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Phil. Trans. R. Soc. Lond. B 1929 **217**, 395-410
doi: 10.1098/rstb.1929.0008

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VIII. Schizopodium Davidi *gen. et sp. nov.—a new Type of Stem from the Devonian Rocks of Australia.*

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Communicated by Prof. A. C. Seward, *F.R.S.*

(Received November 14, 1928,—Read March 14, 1929.)

(Plates 91–93.)

Introduction.

The block of chert containing the fossil plants described in this paper was collected by the late R. L. Jack, when he was the Government Geologist of Queensland, Australia. The block was lent about twenty years ago to Prof. Sir Edgeworth David who was then searching for Radiolaria. Some sections were cut from the block, which seemed to be promising material; but as no Radiolarians were found the material was put away. Recently Sir Edgeworth David realised the nature and importance of the plant remains in it and the whole material was sent by the Queensland Geological Survey to Prof. Seward for examination. Prof. Seward was, at that time, fully occupied with University duties and generously entrusted the work to me.

The specimen is stated to be from the Burdekin beds, Burdekin basin, Queensland, and therefore of Middle Devonian age. There is no reason to doubt that it came from these beds; but there are younger rocks in the neighbourhood, from which it might, possibly, have been collected. A fairly rich fauna of Middle Devonian affinity is known from the Burdekin series (Jack and Etheridge, 1892). The age of these beds has been long accepted as approximately Middle Devonian, and in the more recent work on Queensland Geology (Bryan, 1925), where the full literature is cited, their approximately Middle Devonian age is not questioned. The exact position of the plant-bearing chert in the series is however unknown, so that its age must be regarded as probably, though not certainly, Middle Devonian.

Material.

The material under examination was a small block of chert, the whole of which was eventually cut up into sections. The block was evidently only a fragment of a large nodule, or was possibly from a bed of chert. Four rather imperfect sections had been cut from it in Australia, and I cut some others from detached fragments of the block.

 [Published July 8, 1929.

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The most important sections, however, were cut by Mr. Hemingway, who reported that it was difficult to prepare thin sections because the rock contains numerous cavities which cause it to break up in the final polishing.

The block consists of about 25 silicified *Schizopodium* axes, packed together, with very little unfossiliferous mineral matter between them. The axes lie roughly parallel with one another, but in the course of the 6 cm. or so present in the block they bend through an angle of 60°. There are no other plant remains, not even spores, and no animal remains in the block.

The preservation of the different axes is very unequal, a few are well preserved, but some had rotted considerably before preservation. The rotten axes have been partly bleached and their softer tissues have been compressed as well as decomposed. Even the best preserved stems have been slightly compressed. Stages in the natural maceration of each tissue are available which throw some light on their fine structure and are useful for comparison with other types. A transverse section through several axes in the block of chert is shown on Plate 91, fig. 5.

Description of Schizopodium.

General Description.—All the sections available show similar structure, and it is likely that they may all be from the base of a number of upright shoots. The evidence for this is given on p. 403; it is only indirect. The axis was originally cylindrical, though it is always crushed to some extent, it was from 3–15 mm. in diameter and entirely without leaves or other appendages. It probably branched by equal dichotomy (Plate 91, fig. 4.)

A restoration of a transverse section through an axis of average size and complexity is shown in text-fig. 1. The epidermis is missing; the cortex has three layers, an outer of collenchyma, a middle zone of thick-walled parenchyma, and a broad inner cortex of delicate parenchyma. The stele is composed of a star-shaped mass of xylem surrounded by a very narrow zone of phloem.

Tissues Composing the Axis.—Epidermis.—No axis has a recognisable epidermis, but in several the cortex is surrounded by a delicate brown membrane which may be either the cuticle, or a membrane of ferric oxide precipitated round the axis during petrifaction. It is not likely that the outermost cells of the "outer cortex" are in reality the epidermis, because these cells are just like those deeper in, and because these outermost cells do not always form a definite layer. The outer surface of the cortex is shown on Plate 93, figs. 24 and 34.

Outer Cortex.—The outer cortex is a sheath of collenchyma about eight cells wide in the larger stems, four in the smaller. The cells are sometimes in rather regular layers, but more often they are irregularly placed. The corners of the cells, and to some extent also their tangential walls, are thickened; the radial walls are thin (Plate 93, figs. 24, 34). No intercellular spaces are visible between the cells, but where it is partly decomposed this tissue appears to consist of round, loosely packed cells with evenly thickened

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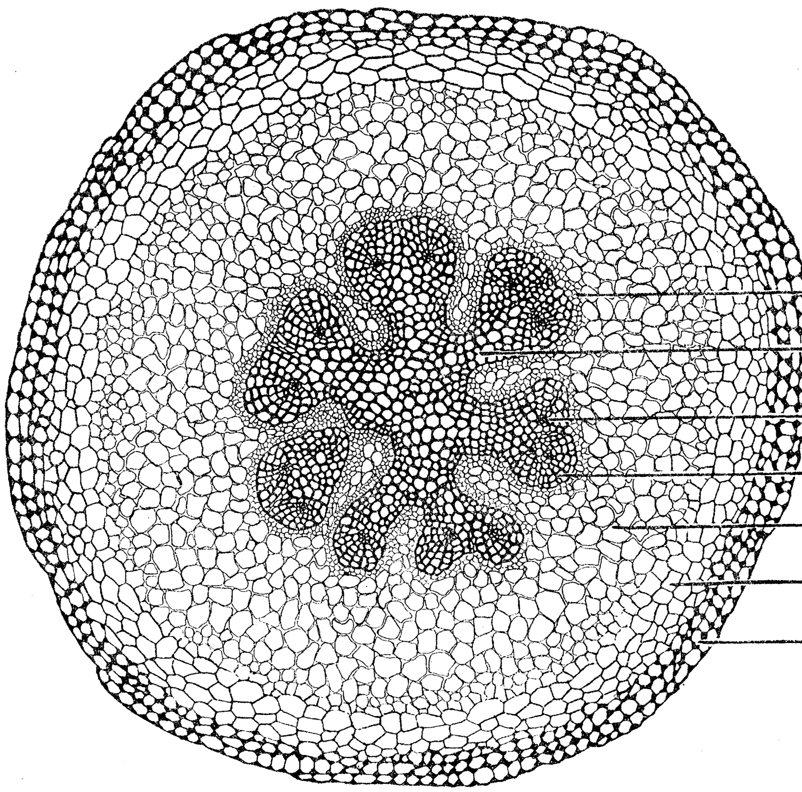
walls. In radial longitudinal section, the end walls are seen to be thin (Plate 93, fig. 26). The radial, tangential and longitudinal dimensions of an average cell of this layer are 22 $\mu \times 30 \mu \times 170 \mu$. On the inside the collenchyma passes by a transition zone of cells of intermediate structure into the middle cortex. In certain stems this transition zone has formed a layer of cork.

Middle Cortex.—The middle cortex is composed of about five layers of polygonal cells (Plate 93, figs. 24 and 30). They are most commonly rather crushed. The cell walls are evenly though not strongly thickened and apparently are unpitted. No intercellular spaces were seen between the cells. The material composing the walls of these



TEXT-FIG. 1.—Restoration of a small axis of *Schizopodium* in transverse section. Magnified about 20 times. PH = phloem, X1 = inner xylem, PX = protoxylem, X2 = outer xylem, C3 = inner cortex, C2 = middle cortex, C1 = outer cortex.

cells is different from that of the outer and inner cortex, since like the xylem, it often remains brown after they have been bleached. It is quite likely it was lignified, while the other two zones were of cellulose. In longitudinal sections (Plate 93, fig. 31) the cells are seen to be about 150 μ long. The transition from the middle cortex to the inner cortex is abrupt.

Inner Cortex.—The area of the inner cortex in a transverse section is probably at least half that of the whole stem, but as it is always somewhat crushed its original extent has to be computed from the perimeter of the outer cortex and of the stele.

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The cells of the inner cortex (Plate 93, figs. 24, 25, 28 and 32) are about 35 μ in diameter and 150 μ long. In transverse section, the cells are rounded or irregular and are separated at their corners by large intercellular spaces. The longitudinal walls are parallel and the end walls transverse or slightly oblique. The cell-walls are very delicate, and this tissue is always the first to be destroyed by rotting. Very often the inner cortical cells are more or less filled with a black substance (Plate 93, fig. 25). This may represent the decomposed remnants of some reserve material these cells once contained. The inner cortex is continuous with the tissue in the grooves in the stele (Plate 93, fig. 29), and when the stele is in separate pieces it is sometimes continuous through it. The first stage in decay is that the inner cortex shrinks, leaving a gap between it and the phloem. The cells then separate, their walls collapse and disappear, sometimes leaving the black contents which are more resistant than the cell-walls.

Cork.—Some of the larger stems are surrounded by a thick zone of tissue composed of cubical cells in radial rows (Plate 93, fig. 27) described here as cork. In these stems the cork is outside the inner cortex, but the outer cortex is missing or unrecognisable. In several small stems, the cells between the outer and middle cortex have divided into radial rows of cells like cork. No doubt this is where the cork originates. This tissue seems to be resistant, as it is usually well preserved; it is described as cork because of its position in the stem, its structure and its resistance to rotting.

Stele.—The term stele is used here for the xylem which is entirely tracheidal, together with the phloem which is composed of uniform thin-walled cells. The stele, thus defined, has a lobed outline in transverse section. In the following account the outward projections of the stele are described as "lobes," and the hollows between the lobes, where the inner cortex projects into the stele, as "sinuses."

The stele in transverse section has almost the same shape as the xylem alone, since the phloem is merely a thin border round the xylem mass. The phloem is omitted in text-fig. 2, where the chief types of stele which have been observed are figured.

The stele is from 1 to 7 mm. wide; in the smaller stems it has four simple lobes, but in the larger stems these lobes themselves branch, so that a complex, though regular, star is formed. In the larger stems also, the branching may be less regular, the four primary lobes may be unequally branched, and there may be more than four of them. The majority of the stems have steles, which agree in size and in complexity with that shown in text-fig. 2, "*d*." Very small steles are uncommon, "*a*" and "*b*" are represented each by only one specimen.

The stele, in several large stems, is discontinuous in cross section. The stages in the formation of separate masses of stelar tissue are: a lobe of xylem connected with the rest of the xylem by a broad band of tracheids; a lobe connected by a narrow neck; a lobe separated from the rest of the wood by phloem; and finally a lobe separated by inner cortex as well as by phloem. These stages were each observed several times, and may all occur in one stem.

The steles of certain stems could be followed in the sections, which form a series,

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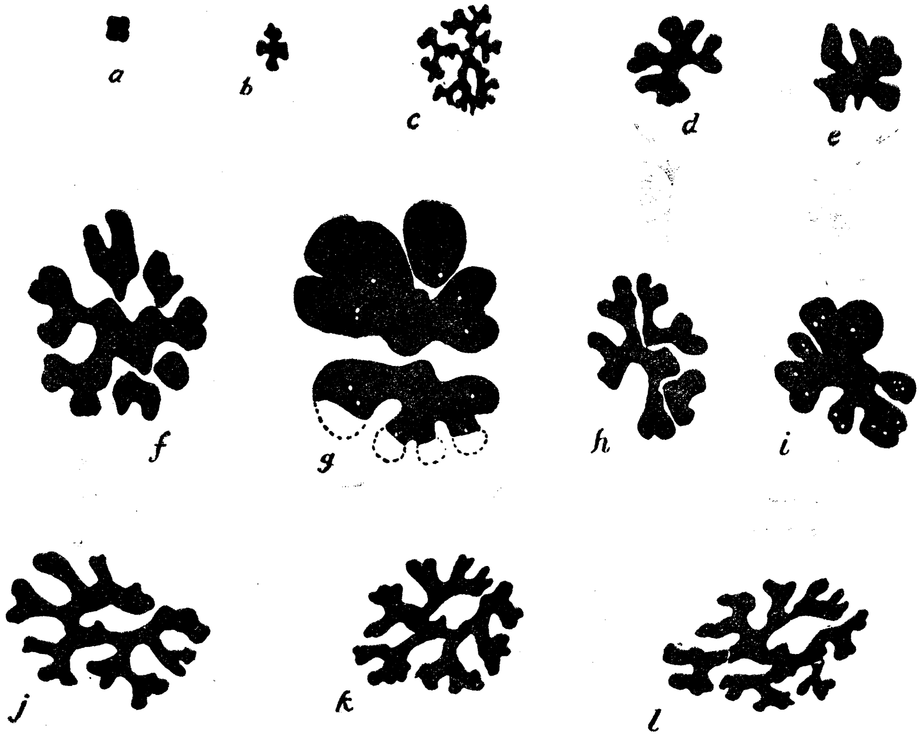
through a distance of 2 cm. The main lobes do not change in this distance, but the smaller ones change slightly (text-fig. 2, *j*, *k*, *l*). The stele shown on Plate 91, fig. 8, is the largest in the block and differs in several respects from the other steles. It is described below as specimen A. The stele is not star-shaped but consists of a large oval mass of " outer wood " enclosing a little " inner wood " and of some smaller oval masses of wood at the side of the large one. The cortex is missing. These strands of wood when traced through the block are continually dividing, shifting and joining with one another. Accurately radial and tangential longitudinal sections through the outer xylem of this stem were prepared by the author from detached fragments of the block, which contained compact masses of outer wood which are almost certainly the continuation of specimen A. Although exceptional in its gross form, specimen A was



TEXT-FIG. 2.—The xylem of *Schizopodium* in transverse section, magnified 6 times. *a–i* represent different stems ; *j*, *k*, *l*, represent one stem at different levels. In *g* and *i* there is outer wood and the protoxylem groups are represented by white dots.

referred to the same species as the other stems, because it agrees with them in the finer structure of both its inner and outer xylem. Part of the largest mass of outer xylem is more elaborately organised in specimen A than it is in other stems, and is described specially, the rest is just like the outer xylem of other stems.

There is no distinct layer of cells at the boundary between the phloem and the cortex which could be described as pericycle or endodermis.

Phloem.—The xylem is bordered by the tissue which is called phloem in this account.

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The phloem consists of thin-walled polygonal cells about 18 μ wide, and therefore only half as wide as the cells of the inner cortex. The innermost cells of the inner cortex are, however, rather smaller than the others, so that the phloem is not sharply distinguished from the inner cortex by the size of its cells (Plate 92, fig. 17). Sometimes when the inner cortical cells have black contents, the phloem remains pale and is then obviously distinct from the inner cortex (Plate 92, fig. 12). Also, when the inner cortex shrinks before preservation, as it often does, it splits away from the stele at the boundary between cortex and phloem (Plate 92, fig. 14).

The zone of phloem is of the same thickness round the lobes as round the sinuses of the stele, but as a rule it is best preserved in the sinuses. The cells of the phloem are not in radial rows; but sometimes the innermost phloem cells form part of the same rank of cells as the tracheids of the outer xylem. There are no intercellular spaces between the phloem cells, but in slightly rotten stems the middle lamella has disappeared and the cells have become round.

Longitudinal sections through the phloem show tubular cells 250 μ long, with more or less oblique end-walls (Plate 93, fig. 32). The cells are commonly longer and have more oblique end-walls than the inner cortical cells. Both the radial and tangential longitudinal walls were searched for sieve-plates. The walls often have thin granular areas like sieve-plates, which, however, may have been caused by decomposition. Similar granular areas are sometimes to be seen on the walls of cortical cells where they are no doubt caused by decomposition.

Xylem.—The xylem may be described as consisting of three parts: protoxylem, inner metaxylem and outer metaxylem. The distinction between the inner and outer xylem is, however, artificial except where they are separated by the protoxylem. The inner xylem consists of tracheids, all similar to one another, but placed irregularly; the protoxylem is a conspicuous group of very small tracheids in the outer part of the lobes of the wood; the outer xylem consists of tracheids in radial rows. The inner wood might have been called primary metaxylem and the outer wood secondary metaxylem, but reasons are given later for preferring the purely descriptive terms "inner" and "outer."

The protoxylem is composed of polygonal tracheids of 8 μ outside diameter and of unknown length. The walls have scalariform thickenings, all the walls are thickened alike, even when in contact with phloem on one side and xylem on the other. Each thickened bar on the walls is connected at the angles of the tracheids with the bar above and the bar below (Plate 92, fig. 19). The thickening on these tracheids is thus definitely scalariform, and no tracheid with annular or spiral thickening was seen.

Even in the best preserved stems there is no sign of xylem elements stretched or broken by the growth of the stem after they were lignified. The scalariform tracheids are called protoxylem because of their structure, there is no evidence that they were lignified before the tracheids with bordered pits. The inner wood consists, in transverse section, of a mass of uniform thick-walled tracheids with a round lumen about

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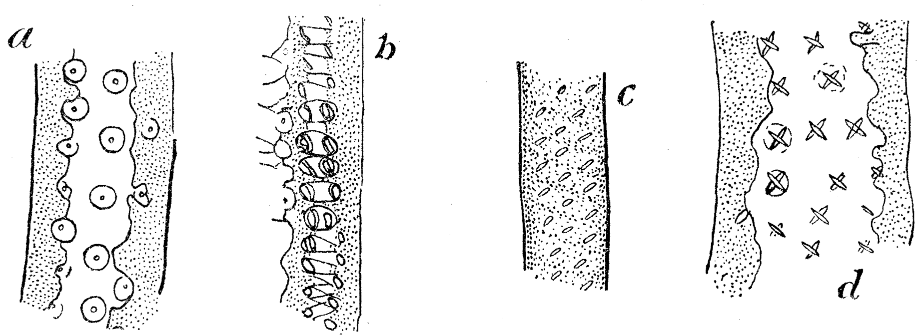
45 μ wide. In well-preserved stems the walls are quite opaque, but in stems bleached by rotting a middle lamella can be seen. There are no intercellular spaces or unlignified cells among the tracheids in this, or any other part of the wood.

The tracheids of the inner wood look the same in a tangential as in a radial longitudinal section through a lobe of the stele, because the pitting on all the walls of the tracheids is the same. The pits are either scattered irregularly over the walls or are in a regular spiral; they are never so crowded as to be in contact with one another. Each pit consists of a round border, 5 μ wide, with crossed oblique apertures nearly as long as the border and about 1 μ wide, text-fig. 3, *d*. There is no sign of any thickening in the middle lamella in the pit. The pit border is sometimes paler than the rest of the tracheid wall, sometimes darker (Plate 92, fig. 23), but more often it is just as dark as the rest of the wall and scarcely distinguishable from it.

In some stems, there is an interesting type of tracheid intermediate in the size of the lumen and in the structure of its walls between protoxylem and metaxylem. It



TEXT-FIG. 3.—*a*, tracheid with bordered pits with round apertures; *b*, tracheid with bordered pits and scalariform thickenings; *c*, tracheid with crowded simple pits; *d*, tracheid with bordered pits. The borders of some of the pits have disappeared. All from one stem, slide 18, × 240.

occurs near the protoxylem, but it is not known whether it belongs to the inner or to the outer wood, as it was only recognised in longitudinal sections. In these tracheids the wall has slender scalariform thickenings between which there are one or two pits, sometimes bordered, sometimes simple (Plate 92, fig. 15), text-fig. 3, *b*. The thickenings of these tracheids look exactly like the bars of Sanio of some coniferous woods. Some of the tracheids of the ordinary metaxylem have very indistinct bars of Sanio, but these transitional tracheids do not occur in all stems.

Outer Xylem.—The outer xylem is more varied than the inner. In stems with only a little outer wood (*e.g.*, Plate 92, fig. 16) the outer wood consists of tracheids exactly similar to those of the inner wood except that they are in somewhat regular radial rows instead of being packed together irregularly. Where there is much outer wood (Plate 91, fig. 8) it consists of tracheids in radial rows, but these pursue a most irregular course; some tracheids are almost cubical, others vertically elongated like ordinary tracheids, some radially elongated like a medullary ray and others are tangentially elongated.

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Their cross-sectional diameter is also variable. All these different types of tracheid can be found in a small piece of secondary wood (Plate 92, figs. 18, 20, 21 and 22).

All these tracheids have multiseriate pits; presumably they were originally bordered, but the only stem with massive outer wood (specimen A) is not very well preserved. It is possible that the short tracheids and the medullary ray-like tracheids may have been living xylem-parenchyma cells, but the pitting on their walls seems to be the same as on other tracheids. One of these "medullary rays" is seen in radial longitudinal section (Plate 92, fig. 10). The ends of one series of tracheids are all curved one way, in the next row underneath they are all curved the opposite way.

Camera-lucida drawings of "serial sections" were made in grinding down the piece of wood shown in Plate 92, fig. 11; by examining the polished surface by light from above, the groups of small cells were shown to be radially continuous, like a medullary ray, but the shape of each group and the number of cells composing it are entirely variable. The different groups sometimes link up with one another temporarily.

The first stage in decomposition of the tracheids with bordered pits is that the round border becomes obscure and disappears. The aperture then seems to become enlarged and tends to merge into the corresponding aperture on the other side of the tracheid, so that at the last stage at which pits are recognisable, the tracheid wall shows a series of irregular and rather indefinite holes through the wall (text-fig. 3, *c*). No further change of importance happens until the wall disintegrates. The pitting of a tracheid in decomposed wood would be described as multiseriate simple pits. It is quite likely that some of the stems which are later compared with *Schizopodium* and appear to have simple pits had originally bordered pits.

In certain very well preserved tracheids the oblique apertures are scarcely shown and the pit appears to have a small round pore 1 μ wide (text-fig. 3, *a*; Plate 92, fig. 23). As some indication of the oblique aperture is, however, always to be found in some of the pits of the same tracheid it seems most likely that this was not an original feature.

Discussion.

Schizopodium seems to have had no leaves. In well preserved axes, the outer cortex was a continuous band of tissue without leaves or leaf-bases. In crushed stems the outer cortex is folded, but the folds are evidently produced after the death of the plant, since the cells at the folds are crushed or torn. In no stem is there anything which could be interpreted as a leaf-trace leaving the stele, and in no section is there anything resembling a detached leaf; all the organic remains can be referred to the axis. However, it is possible that the cortex of only one part of the plant, perhaps the base, is known. The cortex of the smallest axes, which may be ultimate branches, is missing, but in the larger axes it has always the structure shown on Plate 93, fig. 24, and in text-fig. 1. It is noteworthy that there is no assimilatory tissue, and whatever cells contained chlorophyll would seem to be rather unfavourably placed for carbon

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assimilation. This suggests that the stem was not assimilatory and therefore that the part preserved is the base of the stem.

On the other hand, the outer cortex has collenchyma which is characteristic of self-supporting stems rather than of rhizomes and roots, and if the tissue of the cortex looks unfitted for assimilation, it is also unfitted for absorption from the soil. I think that the chert contains the crowded stem-bases of an upright plant preserved parallel to one another in the position of growth.

It would be possible to regard the " inner cortex " as a very broad phloem of unusual structure, and the phloem as a narrow band of conjunctive parenchyma. The reasons for calling the innermost parenchyma phloem are: firstly, that it resembles the phloem of living Pteridophytes in its structure more closely than does any other tissue in the stem, and secondly, it is evidently a similar tissue to what is called phloem in other fossil plant stems, *e.g.*, in *Asteroxylon*. The " phloem " might also be regarded because of its position as a cambium; but it seems very unlikely that it is a cambium, because its cells are irregularly arranged instead of being in radial rows like the tracheids of the outer xylem.

Stele.—The term " stele " is used here for the xylem and phloem, and " cortex " for the ground tissue round the stele and between the lobes of the stele. I have called the tissue between the lobes of the stele as well as the tissue outside " inner cortex " because they are exactly similar. I do not wish to imply any " intrusion " of cortex into stele or vice versa; the " stele " of *Schizopodium* was formed from certain cells near the middle of the apex of the shoot which differentiated into tracheids or elongated parenchyma (phloem) and the " inner cortex " is the name given to cells which differentiated in a third way. There is no fundamental reason why the " stele " should be continuous or discontinuous: in *Asteroxylon* it is continuous; in *Schizopodium* continuous, or discontinuous; in *Cladoxylon* commonly discontinuous. It is better to describe the stem of *Schizopodium* as monostelic than as polystelic, even when the stele consists of widely separated pieces.

In the Filicales the stele often consists of separate strands embedded in a ground tissue. Each of these strands has sometimes been called a stele and the whole axis has been described as polystelic. Now, however, these strands have been shown to be formed from one stele in the individual, and it is believed that they have also originated from one stele in the race. It is thus more convenient to regard the strands as parts of a single stele and to describe the axis as monostelic.

In *Schizopodium*, the separate strands of conducting tissue probably arose, both in the individual and in the race, from a single median strand or stele. The axis should therefore be described as monostelic, not polystelic, although the stages by which a dispersed stele arose in *Schizopodium* and in the ferns are different.

Outer Xylem.—Secondary xylem is understood to mean wood formed by a lateral meristem—the cambium—round the primary wood formed by the apical meristem. The outer wood of *Schizopodium* is intermediate between primary and secondary wood; in

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its structure it resembles secondary, in its formation it resembles primary. To apply the term " secondary " to it is to misuse this term slightly and is to create an artificial distinction between it and the primary wood of other Pteridophytes.

The reasons why the outer wood cannot be considered to be ordinary secondary wood are :—

1. In well preserved axes, there is no cambium; the outermost tracheids are fully lignified and in contact with the phloem.

2. The inner and the outer wood are quite continuous, except where they are separated by protoxylem (Plate 92, fig. 16) and sometimes, *e.g.*, in the stem shown on Plate 91, fig. 9, the tracheids of the inner wood are in rows continuous with those of the outer wood.

3. The delicate tissues of the phloem and inner cortex in the sinuses between the lobes of the stele are not crushed as they would be if the outer xylem were secondary and had encroached on them on both sides. In stems in which secondary wood is formed in a closed space already full of tissue, *e.g.*, in the medulla of *Piper*, crushed tissue is always present. In *Schizopodium* the inner cortical cells in the sinuses are round, or if they are flattened, they are flattened evenly, not crushed. Probably all the cells matured together and the cells of the xylem and of the inner cortex were able to adapt their shape to one another.

Very probably the outer wood was formed as follows :—

1. In certain stems, especially in the small ones, the inner cells of the apical meristem " desmogen strand " formed a star-shaped mass of young tracheids, which all matured about the same time—which was after growth in length of the axis had stopped. The outermost tracheids have the structure of protoxylem (Plate 91, fig. 2).

2. In other stems the protoxylem is not quite at the end of the arms, *i.e.*, it is mesarch. The desmogen cells outside the protoxylem tend to divide radially, which is the one direction in which they can divide freely, while the inner desmogen cells divide irregularly (Plate 91, fig. 6).

3. This radial wood becomes more considerable and the irregular wood relatively and absolutely less (Plate 91, fig. 10), until there is a large mass of radial wood outside the protoxylem and the wood on the inside of it is also nearly all composed of tracheids in radial rows, (Plate 91, fig. 10; Plate 92, fig. 16).

4. Where there is a great mass of radial and very little irregular wood (Plate 91, figs. 8 and 11) it seems quite likely that the outer tracheids were laid down sometime after the inner ones. These tracheids would then be " secondary " in the ordinary sense. In the end, however, the meristem uses itself up entirely by forming tracheids, the last one being in contact with phloem.

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Branching.—On Plate 91, fig. 4, a section is shown which was interpreted as a transverse section through the stele of a dichotomising axis. In the sections on the one side of the one figured, the two halves are to be seen diverging from one another, but in the sections on the other side, this axis is not shown. Although the section figured suggests dichotomy it is also possible that it is through a sharply bent axis and that the two halves are merely two sections through one axis.

Comparison.

Each important feature in the organisation of *Schizopodium* was already known in Middle Devonian plants. The genus is chiefly interesting because it combines features characteristic of different families, and so makes the gap between them seem less.

The following features of *Schizopodium* are important for comparisons :—

1. The axis is slender, and perhaps leafless.
2. The stele is star-shaped ; the xylem is surrounded by a narrow zone of phloem which is not sharply marked off from the cortex.
3. The protoxylem is exarch or mesarch ; when mesarch the xylem outside it is like secondary xylem.
4. The xylem is solid ; there are no pith-cells among the tracheids.
5. The protoxylem has scalariform pits ; the metaxylem has multiseriate bordered pits with oblique apertures.
6. The pitting on all the walls of a tracheid is the same.

Schizopodium is closely comparable with the Middle Devonian genera *Asteroxylon*, *Cladoxylon* and *Palæopitys*. It has features in common with several more recent genera, but these are less striking.

Detailed Comparison.

1. *Asteroxylon.*—*Schizopodium* is so like *Asteroxylon* that it may be placed, provisionally, in the Asteroxylaceæ of the Psilophytales. The two genera have in common : the general Psilophytalean characteristic of a slender axis containing a star-shaped mass of xylem with protoxylem near the ends of the rays of the star. The pitting of the tracheids, while different from that of *A. Mackei*, Kidston and Lang (1920), is rather like that of *A. elberfeldense*, Krausel and Weyland (1923, 1926). The phloem of the two genera consists of elongated parenchyma, not sharply marked off from the inner cortex. The differences between the two genera are :—

1. *Schizopodium* had apparently no leaves, but this must not be emphasised too much since the upper part may, after all, have had leaves. In *A. Mackei* the leafless part of the axis had a round xylem mass, but in *A. elberfeldense* it became stellate below where the leaves appear.

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2. *Schizopodium* has a sort of secondary wood. This wood has, however, been shown to be intermediate between the centrifugal primary xylem of plants with mesarch protoxylem, and secondary wood formed from an ordinary cambium.

3. The stele in *Schizopodium* has the shape of the xylem, which is commonly a star, while in *Asteroxylon* the stele is round, even when the xylem is star-shaped. This fact justifies the generic separation of *Schizopodium* from *Asteroxylon*, but is not sufficient to place them in different families; in stems with no sharp distinction between "inner cortex" and "phloem," the exact position of the boundary cannot be of great importance.

Asteroxylon elberfeldense, KRAUSEL and WEYLAND (1923), has a cavity in the wood filled with some delicate tissue, but it is not known whether this has the characteristics of phloem or of cortex. In any case, the mixture of tracheids and parenchyma, which occurs in the xylem of most ferns, is not known to occur in *Asteroxylon*.

2. *The Rhyniaceæ*.—*Rhynia* and *Hornea*, KIDSTON and LANG (1917, 1920*a*), have branching leafless axes, like those of *Schizopodium*, but a round stele instead of a star-shaped one. It is not yet proved that the whole plant of *Schizopodium* was leafless, so that this point must not be over emphasised; while it certainly resembles *Asteroxylon* in its star-shaped mass of xylem.

3. *Palæopitys*.—*Palæopitys*, KIDSTON and LANG (1923), probably had different primary (inner) wood from *Schizopodium*, since the secondary wood was formed in a ring. The "secondary" wood is very similar in the two genera; in both the tracheids have multiseriate bordered pits on both radial and tangential walls. In both genera there are "medullary rays," but while those of *Schizopodium* are composed of tracheids, those of *Palæopitys* are of parenchymatous cells. *Schizopodium* helps to link *Palæopitys* with Psilophytales.

4. *Aneurophyton*.—*Aneurophyton*, KRAUSEL and WEYLAND (1926), has "secondary" wood, like that of *Palæopitys* and *Schizopodium*; but, from the description given by KRAUSEL and WEYLAND, the pitting of the tracheids is in the form of multiseriate slits rather than bordered pits. The bordered pits of *Schizopodium* lose their borders as a result of rotting, and I think it very likely *Aneurophyton* originally had multiseriate bordered pits. There is nothing to show whether the "secondary wood" of *Palæopitys* and of *Aneurophyton* was ordinary secondary wood, or formed as in *Schizopodium*.

5. The *Cladoxylaceæ*, KRAUSEL and WEYLAND (1926) have obtained a plant—*Cladoxylon scoparium*, KR. and W.—from the Middle Devonian of Germany, which certainly belongs to the *Cladoxylaceæ* and is perhaps rightly placed in the genus *Cladoxylon*. *Cladoxylon* is commonly said to be polystelic; this term seems to imply a distinction between the axis of *Cladoxylon* and those of other plants which are called "monostelic." I think there is no need to maintain this descriptive term for *Cladoxylon*, because it is quite evident (*e.g.*, from KRAUSEL and WEYLAND's figures, especially text-fig. 44) that

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the stele of *Cladoxylon* can be regarded as merely a somewhat dissected star-shaped "monostele," just the same, in essentials, as a dissected *Schizopodium* stele.

Schizopodium agrees in several respects with the Mid-Devonian species *Cladoxylon scoparium*, Kr. and W. (Krausel and Weyland, 1926). In both, the stele consists of radiating bands of xylem surrounded by a little phloem, and the pitting of the tracheid walls is similar. It resembles the carboniferous species in its "secondary wood," which is there also formed in a closed space without crushing the cortex next it.

In *Schizopodium* the stele is normally continuous, but sometimes dissected; in *C. scoparium* it is normally dissected, but still sufficiently continuous to show its continuous origin, while in some other species, *e.g.*, *C. Kidstoni*, Solms-Laubach, it is divided into entirely separate round strands.

The chief difference between the two genera is that the stele in *Schizopodium* is less divided than in *Cladoxylon*, a very small difference. If *Asteroxylon* had been unknown *Schizopodium* might have been placed in the Cladoxylaceæ. I regard the Cladoxylaceæ as a family of robust plants belonging to the Psilophytalean complex, of which *Asteroxylon* is a more slender member. The Carboniferous members of the Cladoxylales are distinct enough from the plants contemporaneous with them to justify their elevation to ordinal rank (Hirmer, 1927). They are, however, very closely linked with the Psilophytales by their earliest member, *C. scoparium*, Kr. and W., and by *Schizopodium*.

Kidston and Lang (1919, p. 666) have already compared *Asteroxylon* with the Lycopodiales, the Psilotales and with the Zygopterid ferns, especially *Stauropteris*. Many of their remarks would apply equally to *Schizopodium* and I think it unnecessary to repeat them. *Schizopodium* is a little closer than *Asteroxylon* to the Zygopteridæ, *e.g.*, *Asterochlœna* (Bertrand, 1911) and *Botrychioxylon* (Scott, 1912), because it has a stellate, not a round stele and "secondary thickening" like that of several of the Zygopteridæ. The resemblance ends here; the differences between them are:—the Zygopteridean axis bore large "leaves," while in the Asteroxylaceæ they are insignificant, the Zygopterid stele usually had pith cells mixed with the tracheids of the wood, and in the Zygopteridæ the cortex is sclerised, as in most ferns, and well marked off from the stele by an endodermis, while in the Asteroxylaceæ the cortex is of more delicate cells, more like the cortex of an Angiosperm.

It is important that the deposit in which this chert occurs should be located and re-investigated. *Schizopodium* is still only incompletely known; but what is known indicates that it is a plant of great interest. The discovery of a bed of fossiliferous chert, with plants as well preserved as this specimen, would rank in importance with the discovery of the Rhynie Chert.

In conclusion, I wish to express my gratitude to the Queensland Geological Survey for lending the material and to Prof. Seward who entrusted the examination to me. Prof. W. H. Lang has been generous enough to spend a considerable time examining the slides and in discussing them with me.

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Diagnosis.

Schizopodium, gen. nov.

Cylindrical, leafless shoots consisting of a broad cortex of three zones—outer of collenchyma, middle of thick-walled parenchyma, inner of delicate parenchyma. Stele star-shaped or dissected, consisting of a solid mass of tracheids surrounded by a thin zone of phloem. Protoxylem composed of scalariform tracheids, metaxylem of tracheids with bordered pits on all their walls. Xylem outside the protoxylem with the appearance of secondary wood, but apparently formed as a primary tissue.

Schizopodium Davidi, sp. nov.—The only species; characteristics as for genus.

The generic name (from σχίζοπους—"with parted toes") was suggested by the diverging branches of the wood seen in transverse section. The specific name is after Prof. Sir Edgeworth David.

Summary.

1. *Schizopodium Davidi*, nov. gen. et sp., is erected for petrified stems from the Middle Devonian rocks of Australia.

2. The only part of *Schizopodium* known is a leafless dichotomously branched axis.

3. The axis has a broad cortex of three zones, the two outer of thick-walled cells, the inner delicate and a stele consisting of a xylem mass surrounded by a thin zone of phloem.

4. The stele is either star-shaped or is disintegrated into pieces, separated from one another by parenchyma resembling inner cortical tissue.

5. The xylem is composed entirely of tracheids; it consists of protoxylem with scalariform pits and metaxylem with multiseriate bordered pits.

6. The metaxylem consists of an inner part composed of irregularly arranged tracheids, and an outer part with the appearance of secondary wood.

7. The outer metaxylem is shown to be not typical secondary wood, but it is intermediate between primary and secondary.

8. The phloem consists of a narrow zone of thin-walled elongated cells.

9. *Schizopodium* is intermediate in the anatomy of its axis between *Asteroxylon* and *Cladoxylon*, and in the structure of its outer metaxylem it resembles *Palæopitys*.

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EXPLANATION OF PLATES 91–93.

All the figures are untouched photographs. C1 = outer cortex, C2 = middle cortex, C3 = inner cortex. Ph = phloem, X1 = inner xylem, X2 = outer xylem, Px = protoxylem.

PLATE 91.—GENERAL FORM OF THE XYLEM IN TRANSVERSE SECTION.

FIG. 1.—Stele of a small axis; slide 1. × 15.

FIG. 2.—A lobe of the xylem with the protoxylem at the outside. The inner cortex has shrunk away from the xylem in the sinus; slide 8. × 50.

FIG. 3.—A large axis showing the outer cortex which has collapsed round the xylem; slide 13. × 7.

FIG. 4.—Xylem of a dichotomising axis; slide 19. × 6.

FIG. 5.—Typical section through the chert block, containing the axes shown in figs. 3 and 8; slide 14. × 1·6.

FIG. 6.—A lobe of the xylem, showing the first recognisable traces of outer wood; slide 13. × 50.

FIG. 7.—A lobe of the xylem with strongly developed outer wood; slide 20. × 37.

FIG. 8.—Transverse section of Specimen A; slide 15. × 10.

FIG. 9.—Transverse section of a large axis in which the stele consists of three separate, unequal pieces; slide 7. × 10.

FIG. 10.—A lobe of the xylem with well-developed outer wood; slide 16. × 50.

FIG. 11.—One of the parts of the stele shown in fig. 8, showing the presence of a little inner wood surrounded by the outer (radial) wood; slide 15. × 37.

PLATE 92.—STRUCTURE OF THE XYLEM AND PHLOEM.

C3 = inner cortex, Ph = phloem, X1 = inner xylem, X2 = outer xylem, Px = protoxylem.

FIG. 12.—A sinus of the stele in which the phloem forms a well-marked zone of pale-coloured cells between the xylem and the inner cortex; slide 20. × 35.

FIG. 13.—Longitudinal section through tracheids of the outer wood showing the oblique apertures of the bordered pits; slide 18. × 350.

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FIG. 14.—A sinus of the stele in which the inner cortex has shrunk away from the phloem (Ph); slide 25 × 200.

FIG. 15.—Longitudinal section through tracheids intermediate between protoxylem and metaxylem. The pits have borders and large oblique pores, and are commonly in pairs, separated by scalariform thickenings, like "bars of Sanio"; slide 18. × 350.

FIG. 16.—A lobe of the xylem showing continuity between the inner xylem (X1) and the outer xylem (X2); slide 13. × 40.

FIG. 17.—A sinus of the stele in which the phloem (Ph) is well preserved and still in contact with the inner cortex; slide 25. × 200.

FIG. 18.—Transverse section through the outer wood of Specimen A. Most of the tracheids are cut transversely, but there is one series of tangentially elongated tracheids; slide 5. × 100.

FIG. 19.—Oblique longitudinal section through a lobe of the xylem showing the scalariform tracheids of the protoxylem; slide 18. × 300.

FIG. 20.—Radial longitudinal section through the outer wood of Specimen A. Certain tracheids are elongated horizontally to form a sort of medullary ray; slide 8. × 80.

FIG. 21.—Tangential longitudinal section through the outer wood of Specimen A. Groups of small tracheids represent the medullary rays of Plate 92, fig. 20.

FIG. 22.—Transverse section through the same piece of outer wood as that shown in Plate 92, fig. 18, taken at about 1 mm. to the right of fig. 18. Most of the tracheids are tangentially elongated or cubical. There is a series of radially elongated tracheids; slide 5. × 100.

FIG. 23.—Longitudinal section through two well-preserved tracheids. In the tracheid to the left, the borders of the pits are pale; in the tracheid to the right they have disappeared, except for one which is darker than the tracheid wall; slide 18. × 350.

PLATE 93.—STRUCTURE OF THE PHLOEM AND CORTEX.

C1 = outer cortex, C2 = middle cortex, C3 = inner cortex, Ph = phloem, X1 = inner xylem.

FIG. 24.—Transverse section through the cortex of a well-preserved axis; slide 16. × 50.

FIG. 25.—Longitudinal section through the inner cortex of a stem in which the cells have dark contents, slide 20. × 100.

FIG. 26.—Radial longitudinal section through the outer cortex showing the thin end-walls of the cells; slide 18. × 250.

FIG. 27.—Cork in more or less radial longitudinal section; slide 15. × 33.

FIG. 28.—Longitudinal section through the inner cortex from a sinus in a stele. The phloem (Ph) is badly preserved; slide 16. × 100.

FIG. 29.—Transverse section through a stem showing continuity between the inner cortex of a sinus of the stele with that outside the stele; slide 18. × 11.

FIG. 30.—Transverse section through the middle cortex; slide 25. × 220.

FIG. 31.—Radial longitudinal section through the middle cortex; slide 18. × 250.

FIG. 32.—Transverse section through the inner cortex in a sinus in a stele; slide 7. × 280.

FIG. 33.—Longitudinal section through the phloem; slide 24. × 100.

FIG. 34.—Transverse section through the outer cortex (C1) and the middle cortex (C2); slide 20. × 160.

Figs. 8, 11, 18, 20, 21 and 22 are of "Specimen A"; figs. 13, 15, 23, 25 and 27 are of a second stem; figs. 19, 24, 26 and 28 are of a third; figs. 9 and 32 of a fourth; and the remaining figures are each from a different stem.

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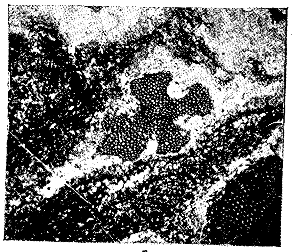

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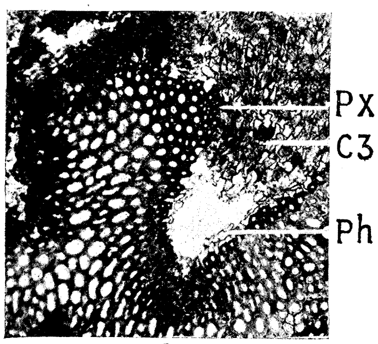

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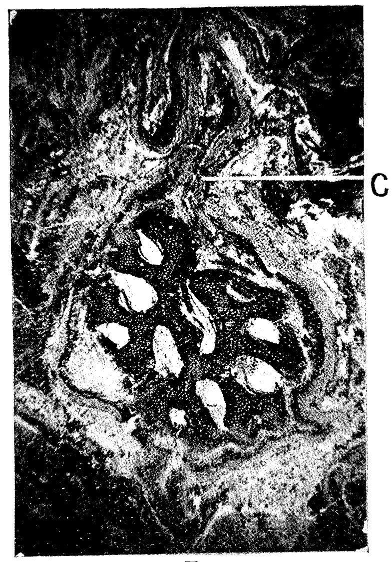

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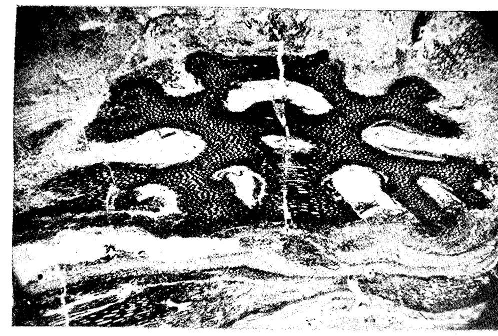

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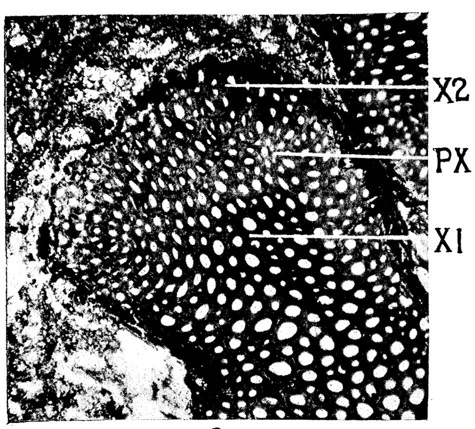

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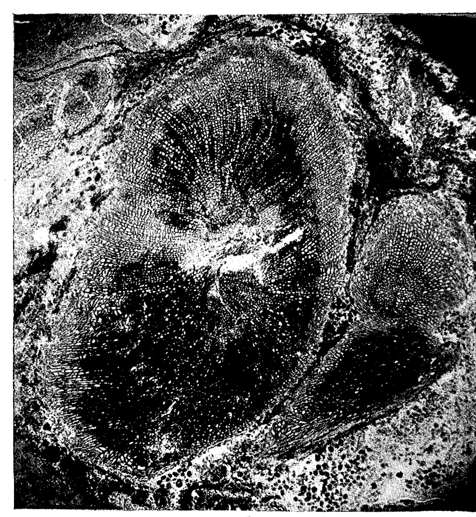

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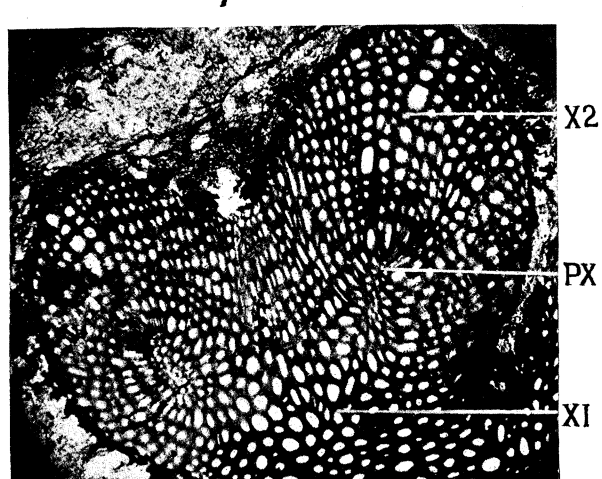

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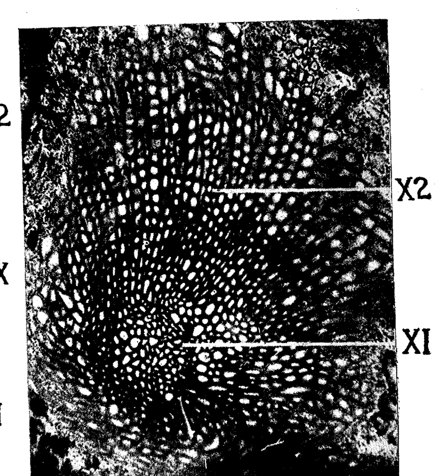

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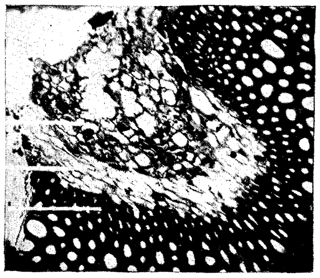

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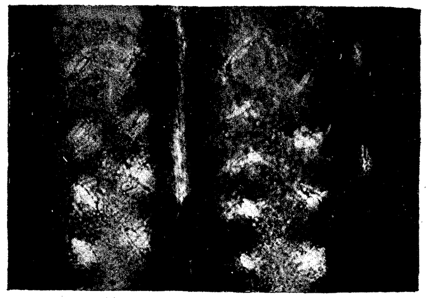

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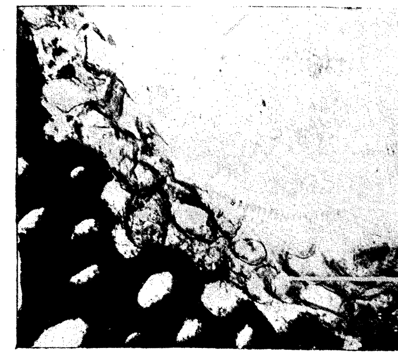

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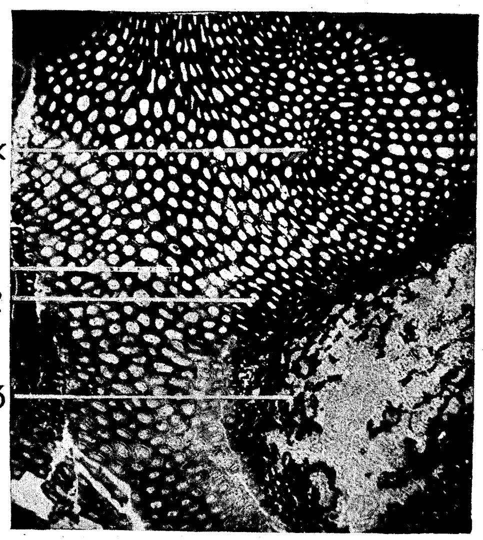

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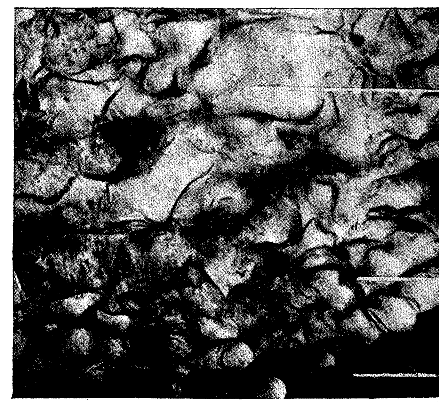

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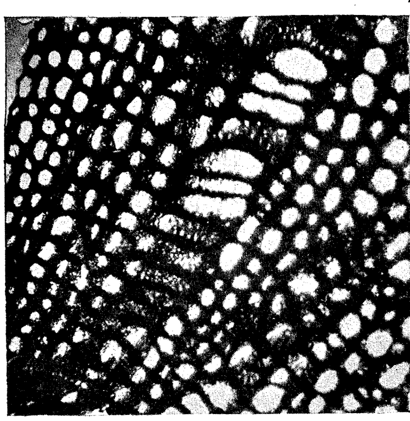

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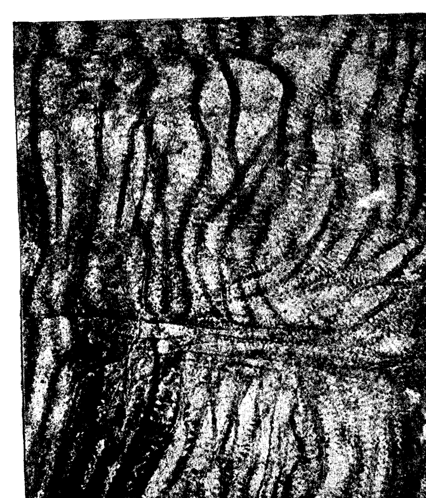

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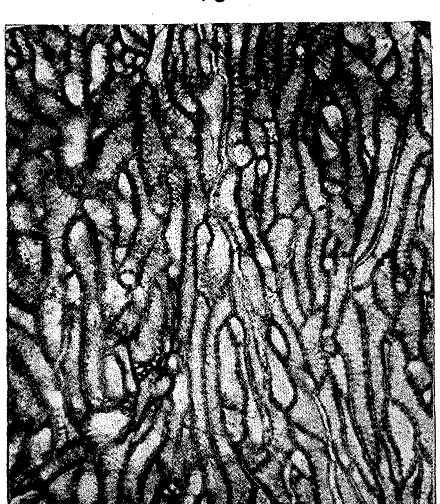

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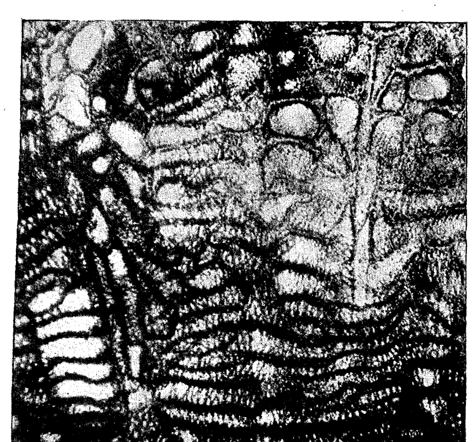

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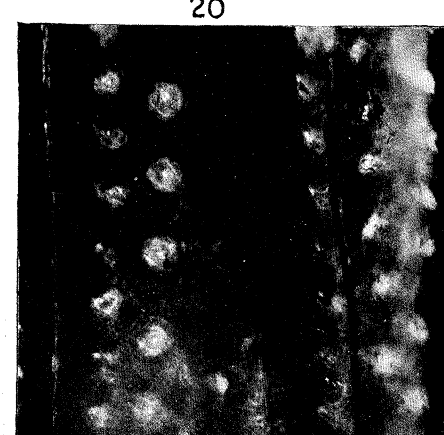

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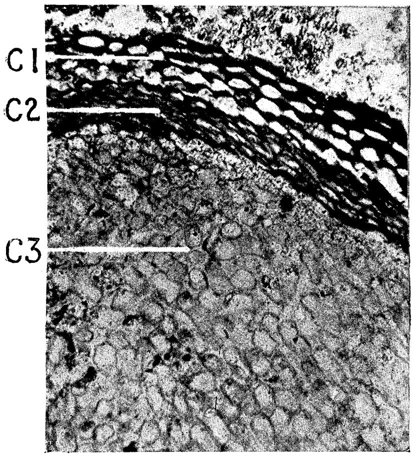

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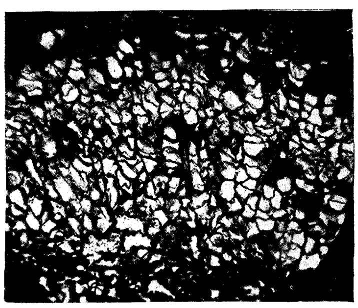
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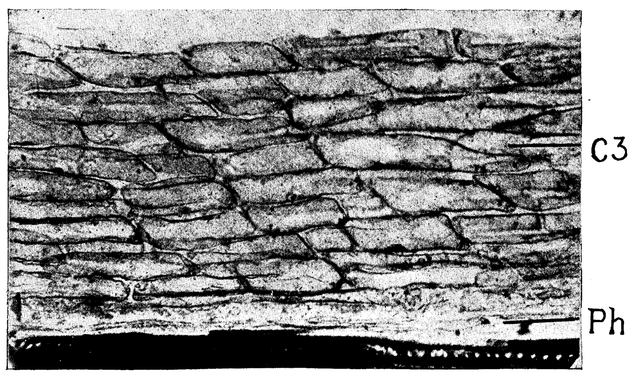

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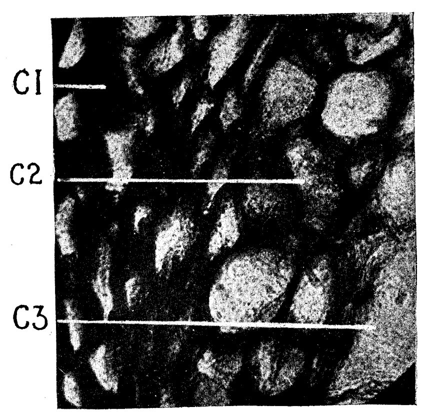

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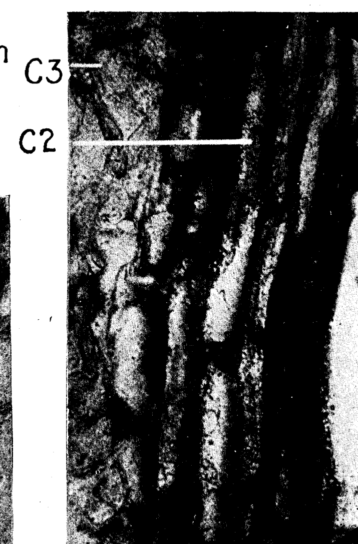

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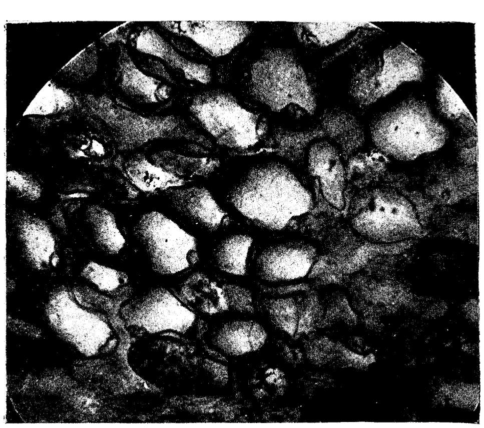
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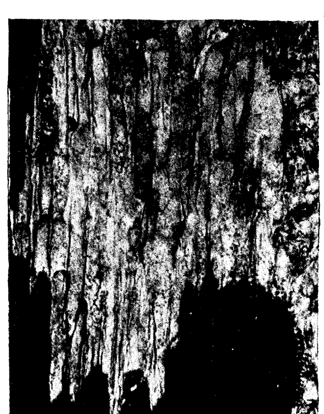
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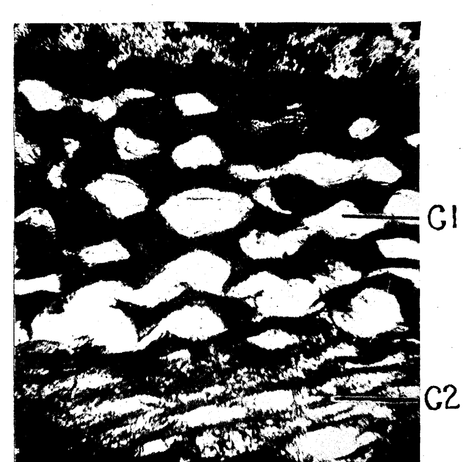

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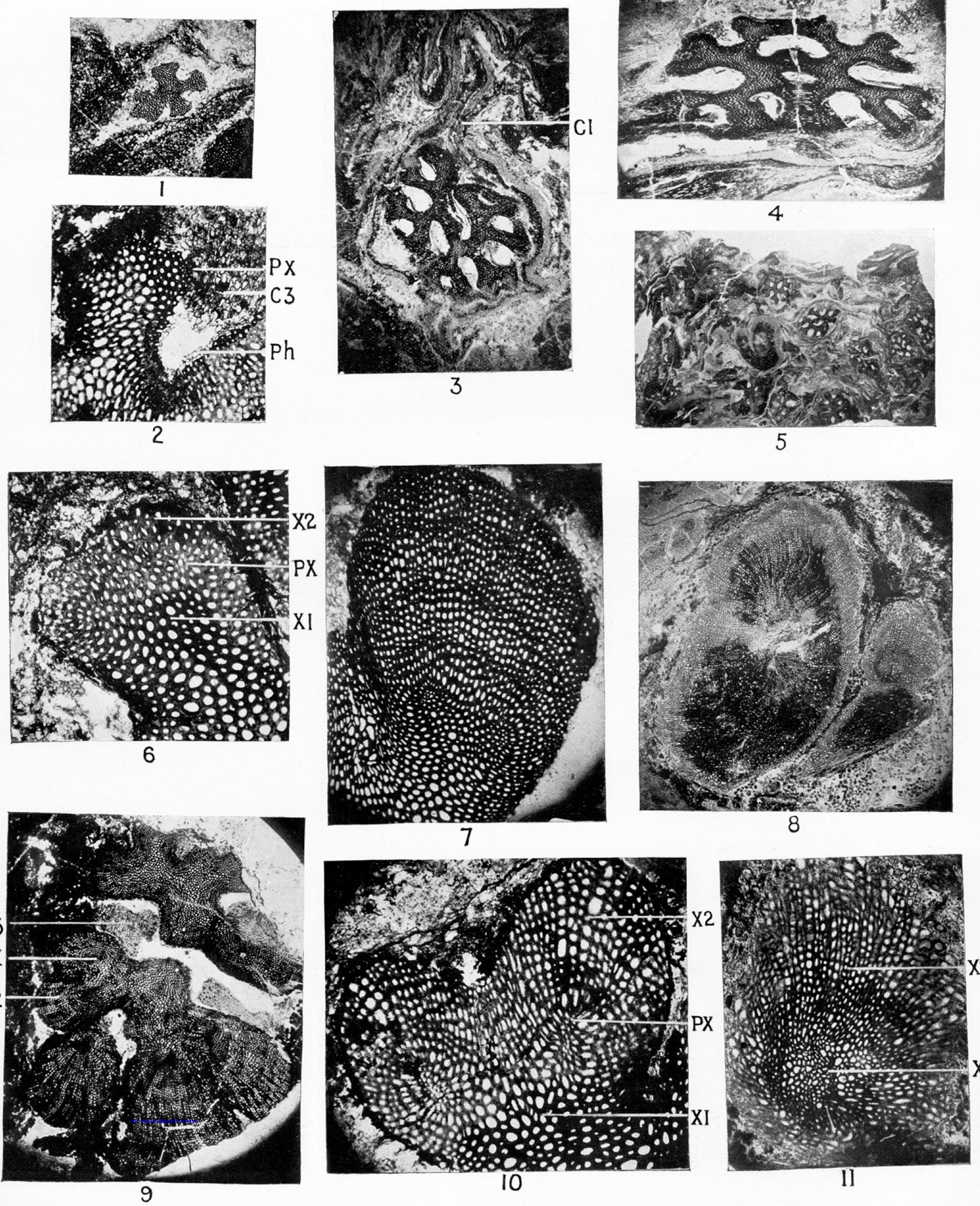

PLATE 91.—GENERAL FORM OF THE XYLEM IN TRANSVERSE SECTION.

FIG. 1.—Stele of a small axis; slide 1. × 15.

FIG. 2.—A lobe of the xylem with the protoxylem at the outside. The inner cortex has shrunk away from the xylem in the sinus; slide 8. × 50.

FIG. 3.—A large axis showing the outer cortex which has collapsed round the xylem; slide 13. × 7.

FIG. 4.—Xylem of a dichotomising axis; slide 19. × 6.

FIG. 5.—Typical section through the chert block, containing the axes shown in figs. 3 and 8; slide 14. × 1·6.

FIG. 6.—A lobe of the xylem, showing the first recognisable traces of outer wood; slide 13. × 50.

FIG. 7.—A lobe of the xylem with strongly developed outer wood; slide 20. × 37.

FIG. 8.—Transverse section of Specimen A; slide 15. × 10.

FIG. 9.—Transverse section of a large axis in which the stele consists of three separate, unequal pieces; slide 7. × 10.

FIG. 10.—A lobe of the xylem with well-developed outer wood; slide 16. × 50.

FIG. 11.—One of the parts of the stele shown in fig. 8, showing the presence of a little inner wood surrounded by the outer (radial) wood; slide 15. × 37.

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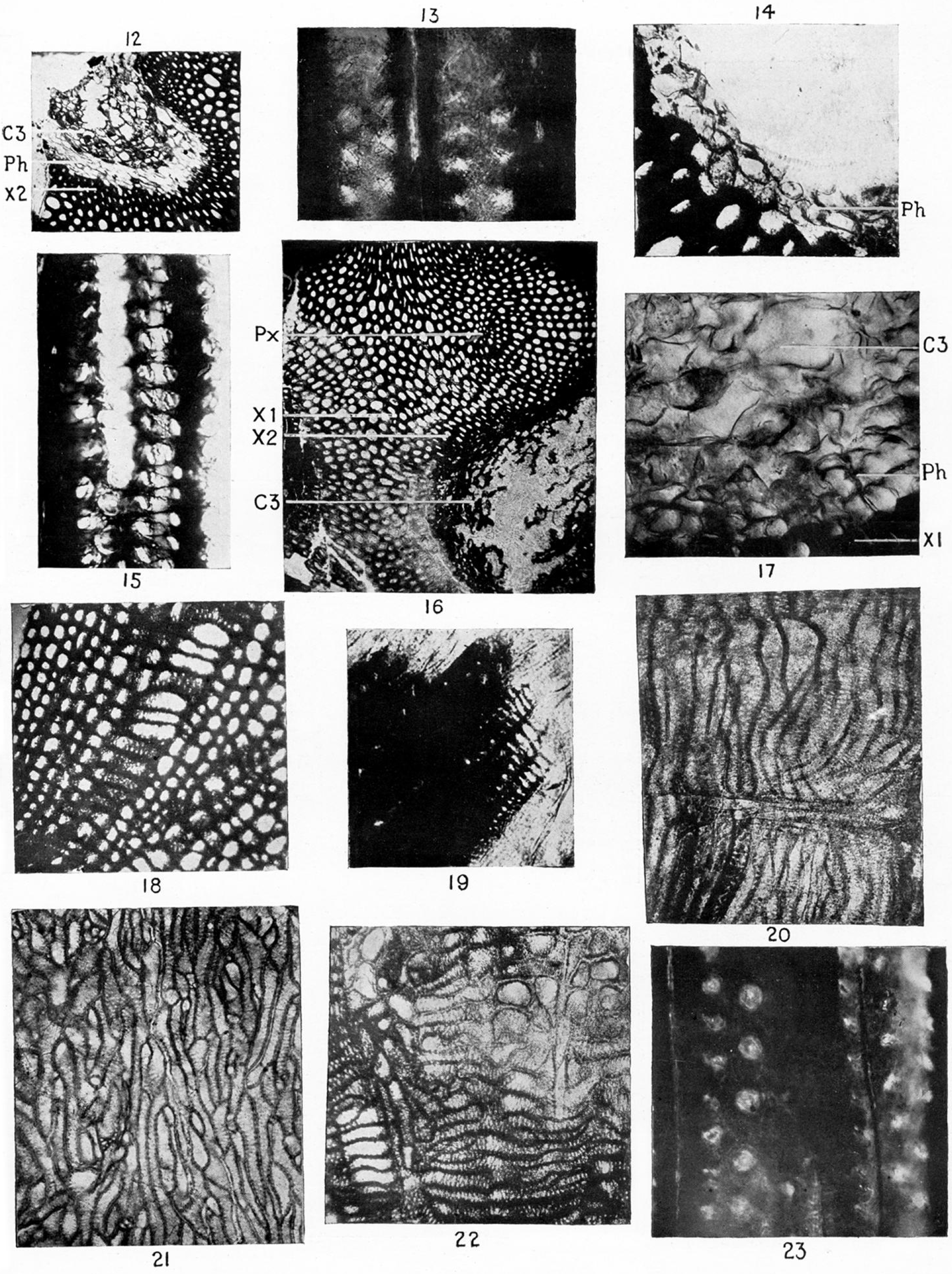

Plate 92.—Structure of the Xylem and Phloem.

C3 = inner cortex, Ph = phloem, X1 = inner xylem, X2 = outer xylem, Px = protoxylem.

Fig. 12.—A sinus of the stele in which the phloem forms a well-marked zone of pale-coloured cells between the xylem and the inner cortex; slide 20. × 35.

Fig. 13.—Longitudinal section through tracheids of the outer wood showing the oblique apertures of the bordered pits; slide 18. × 350.

Fig. 14.—A sinus of the stele in which the inner cortex has shrunk away from the phloem (Ph); slide 25 × 200.

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Fig. 15.—Longitudinal section through tracheids intermediate between protoxylem and metaxylem. The pits have borders and large oblique pores, and are commonly in pairs, separated by scalariform thickenings, like "bars of Sanio"; slide 18. × 350.

Fig. 16.—A lobe of the xylem showing continuity between the inner xylem (X1) and the outer xylem (X2); slide 13. × 40.

Fig. 17.—A sinus of the stele in which the phloem (Ph) is well preserved and still in contact with the inner cortex; slide 25. × 200.

Fig. 18.—Transverse section through the outer wood of Specimen A. Most of the tracheids are cut transversely, but there is one series of tangentially elongated tracheids; slide 5. × 100.

Fig. 19.—Oblique longitudinal section through a lobe of the xylem showing the scalariform tracheids of the protoxylem; slide 18. × 300.

Fig. 20.—Radial longitudinal section through the outer wood of Specimen A. Certain tracheids are elongated horizontally to form a sort of medullary ray; slide 8. × 80.

Fig. 21.—Tangential longitudinal section through the outer wood of Specimen A. Groups of small tracheids represent the medullary rays of Plate 92, fig. 20.

Fig. 22.—Transverse section through the same piece of outer wood as that shown in Plate 92, fig. 18, taken at about 1 mm. to the right of fig. 18. Most of the tracheids are tangentially elongated or cubical. There is a series of radially elongated tracheids; slide 5. × 100.

Fig. 23.—Longitudinal section through two well-preserved tracheids. In the tracheid to the left, the borders of the pits are pale; in the tracheid to the right they have disappeared, except for one which is darker than the tracheid wall; slide 18. × 350.

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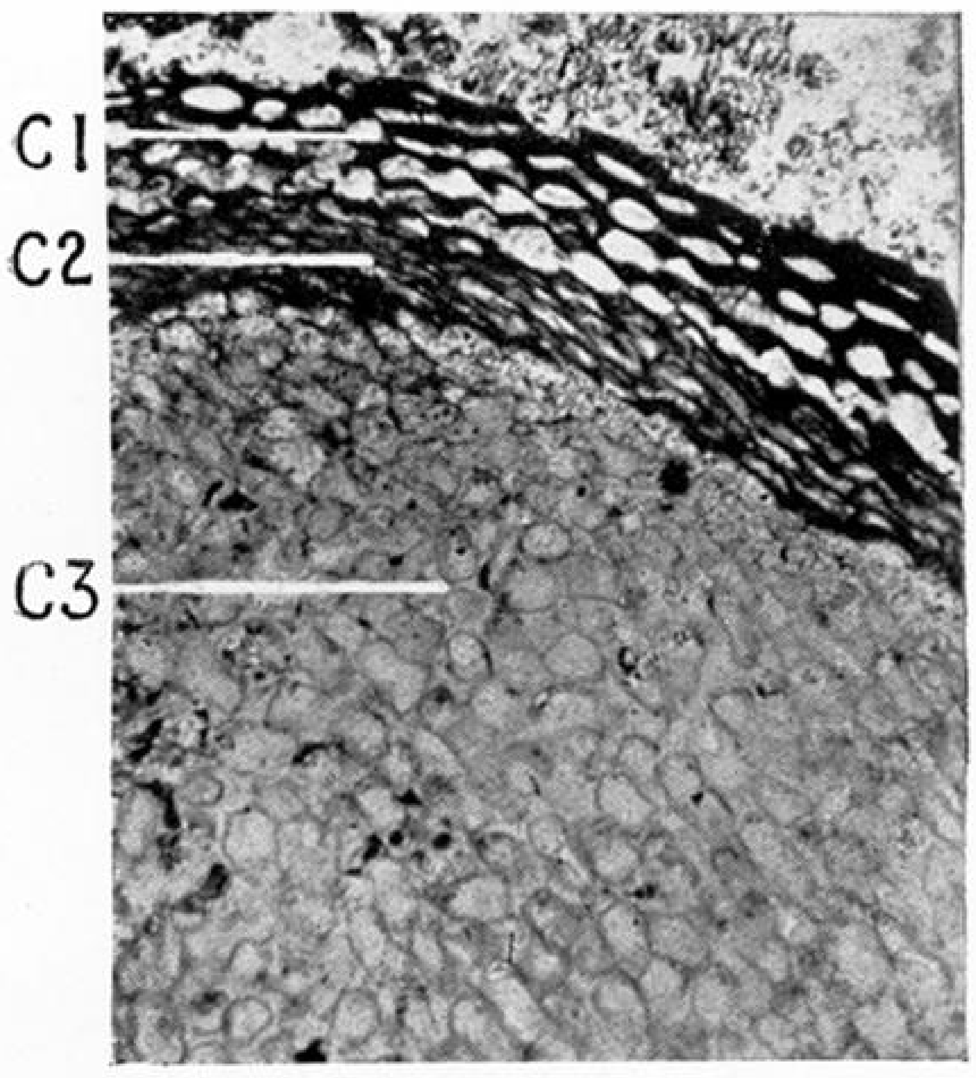

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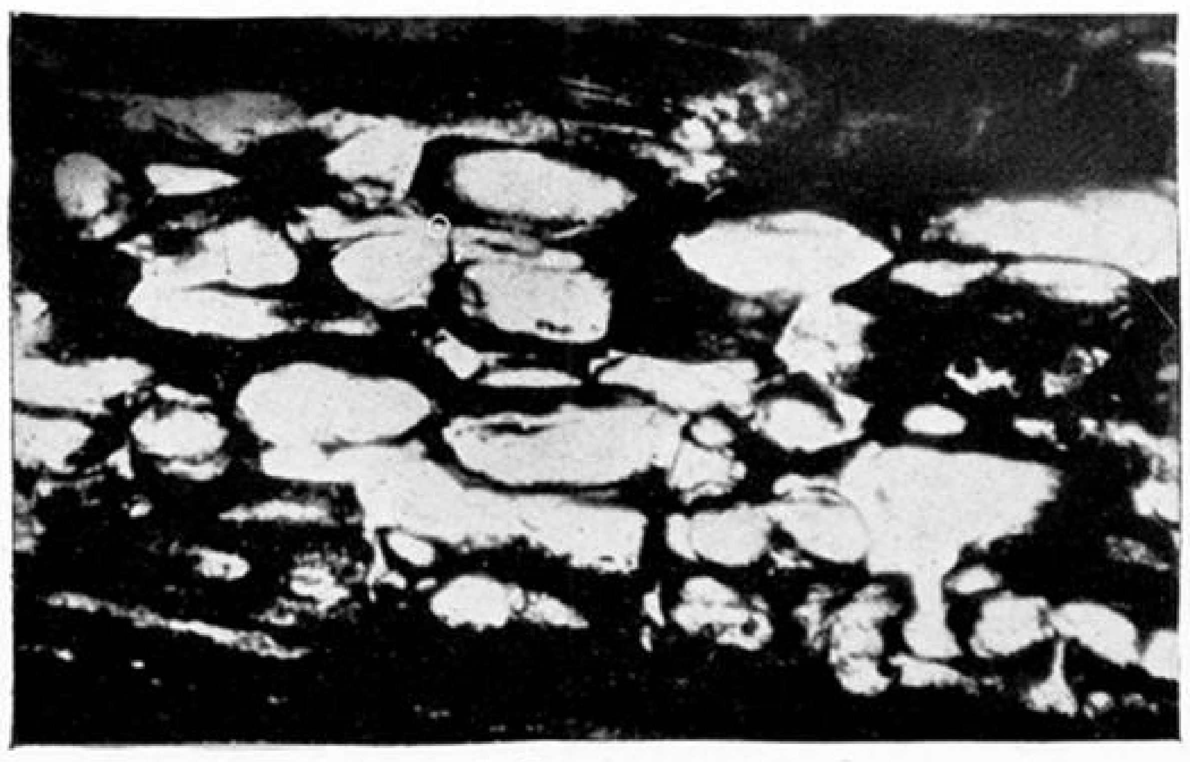
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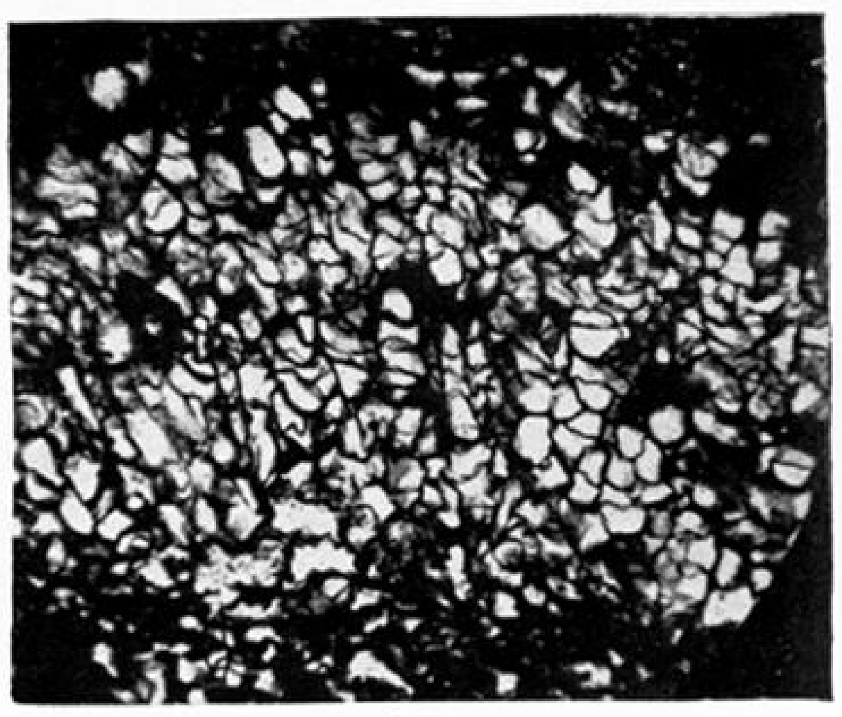
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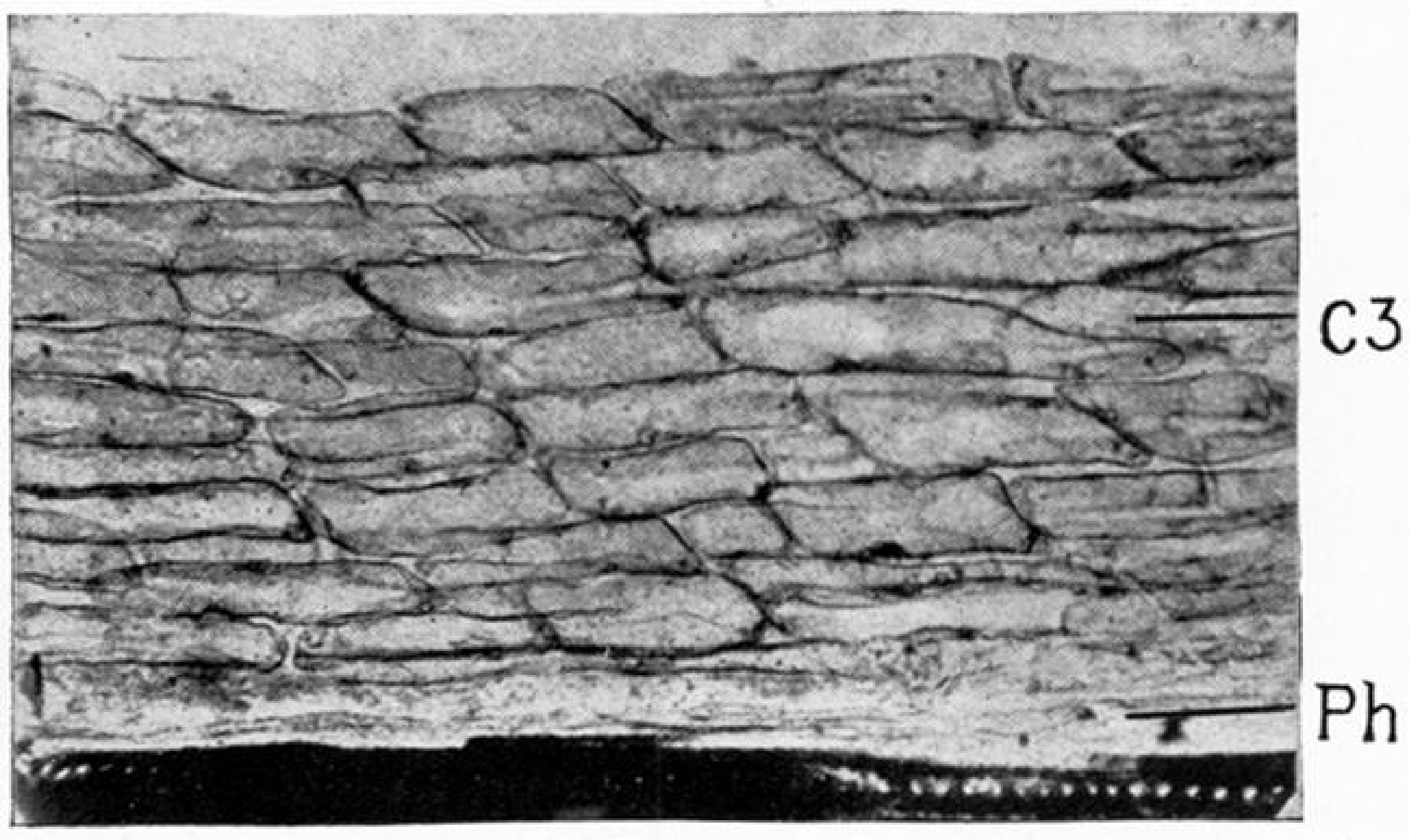

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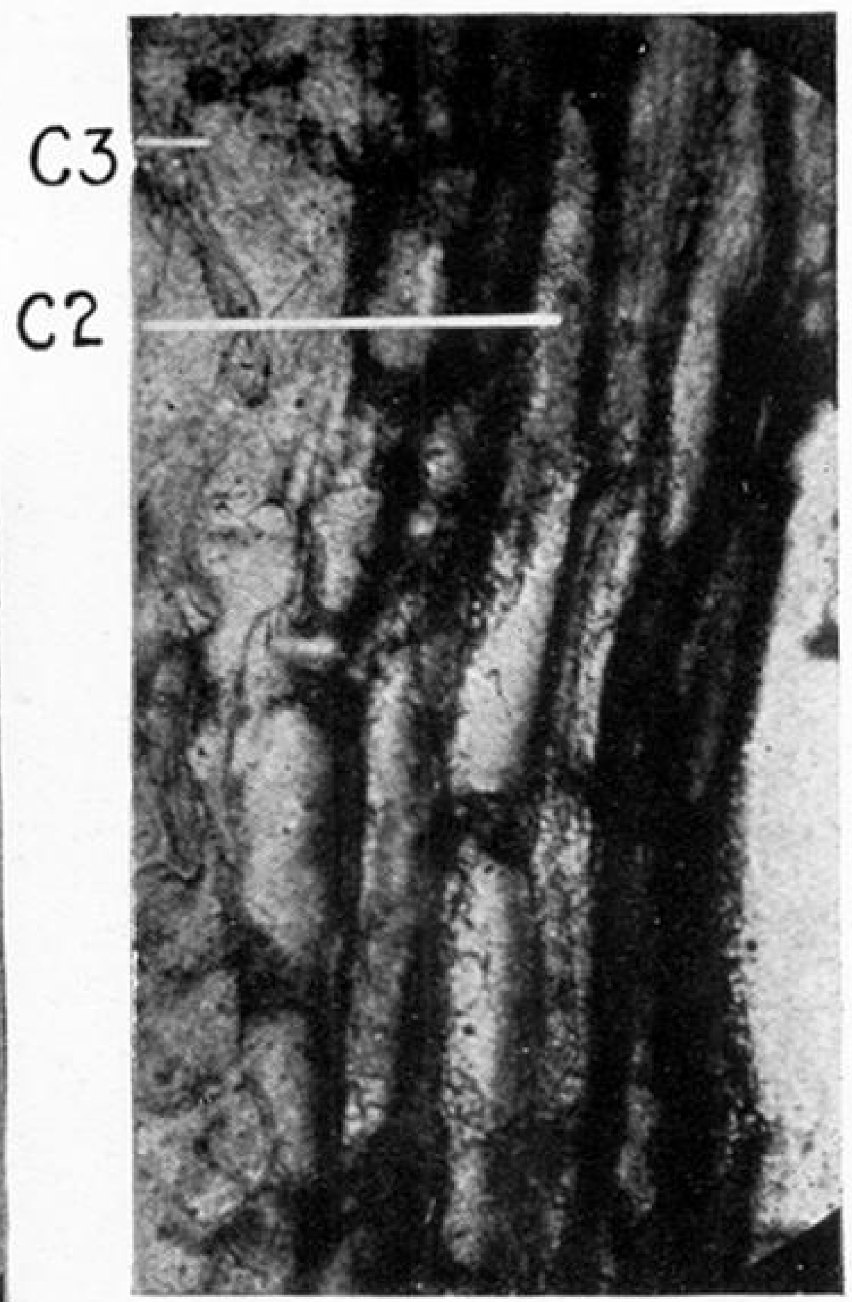

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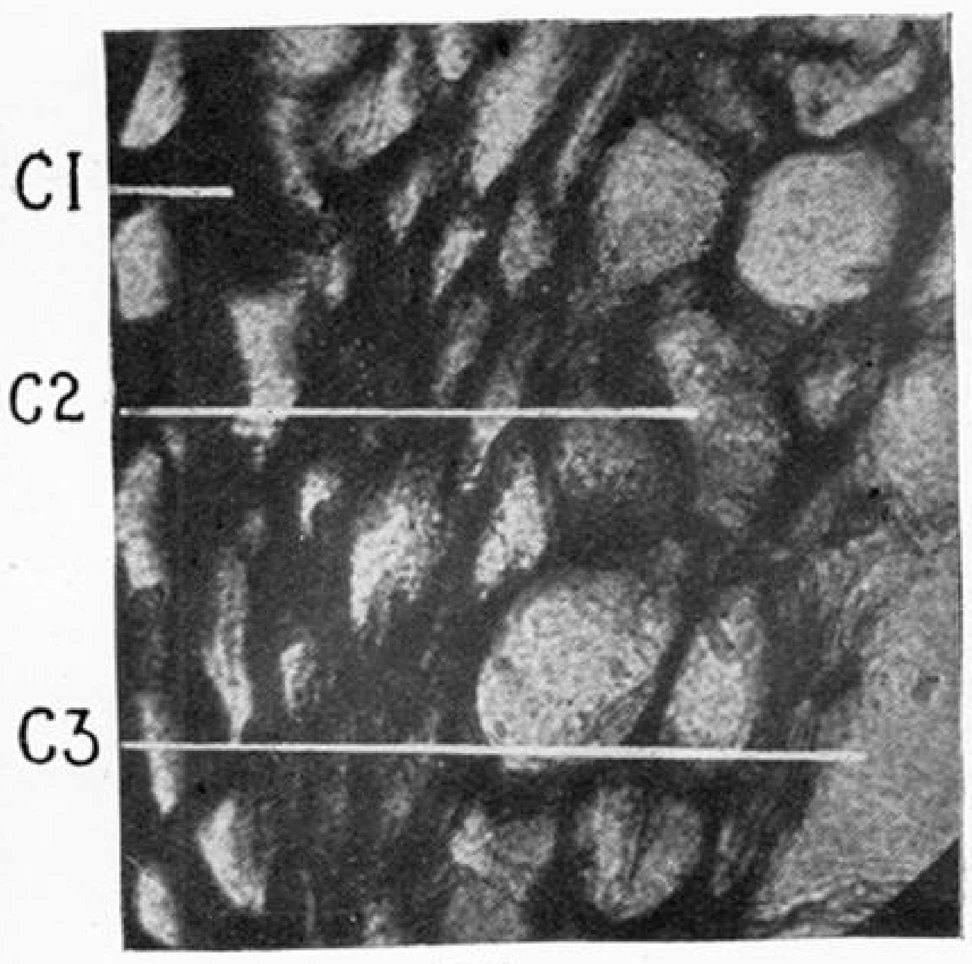

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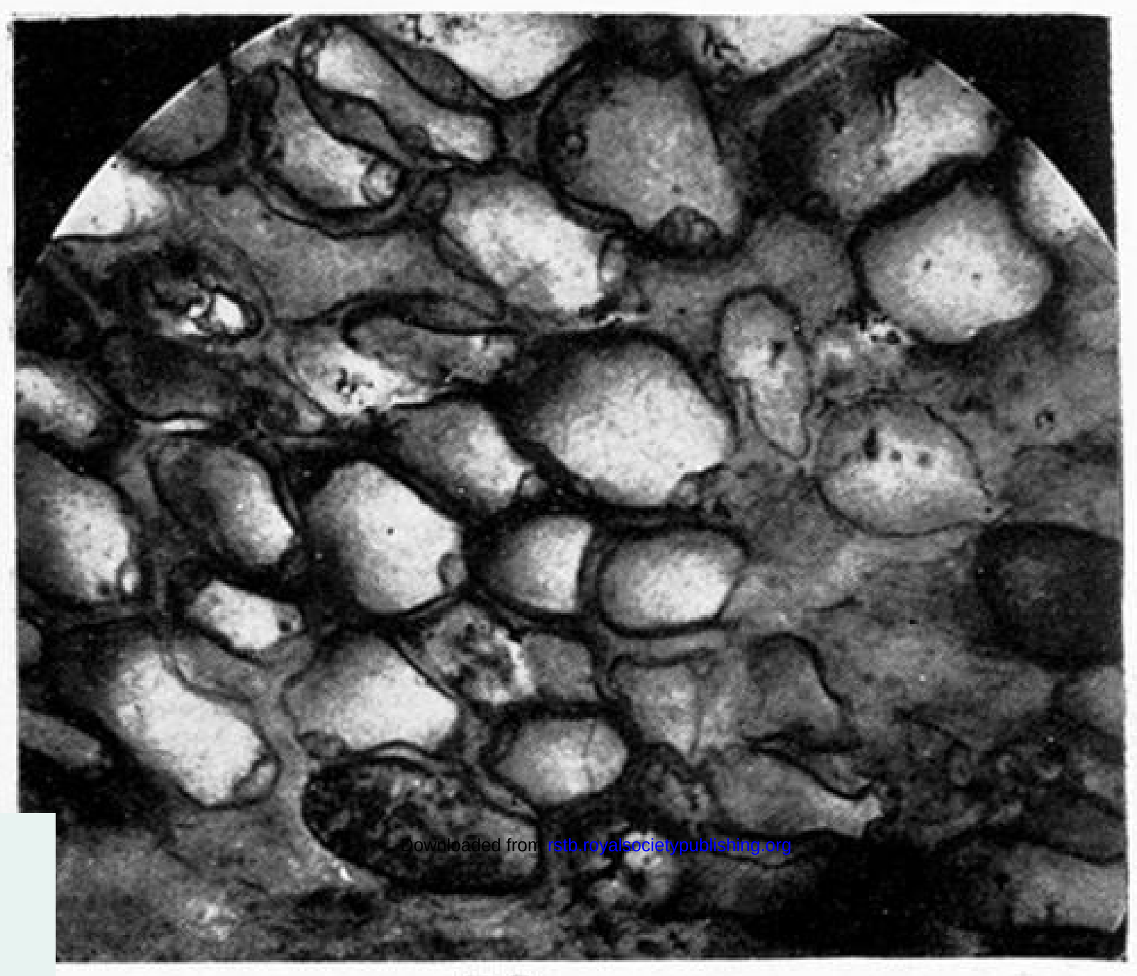
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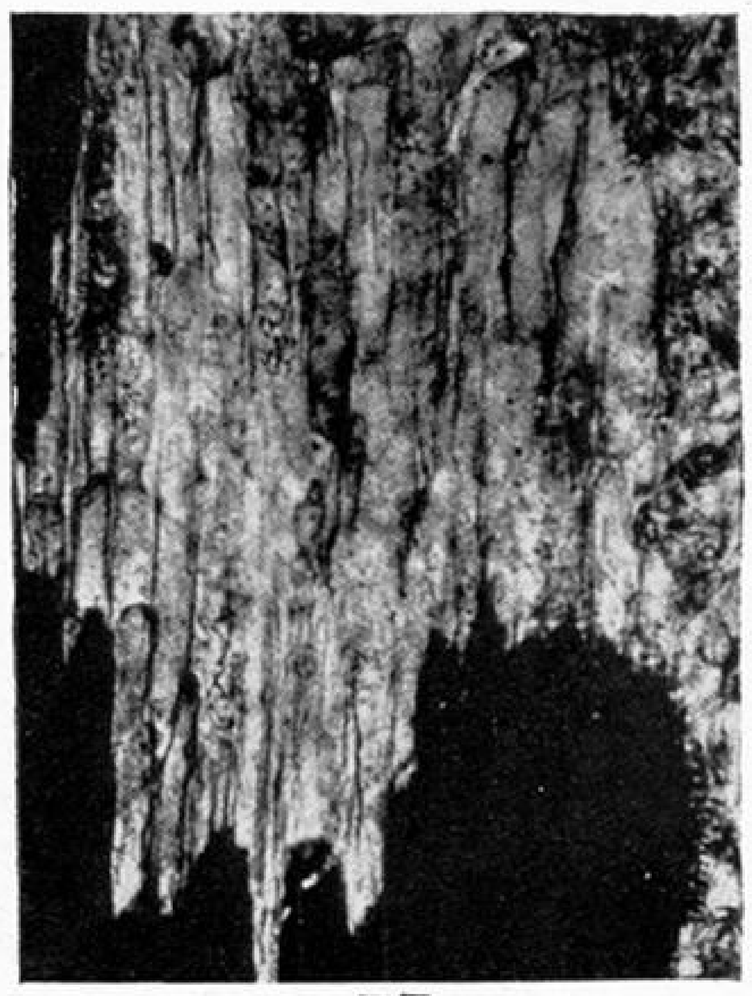
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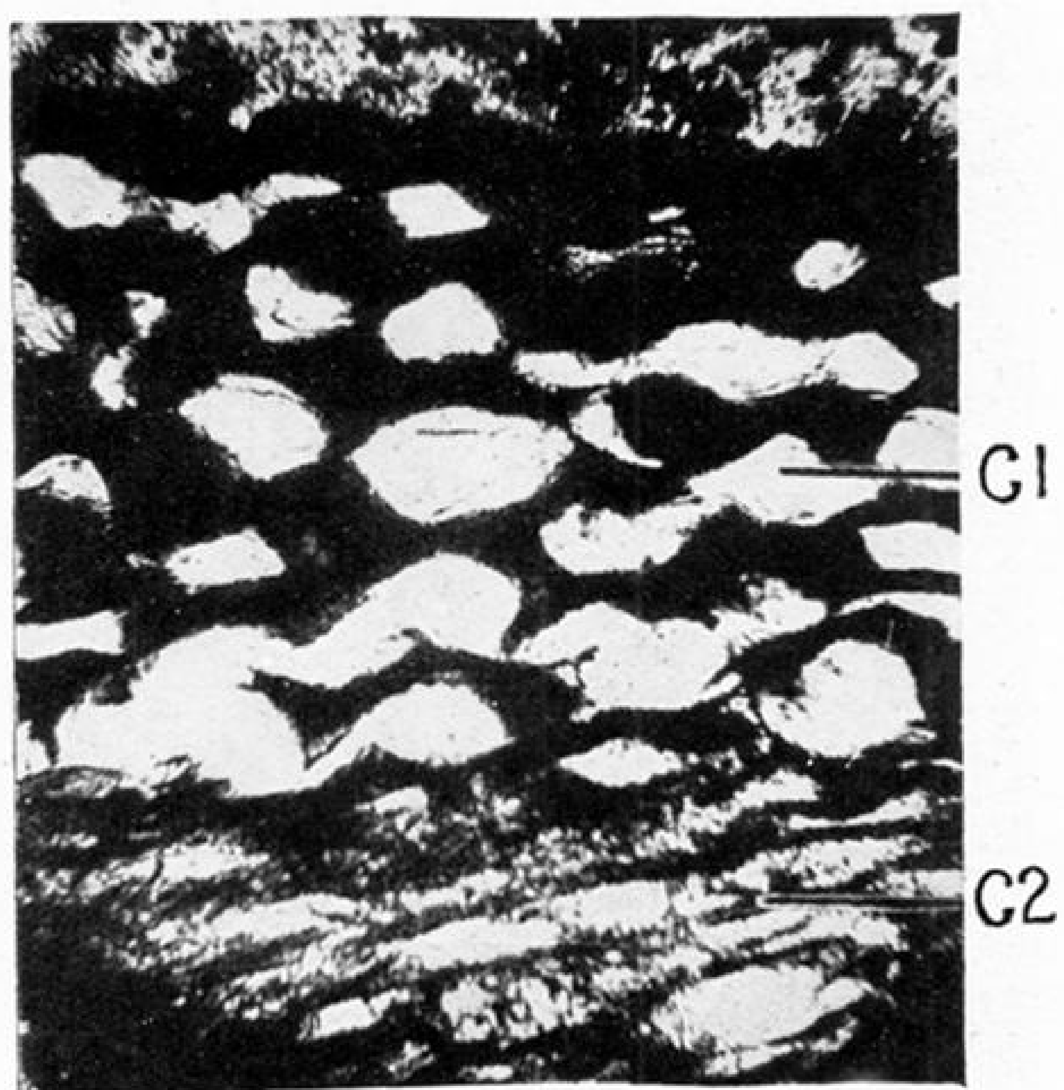

34

PLATE 93.—STRUCTURE OF THE PHLOEM AND CORTEX.

C1 = outer cortex, C2 = middle cortex, C3 = inner cortex, Ph = phloem, X1 = inner xylem.

FIG. 24.—Transverse section through the cortex of a well-preserved axis; slide 16. × 50.

FIG. 25.—Longitudinal section through the inner cortex of a stem in which the cells have dark contents, slide 20. × 100.

FIG. 26.—Radial longitudinal section through the outer cortex showing the thin end-walls of the cells; slide 18. × 250.

FIG. 27.—Cork in more or less radial longitudinal section; slide 15. × 33.

FIG. 28.—Longitudinal section through the inner cortex from a sinus in a stele. The phloem (Ph) is badly preserved; slide 16. × 100.

FIG. 29.—Transverse section through a stem showing continuity between the inner cortex of a sinus of the stele with that outside the stele; slide 18. × 11.

FIG. 30.—Transverse section through the middle cortex; slide 25. × 220.

FIG. 31.—Radial longitudinal section through the middle cortex; slide 18. × 250.

FIG. 32.—Transverse section through the inner cortex in a sinus in a stele; slide 7. × 280.

FIG. 33.—Longitudinal section through the phloem; slide 24. × 100.

FIG. 34.—Transverse section through the outer cortex (C1) and the middle cortex (C2); slide 20. × 160.

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