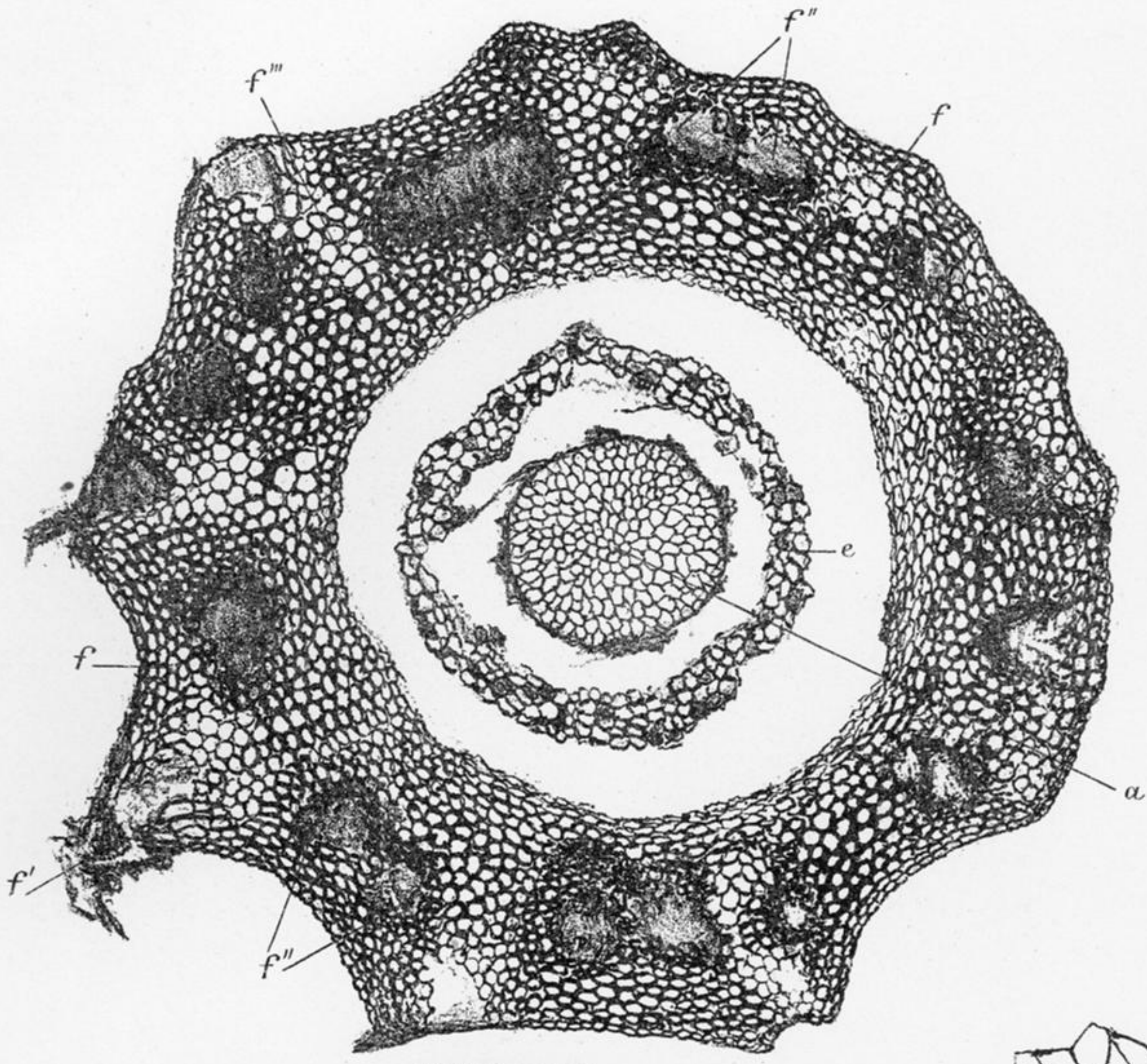


Fig. 23.

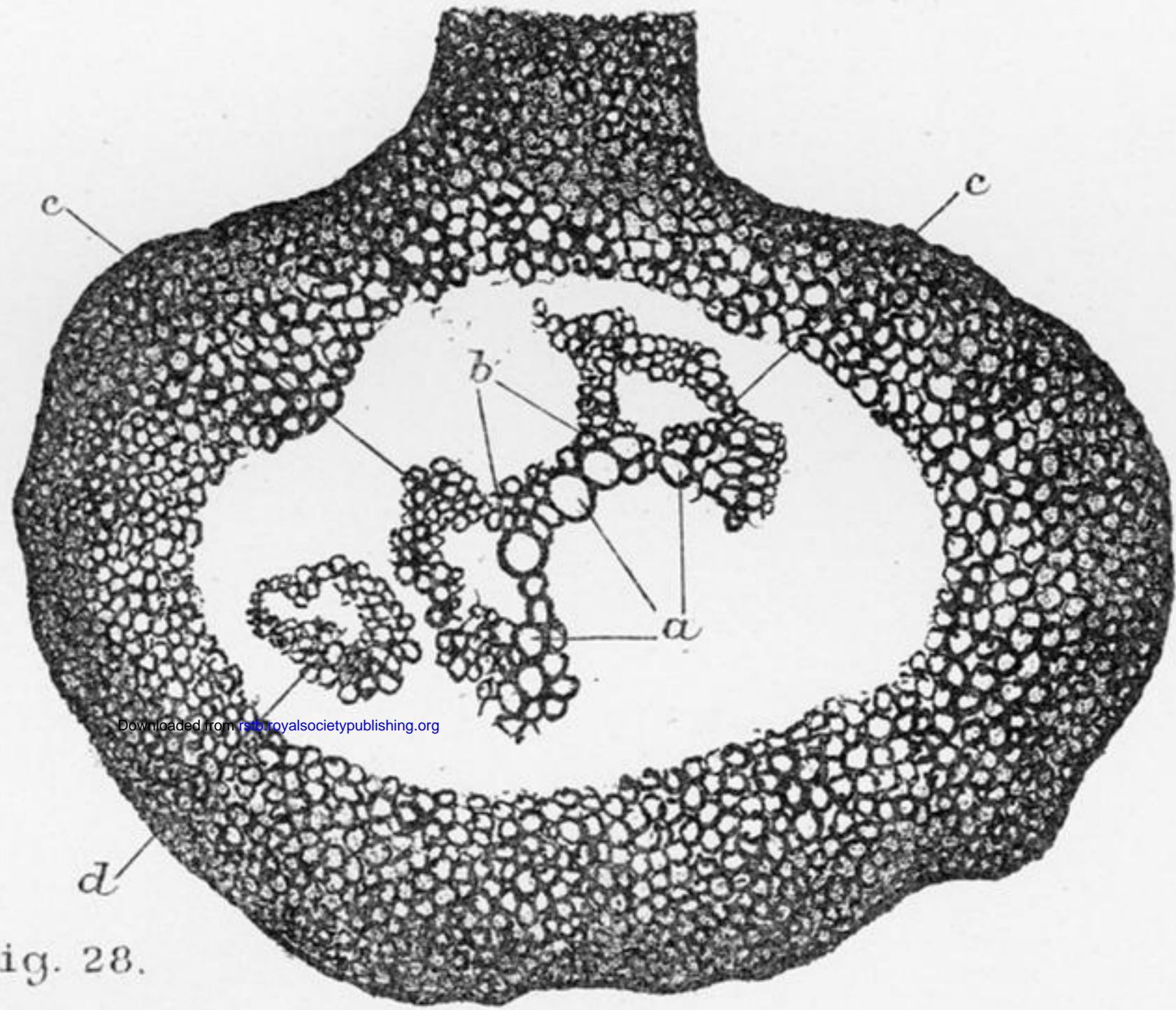
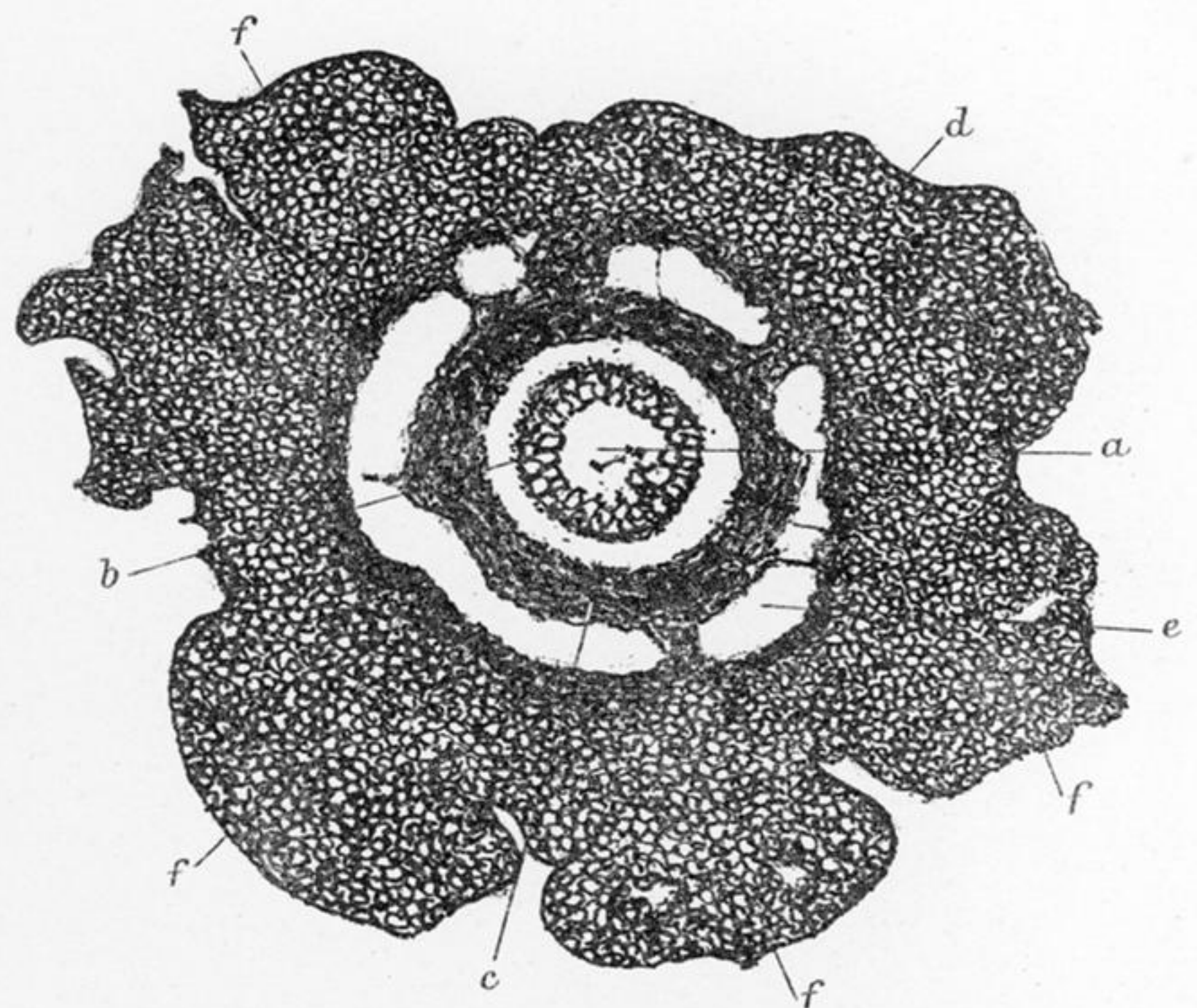


Fig. 27.

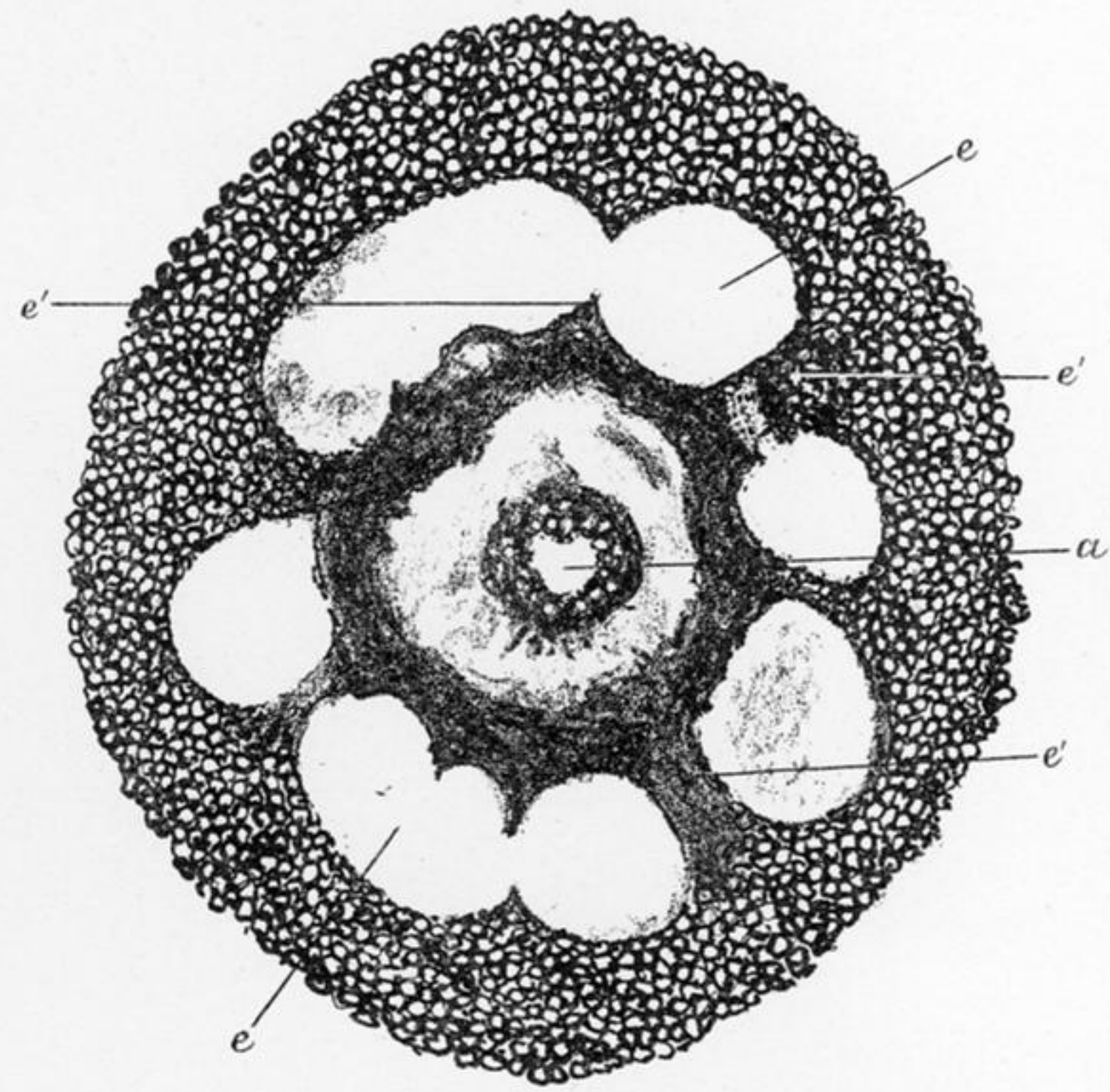


Fig. 24.

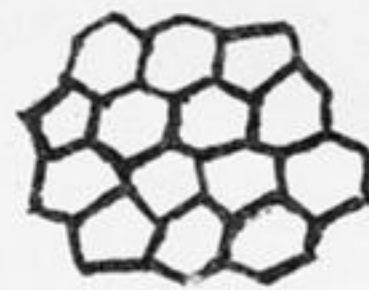


Fig. 26.

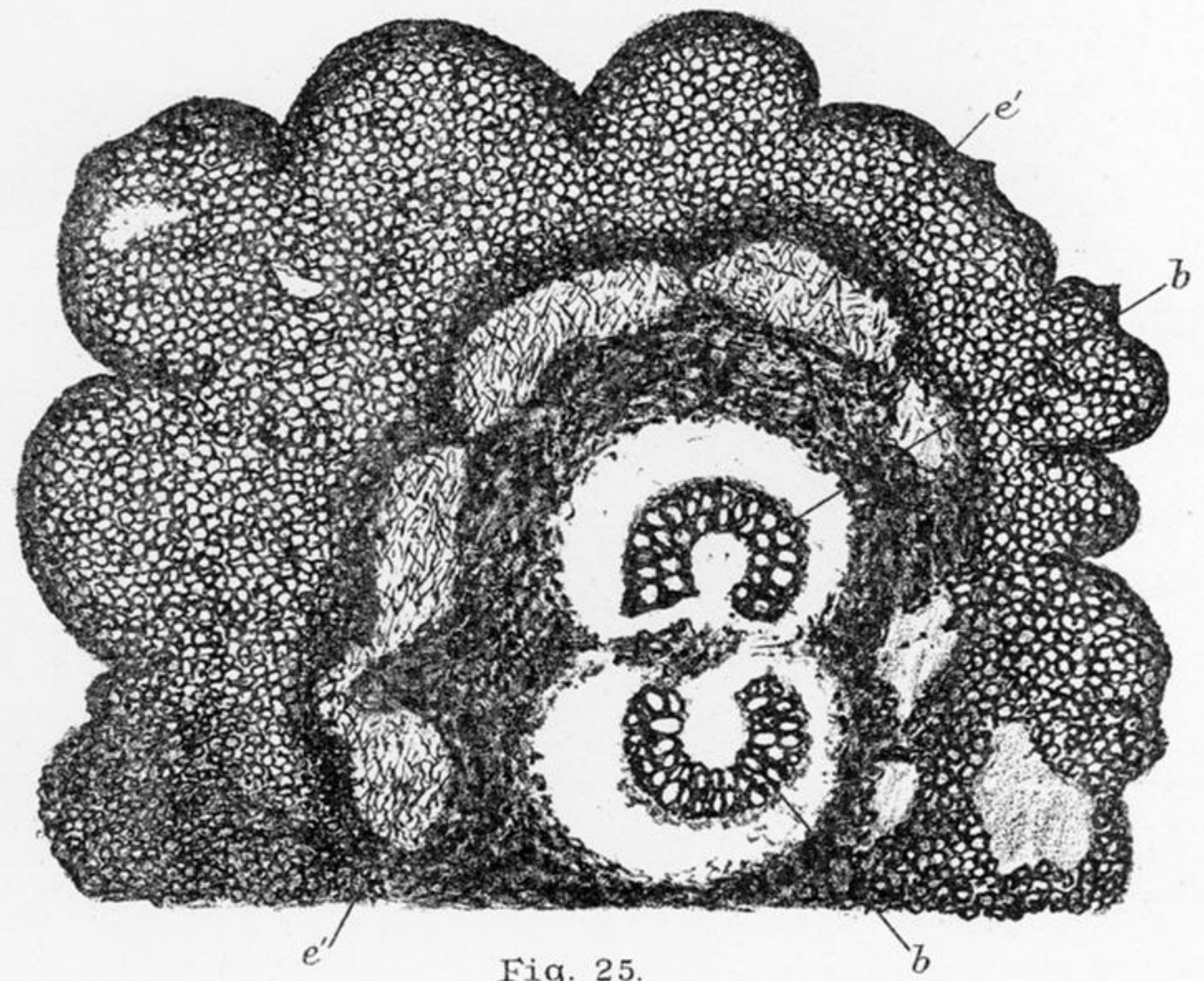


Fig. 25.

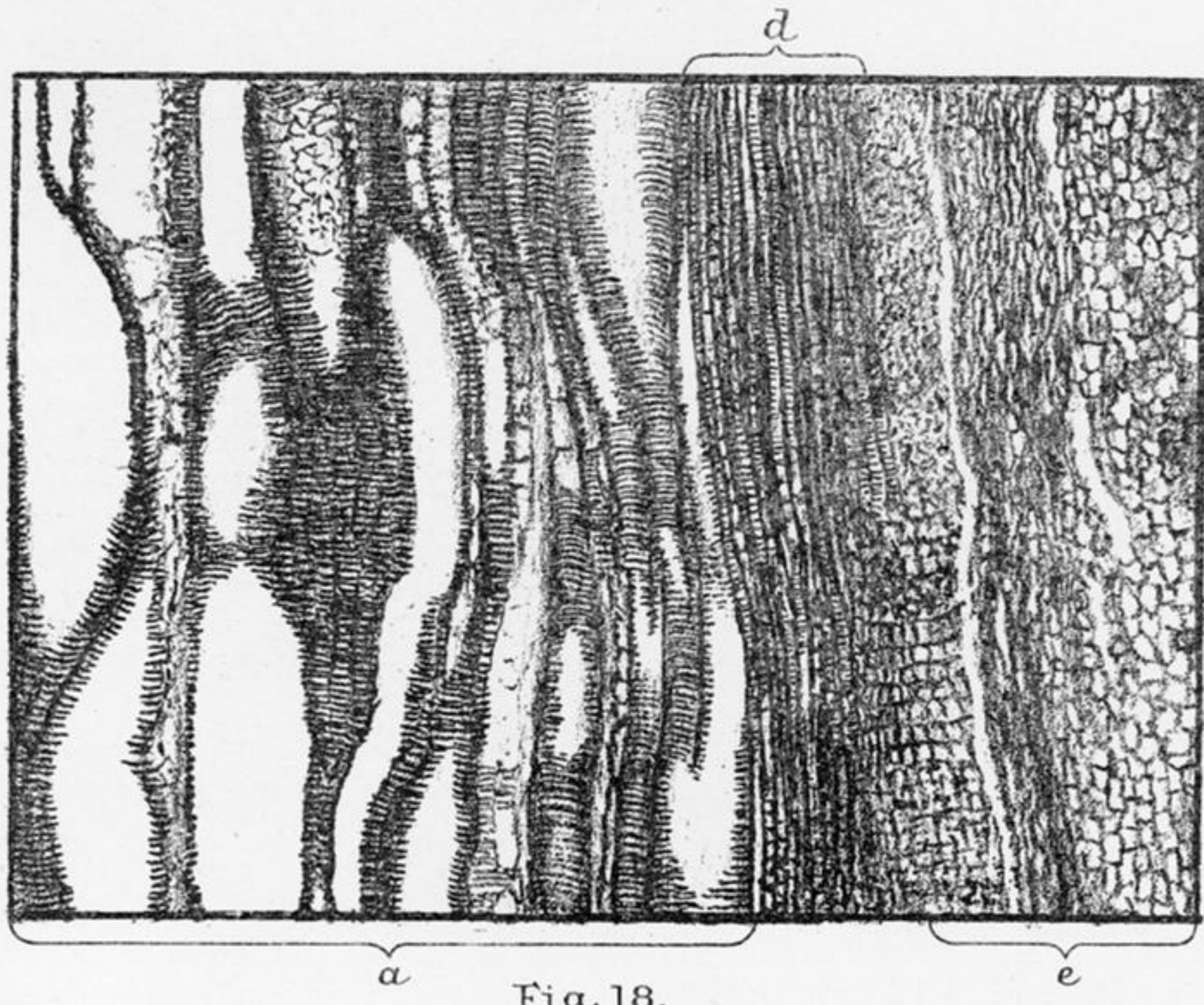


Fig. 18.