A Monograph of Stigmaria Bacupensis, Scott et Lang.

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With Plates I–VII.

INTRODUCTION.

THE purpose of these investigations is the complete study of the general anatomy of the main axis of *Stigmaria bacupensis*, Scott et Lang, and its appendages.

Dr. D. H. Scott was the first who noted the characteristic features of the plant and named the new species. He gave a short account of this type in the catalogue of his splendid collection in the British Museum (Natural History), but never studied or figured it. In the Belgian Coal-balls included in Bouxharmont beds,[1] I found a considerable number of specimens of *S. bacupensis*, some of them being beautifully preserved.

I have to express my thanks to Dr. Scott for his permission to study a plant that he was the first to discover. He also obtained from the British Museum permission for two slides of his collection, nos. 950 and 1773, to be figured in my paper as 'type' specimens (Pl. I, Figs. 1 and 2).

If Dr. Scott made the species, Professor W. H. Lang, though he did not describe it, was the first to figure a *S. bacupensis* under its true name. For that reason, according to the Vienna rules the author of the manuscript name and the author who first published it, must be cited together. Hence the species becomes, *S. bacupensis*, Scott et Lang.

As far as I know specimens of *S. bacupensis* have been already figured by Williamson (17–18), Weiss (15), Gothan (1), Lang (5), Leclercq (16), and Koopmans (4), as *Stigmaria ficoides*, Brong., or without determination, or under its true name. None of them have described in detail either the very characteristic features of the main axis or the appendages, as will be seen in the historical survey.

This species occurs in the English Lower Coal-Measures; it has been

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[1] Bouxharmont beds correspond to the English Lower Coal-Measures. See Leclercq (6).

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found in various localities: Dulesgate, Halifax, Shore Little Borough, Bacup, and Sharneyford. It has been observed in other countries also: in Belgium in Bouxharmont beds (6); in the Netherlands in Finefrau Nebenbank seam (4); in Germany from Katharina horizon (1). However this species seems to be most frequently found in England and in Belgium.

I am indebted to Professor Weiss of the University of Manchester and to Professor Seeward of Cambridge for the kind reception I met with during my stay in these two Universities. I also express my thanks to Mr. Edwards of the British Museum who gave me all possible means of examining the Scott and Williamson collections, I must also especially thank Professor C. Fraipont of the University of Liège for all his kind assistance.

HISTORICAL SURVEY.

In 1881, Williamson (17), for the first time, figured a transverse section of a rootlet of *S. bacupensis* which he attributes to a very young root of *S. ficoides*, Brong. He does not draw special attention to the peculiar anatomy of the appendage. He considers the empty space opposite the narrow parenchymatous band connecting the bundle with the outer cortex, as an accident. (See Pl. I, Fig. 3, of this paper where Williamson's rootlet is re-figured.) He says, p. 292: 'In the specimen figured, some of the cells of the outer zone have become partially detached from the outer ring' This is not quite true. In reality no tissue has been *detached*; the empty space is the result of the *decay* of a larger-celled tissue characteristic of the rootlet (Pl. VI, Figs. 46 and 47), as can be seen in Pl. I, Fig. 4 where a Belgian specimen in the same state of preservation is represented.

Williamson, however, notes the small dimension of the rootlet; he observes, p. 292 'that the diameter of the entire young rootlet is less than that of the central inner bark cylinder of a matured rootlet' of *S. ficoides*, Brong. The small dimension of the rootlet is a particular feature of the *S. bacupensis* appendages as will be seen further below.

In 1887, Williamson's (18) 'Monograph on *S. ficoides*' appeared. The author figures (Pl. IX, Fig. 18) a transverse section of 'an extremely young root of *Stigmaria* and considers it as a small extremity of true root' (p. 15 and 42).

I am inclined to consider Williamson's specimen as a young axis of *S. bacupensis*, Scott et Lang. The disturbed vascular cylinder, the great number of rootlets and their peculiar structure, suggest it. As I had examined the specimen in Williamson's figure only I could not be certain of my determination, so I asked Professor Weiss to clear up this point. He wrote me that he had also noted the resemblance of Williamson's figure to *S. bacupensis*, and that he examined the original preparation when he was at the British Museum. 'The specimen', he says, 'shows some central remains in the pith but no spiral elements are to be seen. The tissues are not sufficiently preserved. Still I think it was very probably a *S. bacupensis*, though it cannot be determined with certainty.'

The presence of spiral elements in the centre of the main axis is one of the characteristic features of *S. bacupensis*, so if they do not occur in Williamson's specimen, the latter is certainly not a *S. bacupensis*. However it might have happened that the delicate spiral elements have become disorganized. In any case the determination is doubtful.

From 1895 to 1923 Dr. D. H. Scott (9) wrote his Catalogue as his collection of slides grew. He gave the following short description of the species: 'Rootlets appear more numerous than in *S. ficoides*, and medullary ray bigger in proportion to bundle of rootlet . . . Stele cut obliquely, shows probably primary tracheides in pith. . . . The middle is almost solid primary wood with small barred tracheides. Periderm and bases of numerous rootlets shown.'

This short description is of course very incomplete. Dr. Scott has noticed neither the peculiar structure of the outer cortex of the main axis nor the peculiarities of the appendages which define the type. These features are particularly well shown in Belgian specimens.

In 1902, Professor Weiss (15) published a very interesting paper on 'The vascular branches of Stigmarian Rootlets'. He investigated rootlets showing fine vascular strands starting out from the protoxylem of the bundle, and running out through the middle cortex to terminate in the outer cortex in connexion with an extensive patch of tracheidal tissue. His study is founded on the examination of *S. ficoides* rootlets and on 'a type not uncommon among stigmarian rootlets', as he correctly noted 'that a careful examination of a large number of rootlets of this type . . . convinces' him 'that it is a somewhat different type of rootlet'. The rootlet figured by Weiss (Pl. XXVI, Fig. 3) is a *S. bacupensis* appendage. A close comparison can be established between these figures (repeated in this paper Pl. I, Fig. 5) and the type specimen (Pl. VI, Figs. 46 and 47). It will be shown that Weiss's undetermined rootlet possesses the characteristic features of a typical *S. bacupensis* appendage (see p. 49 the *S. bacupensis* rootlet diagnosis).

In 1923 M. W. Gothan (1) published a study on the 'Karbon und Perm Pflanzen'. He figures (Pl. XLIII, Fig. 4) a group of rootlets that he determines as stigmarian appendages. The monarch structure of the bundles, its connexion with the outer cortex by a strand of parenchymatous tissue, and the diameter of the rootlets are characteristic features of *S. bacupensis* rootlets.

The comparison between Gothan's appendages group and the group of *S. bacupensis* appendages (Pl. VI, Fig. 47) shows the identity of the rootlets. In the same year, Professor W. H. Lang (5) gave a very interesting account

'On the apparently endogenous Insertion of the Roots of *Stigmaria*'. His investigations are founded on the examination of a young axis of *S. bacupensis*. His researches concern the relation of the rootlets to the outer tissue of the Stigmarian axis. He does not describe the species, but for the first time, as it has been noted in the introduction, he figures that species with its true name.

Two years later (1925) I published a paper (6) in which I pointed out the presence of two *S. bacupensis* specimens in the coal-balls of Bouxharmont. The first one, figured on Pl. XXVIII, Fig. 5, is a young axis magnified (thirty times) to show on the photograph the numerous rootlets, cut in various directions, which surround it. A transverse section made through that specimen is figured in this paper (Pl. I, Fig. 6); the second specimen figured on Pl. XXVII, Fig. 3, of my paper of 1925, is a rather stout axis. The stele alone is preserved and shown magnified only ten times. This specimen named *Stigmaria cf. bacupensis* is not correctly determined. If the secondary wood is broken down in numerous narrow bundles as is usual in *S. bacupensis*, the primary wood lay here at the inner end of each wedge. It is formed by smaller and not very regular elements disposed in a centrifugal manner such as *S. ficoides*. The distinction between primary and secondary xylem is not sharp as in *S. bacupensis* (Pl. II, Fig. 9). The centre of the stele is hollow; it has been certainly occupied by a fair-sized pith which is not preserved, and is replaced by a Stigmarian appendage running over. No traces of spiral elements belonging to the primary wood can be seen in the centre, as always occur in *S. bacupensis* axis.

For that reason I will call that specimen *Stigmaria* sp. till I have found another specimen surrounded by a cortex.

In 1927 Dr. M. Hirmer[1] (2) published his 'Handbuch der Paläobotanik', in which he re-figures (p. 294, Fig. 346) Gothan's undetermined group of Stigmarian appendages and names them *Stigmaria ficoides*, Brong. For the reasons stated above, I consider these appendages as belonging to *S. bacupensis*. In the same paper M. Hirmer gives (p. 296) a short account of *S. bacupensis*; he says: '*St. bacupensis*, Scott. Lower Coal-Measures of England and Belgium. In transverse section the primary xylem consists of very numerous and small elements. Rootlets of evident endogenous formation.'

In 1928 appeared R. G. Koopmans 'Researches on the flora of the coal-balls from the "Finefrau Nebenbank" Horizon in the province of Limbourg (the Netherlands).' The author (4) figures (Pl. XII, Fig. 93) a transverse section of two steles without cortex, of *St. cf. bacupensis*, Scott. He considers it possible that these specimens belong to that later

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[1] Hirmer, M.: *St. bacupensis*, Scott. Lower Coal-Measures von England und Belgien. Primary xylem Partieen im Querschliff sehr schmal und zahlreich. Wurzeln offenbar von endogener Entstehung (p. 296).

species, though his determination is only founded on the examination of the figures published in my paper, 'Les coal balls de la couche Bouxharmont des charbonnages de Werister'. His determination seems to be correct.

DESCRIPTION OF *STIGMARIA BACUPENSIS*, SCOTT ET LANG.

Stigmaria bacupensis.

1895–1923: Scott, Manuscript.
1923: Lang, Mém. Proced. Manch. Litt. Phil. Soc., vol. lxvii, Part II, p. 101, Pl. II, Fig. 1.
1925: Leclercq, S., Mém. in 4°. Soc. Géol. de Belg., tom. vi, p. 47, Pl. XXVIII, Fig. 5.
1928: Koopmans, R. G., Géol. Ber. voor het Néderl. Myn., i, p. 17, Pl. XII, Fig. 93.

Stigmaria ficoides.

1881: Williamson. Royal Society. On the Organization of Fossil Plants, Part XI, p. 292, Pl. LIII, Fig. 16.
1887: Williamson, Monograph on *S. ficoides*, Paleontograph. Soc., pp. 15 and 42, Pl. IX, Fig. 18.
1927: Hirmer, Handbuch der Paläobotanik, München und Berlin, p. 294, Fig. 346.

Stigmaria, sp.

1902: Weiss, F. E., Ann. Bot., p. 565, Pl. XXVI, Figs. 3 and 4.
1923: Gothan, W., Leitfossilen, Berlin, p. 156, Pl. XLIII, Fig. 4.

ANATOMICAL STRUCTURE.

As already mentioned, the species *S. bacupensis* was made by D. H. Scott as the result of the examination of English specimens now in the British Museum. I have shown in this paper as type specimens (Pl. I, Figs. 1 and 2), two examples nos. 950 and 1773 borrowed from the Scott collection, though the whole study of the species is based largely on the examination of Belgian specimens found in coal-balls of the Bouxharmont beds. The Belgian coal-balls examined are nos. 2, 624, 678, 802, 724. They have supplied very numerous preparations. For ease of text transcription, the specimens will be designated by the number of the preparation in which they are found. For instance when it is said that in no. 624, the glandular zone of the outer tissues of the main axis is the most striking, it means that in the specimen of *S. bacupensis* included in preparation no. 624, the glandular zone of the outer tissues of the main axis is the most clearly seen.

We have now to consider the internal structure of the main axis (vascular cylinder and cortex) and its appendages.

THE MAIN AXIS.

The dimensions of the whole axis (stele and bark), vary according to the age of the specimens. In apparently well-developed specimens (like nos. 624 and 678; Pl. I, Figs. 7 and 8), the bark must have had a circumference of 25–35 mm. while the central cylinder diameter is 3–4 mm. only.

(*a*) VASCULAR CYLINDER.

The primary wood. One of the most striking features of the anatomy of *S. bacupensis* is the structure of the primary wood of the vascular cylinder. This differs in essence from all the other species of *Stigmaria* in being neither centrifugal nor centripetal in its development. Towards the centre of the axis, the secondary tracheides become smaller without losing anything of the regularity of their arrangement (Pl. II, Fig. 9) as will be seen below. Then within the cylinder of secondary wood we come to a very definite primary wood beginning with small spiral elements on the outside (Pl. II, Fig. 9) followed on the inside by a tissue consisting of numerous rows of spiral elements and small barred tracheides of various dimensions (Pl. I, Fig. 1; Pl. II, Fig. 10). No pith is present. The transverse sections (Pl. II, Fig. 10) show clearly that within the small elements of the periphery, as we advance further inwards, elements of various size are mixed. Some of them are twice the size or more of the peripheral elements, others are as small as these or still smaller. This fact is well illustrated in the specimen 624 (Pl. II, Fig. 11) where a rather wide element, situated in the centre of the axis is surrounded by seven smaller elements (Pl. II, Fig. 11) and also in specimen 624, 1–7 (Pl. I, Fig. 12) where a row of elements of various dimensions joins the ring of secondary wood.

Beyond that, specimen 624 only shows in a transverse section, wide elements with reticulate thickening (Pl. II, Fig. 13) like the characteristic reticulate tracheides of *Lepidodendron selaginoides*, Stern. No ring forming a broad continuous zone of primary wood can be found, and as Dr. Scott says in his catalogue 'The middle (of the axis) is almost solid primary wood, with small barred tracheides'.

The elements of primary wood being thin walled and of small zone do not offer a great resistance to the intrusion of the stigmarian appendages; these latter, very frequently, run over the centre of the axis, crushing the primary xylem (Pl. I, Fig. 8). For that reason good radial sections are rare. However, the radial section (Pl. III, Fig. 14) shows very narrow elements at the outside of the wood exhibiting spiral, annular, and barred marking (Pl. III, Figs. 14 and 15). Further inwards, the wood consists of elements showing the same thickening but of various dimensions (Pl. III, Figs. 14, 15, and 16). It is not possible to say if the primary wood consists in protoxylem and metaxylem; the differentiation and the direction of the woody elements in which they are developed are not clear enough.

In three radial sections made through the woody cylinder of two Belgian specimens, nos. 624 and 678, we have found mixed with the primary wood elements, a thick bearded mycelium (Pl. III, Fig. 17). The same fungus has been met with among the primary wood of one of the two English specimens (no. 1773) figured in this paper (Pl. I, Fig. 2). Though four other specimens have been investigated to see if the association of the two plants was constant, we are not yet able to assert it with certainty. It is very difficult to obtain good and clear radial sections through the delicate primary wood whose elements are generally crushed by intruded Stigmarian appendages. Yet the presence of the same fungus in three well-developed main axes seems to remove the possibility of an accidental invasion. It must be said, however, that young axes appear not to have been invaded.

The secondary wood is generally well preserved and of normal type. It consists of a well-developed vascular cylinder divided up into numerous narrow bundles by the numerous principal medullary rays (Pl. I, Figs. 1 and 8; Pl. II, Fig. 9). The bundles consist of radially arranged scalariform tracheae showing only slight irregularity where new rays of wood elements become added, as secondary growth proceeds. The tracheides are of medium size, and square in transverse section. Towards the inner margin, though the distinction between primary and secondary xylem is sharp, the inner end of each wedge is loose. In addition to the principal rays, numerous narrow secondary rays traverse the wood; their thinner tissue has undergone some disorganization so that they appear on the transverse section more like long gaps (Pl. I, Fig. 1; Pl. II, Fig. 9).

The secondary xylem tracheae present scalariform pits on both radial and tangential walls (Pl. III, Figs. 18 and 19) and show the spaces between the transverse bars bridged across by fine threads as has been noted and figured by Williamson for *Lepidodendron mundum* as well as in the tracheae of other *Lepidodendra*. The numerous parenchymatous rays, generally one cell thick and one to forty cells in height, can readily be seen on the tangential longitudinal section (Pl. III, Fig. 18). The radial sections show clearly the secondary tracheides becoming smaller from the outside to the inside and joining closely the narrow spiral elements of the primary wood (Pl. III, Figs. 15 and 19). No pith is present. A feature which distinguishes this type of *Stigmaria* from the *Stigmariae* with a solid primary wood, is the woody cylinder broken up into numerous and narrow distinct wedges. The frequent presence of broad medullary rays traversed by the appendages bundles split up the woody ring. The tangential section shows (Pl. III, Fig. 18) the narrow bundles anastomosed laterally with each other, forming a network, with numerous meshes in which medullary rays and the appendages bundles are enclosed. Radial sections show the secondary wood very divided for the same reason (Pl. III, Fig. 19; Pl. V, Fig. 37).

In conclusion, I should like to mention the characteristic features of the vascular cylinder: *Solid primary xylem with small spiral, annular, and barred-marking elements of various size. No evident direction in the development; no pith. Secondary xylem broken into numerous narrow bundles, the inner end of these latter is loose; numerous medullary rays.* The delicate tissue of the cambium and the phloem has not been observed in the preparations examined.

(*b*) THE CORTEX.

From the outer tissues, the outer cortex is generally well preserved. Remains of inner and middle cortex are rare. The space left by the decay of these soft tissues is usually largely invaded by stigmarian appendages (Pl. I, Fig. 8; Pl. II, Fig. 9).

In the outer cortex, it is possible to distinguish four zones. These are from within outwards (1) an irregular periderm (Pl. III, Fig. 20); (2) a zone with dark-coloured group and tangentially elongated parenchymatous cells (Pl. II, Fig. 9); (3) a clear zone of tissue made up of moderate sized cells which may show indications of tangential and radial divisions (Pl. II, Fig. 9); (4) more or less complete remains of an outermost zone of very small-celled tissue (Pl. I, Fig. 6; Pl. V, Fig. 36).

The *periderm* consists of a prosenchymatous tissue formed by cells with parallel sides and pointed ends, mixed with wide-celled files (Pl. IV, Fig. 22).

In transverse section, the prosenchymatous cells are radially elongated except the inner-cells which are more tangentially extended (Pl. IV, Fig. 21).

Their layers, generally arranged in definite vertical files, are separated throughout the width of the periderm by a wide-celled portion (Pl. III, Fig. 20), and against the dark-coloured group of zone II (Pl. II, Fig. 9; Pl. III, Fig. 20).

Sometimes files do not quite reach to the outer border of the secondary tissue and taper away before reaching the outer margin (Pl. III, Fig. 20).

Very probably in some cases short files may be produced by subsequent division of the cells of the periderm. The number of the layers increases with the age of the specimens.

The wide-celled files, typical of stigmarian periderm are rather frequent in *S. bacupensis*. In well-developed periderm formation, they form lighter lenticular areas enclosed by dark prosenchyma files (Pl. III, Fig. 20; Pl. IV, Fig. 21).

In younger axes they appear rather wedge-shaped in transverse section, increasing in size towards the periphery or the inner margin (Pl. II, Fig. 9). They are formed among the ordinary radial files by a certain number of the cells being left thin-walled and becoming extended in the tangential direction. They have a great power of division and show numerous radial septa (Pl. III, Fig. 20; Pl. IV, Fig. 21).

It is in the tangential section that the heterogeneous nature of the cells of the periderm is the most striking. The prosenchymatous cells are as already mentioned, narrow parallel-sided and with pointed ends (Pl. IV, Figs. 22 and 23). They are commonly narrower towards the inside where they constitute the largest portion of the periderm. The thin-walled wide cells occur rather in definite vertical files than in lenticular areas (Pl. IV, Fig. 22). They are divided by horizontal septa into chambered-cells, and each segment may undergo further vertical division, so that later, the outline of the original extended prosenchymatous cells is lost (3, p. 306) (Pl. IV, Fig. 23), but sometimes the occurrence of the pointed end-segments still gives the clue of the origin of the mesh. Sometimes very simple chambered-cells are met with which consist of cells with a few horizontal septa.

In radial section the prosenchymatous cells consist of fairly straight rows of tissue, narrower towards the interior (Pl. IV, Figs. 24 and 25). The chambered-cells with their numerous daughter-cells form a large conspicuous parenchymatous strand surrounded by dark prosenchymatous formation (Pl. IV, Fig. 25).

We will now consider in which direction the periderm has been formed. In none of the specimens we have investigated, have we found the phellogen preserved, but it has been already mentioned, in transverse sections, toward the interior, the prosenchymatous cells are more tangentially extended (Pl. III, Fig. 20; Pl. IV, Fig. 21), that is to say, that recently formed tangential walls have occurred and probably represent an early stage in the development of periderm.

In radial section made through the periderm formation the straight lines tissue is narrower towards the inner margin (Pl. IV, Figs. 24 and 25). For these reasons I am inclined to determine the position of the phellogen near the inner margin, and to consider the periderm development as centripetal.

In her paper on the 'Physiological anatomy of the periderm fossil Lycopodiale' Kisch (3, p. 294) noted in *Stigmariae* two distinct types *at least* in regard to the position of the phellogen. In the case of irregular periderm with wide-celled outer portion, she locates the phellogen in the middle of the periderm formation just at the junction of the regular radially disposed cells, and the irregular wide-celled outer portion.

'In this type,' she says, 'though a disorganized band of cells is all that can generally be distinguished, the phellogen is probably at the junction of the two different kinds of tissue and forms the wide-cells to the exterior and the narrower files on its inner surface by means of further radial divisions.'

I do not agree with this view in the case of *S. bacupensis*. In all the specimens of that species I have examined (and some of them have perfectly preserved periderm) I never found in the middle of the periderm formation either meristematic cells or a disorganized band of cells which may be distinguished as phellogen. If the periderm is of an irregular formation a sharp distinction between a wide-celled *outer portion* and a regular radially disposed cell *inner portion* does not occur in *S. bacupensis*. In transverse section, the chambered-cells ol the somewhat lenticular areas run the whole width of the periderm. If their maximum width most frequently occurs towards the exterior, the extremity of the decreasing lenticular strand also reaches the inner margin (Pl. II, Fig. 9; Pl. III, Fig. 20; Pl. IV, Fig. 21).

The irregular periderm formation of *S. bacupensis* is quite easy to explain when the phellogen is situated towards the inner margin. In very young specimens, regular prosenchymatous tissue only is formed on the outer side of the phellogen. A little later, in a somewhat older example some cells are left thin-walled by meristematic cells and are transformed into chambered-cells (wedge-shaped and afterwards lenticular area transverse section). In very old specimens, the increasing girth of the axis forces the gradual increase of the outer tissues. This enlargement is assured by the multiple divisions of the chambered-cells which have such a great power of division that they may loose their original outline. In such old examples, where periderm formation is well developed, a regular inner portion in which no wide-cells are found, may occur. The chambered-cells have been located towards the middle and the exterior periderm up to the point where the increasing girth of the axis results in numerous divisions of the outer tissue to keep pace with its enlargement.

To sum up the characteristic of the first zone of the outer cortex it may be said that *the periderm is of an irregular type consisting of normal prosenchymatous tissue mixed with wide-celled portions. The position of the phellogen is on the inner margin, consequently tbe periderm is developed in a centripetal direction.*

The *second zone* of the outer cortex is equivalent to the band of cells characterized by dark contents noted in the outer tissues of *Stigmariae*. This zone in *S. bacupensis* is highly specialized, and one of the most striking features of the species.

In transverse section, at fairly regular intervals, groups with dark contents appear; these are generally distributed in a single row, though two groups may occur on the same ray (Pl. I, Fig. 8; Pl. II, Fig. 9).

They consist mainly of circular or oval areas (Pl. IV, Figs. 26 and 27), whose diameter is generally uniform, though groups of various sizes occur. They are connected by a wide-celled parenchyma tangentially, and sometimes radially extended (Pl. II, Fig. 9; Pl. IV, Figs. 26 and 27) which shows few horizontal or vertical secondary septa. Just opposite the rootlet's base the dark group is missing, and a dark small-celled tissue with thick walls fills its place (Pl. I, Fig. 6; Pl. II, Fig. 9).

Of all the specimens which have been investigated, no. 624 shows the most highly specialized glandular parenchyma (Pl. I, Fig. 7; Pl. II, Fig. 9). In a small axis like number 2 (Pl. I, Fig. 6) dark groups are rare; they are just beginning to develop. In the example with well-developed periderm, the parenchyma connecting the dark areas is more or less crushed (Pl. I, Fig. 8; Pl. III, Fig. 20). The nature of the content of the group is not easy to determine. It cannot, however, be interpreted either as sclerotic nest or as imperfectly preserved fungal hyphae for, in transverse section as well as in radial and tangential, the groups are filled up by black bodies which may be remains of cell-wall and products of secretion (Pl. IV, Figs. 26 and 27). On the other hand, some of the glandular strands seem to have a somewhat central reservoir (Pl. IV, Fig. 27). The formation of such a passage is shown in a young branched axis. In a transverse section, a glandular strand in formation shows one of its cells which has been divided in two by a radial septa (Pl. IV, Fig. 28). In the width of that septa a lenticular intercellular space, bordered by two cells, is formed; the whole structure is like a stomata. This pseudo-stomata is the first indication of a central passage. The adjoining cells probably underwent further analogous divisions, and constituted a definite strand of secretory cells. Yet disorganization is so advanced in glandular strands which have reached full development, that no peripheral layer of glandular cells occurs with certainty.

However, if the slides I have examined have not shown very young axes in which it would have been interesting to follow the glandular sacs development, Professor Lang (5), as already mentioned, has figured a portion of the outer cortex of a small axis of *S. bacupensis*, in which early stages of glandular sac development are seen. Prof. Lang distinguishes three zones in the outer cortex. His zone '*a*' is equivalent to our zone II. He says, 'the zone "*a*" consists of cells, the walls of which are often dark, and which may show indications of tangential divisions'. The zone '*a*' is shown in Pl. II, Fig. 5 of his work. In the right part of the figure, a small black mass occurs; eight parenchymatous cells are disposed around it (see Pl. IV, Fig. 29). On the left of the figure a second black mass is seen, in the middle of which occurs a somewhat light spot, which may represent an early stage of the formation of the central canal. The dark substance is surrounded by six large cells; one of these seem to be just divided by a radial septa.

I am inclined to consider the whole as a different stage of glandular strand development. As is known, in order to form a glandular strand, all the cells of a vertical row divide themselves into four cells by two perpendicular divisions. Between the four resulting daughter-cells an intercellular space occurs, which increases in size by further radial and tangential divisions, undergone by the adjoining cells. The surrounding cells of the dark mass of Lang's photograph would be this layer of glandular cells, disorganized, in mature axes.

If the presence of cells showing signs of recent divisions is unusual in secretory tissue, it is normal to meet them in quite immature secretory sacs, and we know that Lang's specimen is a very young axis.

The investigations we have carried out show that the secretory sacs seem to have a schizogenous development; they belong to the primary cortex.

The tangential section shows that the secretory sacs do not form either an anastomosing system or continuous large ducts, but consist of isolated sacs of various lengths and width, rarely branched, and ending blindly (Pl. V, Fig. 30). Their distribution in the surrounding parenchyma is very irregular. Pl. V ,Figs. 31, 32, and 33 show various aspects of the secretory sacs. Some of them (Pl. V, Figs. 31, and 32) are wide lenticular areas connected to one another by two rows of large cells elongated tangentially. Some others are long and narrow (Pl. V, Fig. 33), or short and narrow (Pl. V, Fig. 30), but all are surrounded on both sides by wide cells tangentially elongated, which distinguish them from the well-known wide-celled portion of the periderm not being chambered in numerous secondary cells.

Sometimes a group of small cells is located within the secretory sacs (Pl. V, Fig. 34); this explains the group of small cells without dark contents found in the transverse section in the place of secretory areas.

The presence of a divided secretory strand explains also the double rays of the group and the narrow canals observed in the transverse section. Whatever shape they may have, the secretory sacs are occupied by dark bodies or rods of various size and form, which may be the remains of dissolving cell-walls mixed with waste product (Pl. IV, Figs. 26 and 27; Pl. V, Fig. 31).

Generally the secretory sacs show a diffuse central passage (Pl. IV, Fig. 27; Pl. V, Figs. 31, 32, 33, and 34), and remains of periphery glandular cells, but these latter appear either disorganized or like two black layers surrounding the canal. The radial section confirms the somewhat lenticular aspect of the secretory sacs observed in the tangential section; Pl. IV, Fig. 24 and Pl. V, Fig. 34 show some of them cut radially. In the magnified glandular strand (Pl. V, Fig. 34) we see the dark content in the diffuse central passage, and the dark peripheral layer of glandular cells. This latter joins, on the inner side, the straight line tissue of the periderm which abuts against it, and on the outer side, a wide-celled parenchyma elongated radially, well seen in transverse section (Pl. IV, Figs. 26 and 27); without and within are narrow thick-walled cells.

Where the sections show the point where the periderm touches the secretory sacs, these latter are surrounded on both sides by parenchyma elongated radially.

On the whole *the second zone is characterized by glandular strands (sacs) of schizogenous formation, in which the central passage is occupied by remains of cell-walls and waste-products. In transverse section they are disposed at fairly regular intervals in a single circle. They consist of circular or oval areas generally connected by a wide-celled parenchyma, tangentially, and sometimes radially extended.*

In tangential and radial sections they cousist of isolated sacs of various length and width, rarely branched, and ending blindly. Their distribution in the surrounding parenchyma is irregular.

It is not the first time that glandular strands have been noted in Stigmarian cortex; Professor Weiss (14) has described a secretory strand in *Stigmaria radiculosa*, Hick. This secretory strand was exactly like those found in a corresponding position in *Lepidodendron fuliginosum*, Will.

Zones III and IV. The two later zones of the outer cortex present no particular feature.

In transverse, tangential, and radial sections (Pl. II, Fig. 9; Pl. IV, Fig. 24; Pl. VI, Fig. 44) zone III shows a parenchymatous tissue with an average breadth of eight to twelve rows of moderate sized cells, which may undergo further tangential and radial divisions (Pl. V, Fig. 35).

The outermost zone (IV) is rather defective. It consists of somewhat broken-down small-celled tissues of ten to twelve layers in thickness (Pl. V, Fig. 36; Pl. VII, Fig. 54).

This soft parenchyma, usually crushed or broken by the appendages, is left ill preserved in most of the preparations (Pl. VI, Fig. 44; Pl. VII, Fig. 54).

In conclusion, I should like to sum up the characteristic features of the outer tissues of *S. bacupensis.*

The outer cortex includes four zones:

I. A periderm centripetally developed consisting of normal prosenchyma mixed with chambered-cells.
II. A particular zone of isolated schizogenous glandular strands whose shapes vary in length and width, and end blindly.
III. A parenchymatous tissue made up of moderate-sized cells which show power of division.
IV. A delicate small-celled tissue generally broken down.

THE APPENDAGES OR ROOTLETS.

The above account has described the anatomy of the whole axis; it remains now to describe the appendages.

The relation of these latter to the main axis will be considered first, and afterwards their characteristic structure when they are free, will be investigated. The true morphological nature of the appendages is still unknown, but, for facility of text transcription the figurative term 'rootlets' will be used.

By means of radial sections made through the whole principal axis, the rootlet's bundle-course is readily followed. The vascular strands start from the outer margin of the primary wood carrying with them some protoxylem elements. They bend sharply outwards and pass horizontally through the whole width of the secondary wood (Pl. V, Fig. 37), splitting up the woody cylinder in distinct wedges (Pl. I, Figs. 1 and 6; Pl. II, Fig. 9). This horizontal course of the rootlet bundle through the secondary wood is usual in the *S. ficoides* appendages. On emerging from the secondary wood, they incurve bluntly (Pl. VI, Fig. 38), and pursue a nearly vertical course through the middle cortex region (Pl. VI, Fig. 39). Afterwards they enter the outer cortex horizontally, which direction is maintained through the thickness of the cortex until the base of the appendage has been reached (Pl. I, Figs. 2 and 6; Pl. II, Fig. 9).

Four different tangential sections through the woody cylinder and the outer tissue in the main axis, give an idea of the rootlet's bundle structure at various stages of its course.

The first one shows the vertically-elongated lenticular cavity of the medullary rays, in which are the wedge-shaped rootlet's bundle (Pl. III, Fig. 18). The structure of these latter agree with the characteristic tongue-shape appearance of the appendage bundle found in *Stigmaria*, where the primary wood is centrifugal. The amount of secondary wood which takes part in the formation of the appendages in *S. bacupensis* is, however, less than in *S. ficoides*; it consists only of one, two, or three rows of secondary tracheides, generally connected with the secondary wood of the main axis (Pl. III, Fig. 18; Pl. VI, Figs. 40 and 40 *bis*.).

The second tangential section passing through the periderm shows a bundle cut transversally, consisting of a few ligneous elements, closely surrounded by the dark prosenchymatous cells (Pl. VI, Fig. 41).

In the third one, the transverse section of the rootlets increase in size (Pl. VI, Fig. 42). The bundle is surrounded by a dark ring of cell-walls which seem similar to the dark cells found in the place of the glandular strand, just opposite the base of the appendage in the second zone of the cortex of the main axis (Pl. I, Figs. 6 and 7; Pl. II, Fig. 9).

In passing through the third zone of the outer cortex of the principal axis, a second ring, consisting of layers of thin-walled cells, encloses the inner dark circle (Pl. V, Fig. 30; Pl. VI, Fig. 43). This second lighter ring is derived from zone III of the main axis. The rootlet's cortex, from that moment, is definitely formed, for the appendages in going out, break down the last zone of the main axis cortex without taking with them some of its elements. In his paper on the roots of *Stigmaria*, Professor Lang (5, p. 104), notes that the smaller celled-tissue of the outermost zone of the main axis 'gives the impression of a layer through which the root has broken'. This is quite true. Projections of this tissue are found between the rootlet bases and crushed against their sides (Pl. VI, Fig. 44; Pl. VII, Fig. 54). In reality, the continuity of the outer cortex of the main axis with the rootlet's base tissue is only partial. Old specimens could have given the impression that the continuity was complete when their outermost zone was decorticated.

It may be stated here that a particular feature of *S. bacupensis* very well seen in radial section, is the great number of appendages starting from the main axis (Pl. VI, Fig. 39), which show numerous vascular strands running obliquely through the disorganized middle cortex. In that region, the section of the rootlet's bundle is of a triangular shape, consisting of three or four rows of secondary tracheides, three or six layers in thickness, converging to the apex where the protoxylem occurs (Pl. VI, Fig. 45).

When free from the parent axis, the rootlets of *S. bacupensis* show a definite structure very uniform on the whole. Their dimensions do not vary greatly, the diameter ranging from 1 or 1½ mm. or less. Their structure consists of an outer, middle, and inner cortex surrounding the vascular strand (Pl. VI, Fig. 46). The outer cortex, which is generally well preserved, is divided into two zones. The outer one is only two or three layers in thickness; this tissue consists of narrow and thin-walled cells which are frequently considerably larger, just opposite the protoxylem point of the bundle, than in any other part of the circumference (Pl. VI, Figs. 46 and 47). When the state of preservation is perfectly good, some cortical tracheides with wide thickening walls, are seen in that patch of large-celled parenchyma. The inner zone is generally three or five rows of cells in thickness, these cells being small in size, with thicker walls (Pl. VI, Figs. 46 and 47). Within the external zone there is usually a wide empty space, bridged by a strand of parenchyma. Occasionally at the base of the rootlet, or in rootlets situated near the main axis, some remains of the middle cortex is still found (Pl. VII, Fig. 54). It consists of one or two rows of large cells with thin walls, which extend themselves radially until their thin walls break. Pl. VI, Fig. 48 shows a rootlet still near the main axis and cut transversally. On the left of the photograph wide cells are still in connexion with the inner cortex layers; on the right, three cells have their delicate radial walls much extended and detached. Some of the rootlets

(Pl. VI, Fig. 47), though they have reached their full development, still show some of the radial walls of the disorganized wide cell.

The internal cortex forms a ring of some rows of cells enclosing the vascular strand. It consists of a few layers of delicate parenchyma connected with the outer cortex by a strand of parenchyma (Pl. VI, Figs. 46 and 47).

We shall now describe the vascular strand. In the middle cortex of the main axis, the transverse section of the bundle's appendages seems to be more important than in the free rootlet. That appearance is due to the obliquity of the bundle course through that region in the main axis. Generally, in the bundles of the free rootlet, the wood only remains, the phloem and the cambium are decayed. The xylem consists of a small strand of scalariform tracheides (eight or nine) with a somewhat triangular transverse section (Pl. VI, Figs. 46 and 47). At the more prominent angle the protoxylem is formed by three or four spirally thickened elements which generally abut against the surrounding parenchyma.

This vascular strand is monarch, and does not at all reproduce the mesarch structure characteristic of *Stigmaria* with primary centripetal wood,[1] though its main axis possesses spirally thickened elements in its centre. A noticeable feature of this *S. bacupensis* rootlet is the connexion of the bundle with the outer cortex by a strand of parenchymatous cells (Pl. VI, Figs. 46 and 47). In *S. ficoides* appendages and the rootlet probably related to *Lepidophloios fuliginosus* (14), the stele lies freely in the space left between the inner and outer cortex, by the decay of the middle cortex. The connexion of the bundle with the outer cortex is not an attribute of very young roots only, as Williamson points out (1, Pl. LIII, Fig. 16), for a large number of fully developed rootlets show this peculiar structure (Pl. I, Fig. 6; Pl. VI, Fig. 47).

In the parenchymatous bridge one, two, or three groups of spirally-marked tracheides frequently occur in close proximity to the protoxylem (Pl. VI, Fig. 46). These little strands of tracheides are the elements that Renault (Renault, B., Cours de Botanique fossile, Pl. XX, Fig. 4, Ann. des Sc. Géol. 1882, Pl. II, Fig. 8) had regarded as indicating a mode of branching distinct from the usual dichotomy. Professor F. E. Weiss (15) in 1902 has clearly investigated these structures. He confirms Renault's observations, but finds that 'these strands do not pass out to lateral rootlets as suggested by Renault, but terminate in the outer cortex, sometimes in connexion with distinct groups of large parenchymatous cells'. He points out that these fine vascular strands are given off from the protoxylem group of the bundle and pass out obliquely or horizontally, through the middle cortex, and terminate in connexion with an extensive patch of tracheidal tissue in the outer cortex.

[1] *S. weissiana*, *S. lohesti*, *S. brardi*.

The rootlet represented in Pl. VII, Figs. 49 and 49 *bis.* is cut longitudinally, and shows a delicate strand of tracheides surrounded by a layer of parenchymatous cells starting from the stele, and running obliquely through the space between the vascular bundle and the outer cortical cylinder, to the patch of large-celled parenchyma of the outermost zone of the cortex. The origin of the delicate vascular branch is unfortunately not clearly shown. The terminations of these few vascular strands in the outer cortex are not so easily observable in rootlets of *S. bacupensis* as in those of *S. ficoides,* where the outer cortex is a thin-wall tissue, much lighter than the dark-coloured zone of the outer cortex of *S. bacupensis* appendages. However, in Pl. VII, Fig. 50, a radial section passing just through the large-celled portion of the outermost cortex, shows wide spirally-marked tracheides running continuously along the rootlet. These elements are confined to those regions where the fine vascular branch terminates in the outer cortex (Pl. VII, Fig. 51).

The above description shows that the rootlets of *S. bacupensis* have numerous characteristic features which may be summed up as follows: *the monarch vascular bundle is generally connected with the outer cortex by a definite strand of parenchymatous tissue. In this latter frequently occur fine vascular strands which connect the woody elements of the bundle with the cortical tracheides. The outer cortex is divided in two zones; an inner dark one, three or five layers in thickness, and a lighter outer zone, two or three layers thick; the latter has its cells considerably enlarged just opposite the protoxylem point of the bundle where the cortical tracheides are located.* These peculiar features define plainly a type of rootlet that is of species value.

The normal type of rootlet of *S. bacupensis* may, however, undergo a few modifications. For instance, where the external zone of the outer cortex has peeled off by disorganization, the cortex of the rootlet is reduced to the few layers of the inner dark zone. Such a rootlet has been noted and figured by Williamson (17, Pl. LIII, Fig. 16) as a young *S. ficoides* rootlet. Pl. I, Fig. 4 shows a rootlet in the same state of preservation. When a rootlet has just escaped from the main axis its outer cortex is thicker than in the normal type. The outer zone of its outer cortex is five or eight layers in thickness, and the rootlet looks much more massive than the normal ones. Such a rootlet is shown in Pl. VII, Fig. 52.

A curious fact which must be pointed out is the complete absence of a glandular strand in the cortex of the normal rootlet. When (pp. 44 and 45) the course of the rootlet bundle through the outer tissue of the main axis was studied, it was pointed out that the two zones of the rootlet's cortex show a continuity of structure with the zones II and III of the main axis. The parenchymatous cells of the inner dark zone of the cortex of the rootlet are much more like the dark small-celled group found in zone II of the main axis cortex just opposite the base of the rootlet, but no secretory strand surrounded by elongated parenchymatous cells occurs. If numerous rootlets had not been found associated with the main axis of *S. bacupensis* (Pl. I, Fig. 6), identifying them with certainty, the peculiar structure of a new rootlet species *S. arachnoidea* created by Dr. Koopmans would probably have been described as belonging to *S. bacupensis.* That rootlet possesses in its cortex very conspicuous dark groups regularly distributed, connected to one another by parenchymatous cells which are tangentially elongated. The short description and the published figure repeated (Pl. VII, Fig. 53) correspond reasonably with what has been said about the glandular strand of the outer tissue in *S. bacupensis.* Yet the author considers the dark groups of *S. arachnoidea* as sclerotic nest. This is absolutely not the case in *S. bacupensis.* Such rootlets being present in Belgian coal-balls (4, p. 18, Pl. VIII, Fig. 72, Pl. XII, Fig. 92), special attention will be drawn to them in a later paper.[1] But the analogy of structure between *S. arachnoidea*, Koop., and the outer tissues of *S. bacupensis,* Scott et Lang, is, I think, interesting to note. That example proves that, however striking a similarity of structure may be, it is never a sufficient argument to establish a relationship between two plants.

SUMMARY AND CONCLUSIONS.

The morphological and histological features which have been described show complete justification for considering *S. bacupensis* as a new species. The most striking features of the species are: the massive primary wood of the main axis consisting of spiral and barred marking elements developed without apparent direction; the glandular zone of principal outer cortex; and the well-defined structure of the free rootlet.

The first of these characteristic features is sufficient in itself to distinguish *S. bacupensis* from all known *Stigmariae.* For so far as primary wood is concerned, the *Stigmariae* may be divided into three types:

TYPE I. *Stigmaria* with a centripetal solid primary wood consisting of scalariform tracheides. No pith.	*S. augustodulensis*, Renault. *S. Lohesti*, Leclercq (6). *S. dubia*, Scott (9).
TYPE II. *Stigmaria* with a well-defined ring of centripetal wood lining the pith.	*S. brardi*, Renault, primary xylem formed by strand of crescentic transverse section. *S. weissiana*, Leclercq, primary xylem consisting of two or three continuous layers.

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[1] The author commits an error when he says (p. 18) that these rootlets are not present in any of the slides he has seen from Belgium.

TYPE III. *Stigmaria* with centrifugal primary wood: the centre of the axis seems to be hollow.	*S. ficoides*, Sternb. *S. radiculosa*, Hick. *S. petticurensis*, Scott (9).

What place shall we confer to *S. bacupensis*? It appears that it cannot be classed in any of the above-mentioned types, for the anatomy of *S. bacupensis* seems to represent an intermediate structure between *Stigmariae* with centripetal or centrifugal primary wood.

S. bacupensis new type would then be placed between the second and third type already described:

Stigmaria with solid primary wood consisting of spiral and barred thickening elements, developed in no apparent direction. No pith.	*S bacupensis*, Scott et Lang.

If *S. bacupensis* possesses a solid primary wood like *S. augustodunensis*, Ren., and *S. Lohesti*, Lecl., its secondary wood breaking out in numerous distinct wedges, the monarch structure and somewhat triangular form of the bundles of the rootlet and the course of the former, present, as has been said above, a similarity in structure to *Stigmariae* with centrifugal primary wood like *S. ficoides.*

Generally *Stigmariae* with solid primary wood developed centripetally have a compact secondary wood, very few appendages, and more or less numerous mesarch rootlet bundle. Such anatomical changes have not been introduced in *S. bacupensis* structure. I am inclined to consider the small spiral and barred elements of its primary wood as a protoxylem enlarged somewhat excessively. That hypothesis would explain the absence firstly, of direction in the primary wood development, and secondly, of the features peculiar to *Stigmariae* with a centripetal solid primary wood mentioned above.

The above classification established on a single feature has of course no specific value, but has the merit of showing that among all the *Stigmariae* known, specimens with centripetal primary wood are more numerous than specimens with centrifugal primary wood. *S. ficoides*, which is generally the very commonest of all fossils in coal-balls, has consequently been investigated first. In all handbooks the knowledge of the anatomical structure of the *Stigmariae* is based on the description of *S. ficoides*, which, however, might easily not represent the commonest structure of the *Stigmariae.*

It is advisable now to sum up the whole features of *S. bacupensis*, Scott et Lang. The dimensions of the whole axis, stele, and bark vary according to the age of the specimens. The vascular cylinder consists of a solid primary xylem made up of small spiral annular and barred marking elements of various size, developed in no apparent direction, and of a secondary xylem broken down in numerous bundles by numerous medullary rays. The inner margin of the bundle is loose. No pith is present in the centre of the stele. Inner and middle cortex are ill preserved. The outer tissues include four zones: first, a centripetal periderm of an irregular type made up of normal prosenchyma mixed with chambered-cells; secondly, a particular glandular zone which consists of schizogenous isolated sacs of various length and width ending blindly, and filled largely with remains of cell-walls and waste products (these glandular strands are generally connected by a wide-celled parenchyma); thirdly, a parenchymatous tissue made up of moderate-sized cells which show power of division; fourthly, a delicate small-celled tissue generally broken down. A particular feature of the main axis must still be added: vascular cylinder branched off frequently. It is not uncommon to find two or more steles in a single preparation.

In relation to the main axis the monarch bundle of the rootlet shows a structure and course similar to *S. ficoides* appendages.

The free rootlet has a typical structure. The monarch bundle is connected with the outer cortex by a definite parenchymatous bridge. In this latter there frequently occur fine vascular strands which connect the woody element of the bundle with cortical tracheides. The outer cortex is divided into two zones: an inner dark one, and an outer clear one enlarged just opposite the protoxylem point of the bundle, where a patch of cortical tracheides is located. The rootlets are of small dimension, their size ranging from 1 to 1½ mm., and they are extremely abundant. The rootlets of *S. bacupensis*, which are common in calcareous section and which cause disorganization in the structure of the plants they invade, can now be easily distinguished and identified. It will also be possible to determine with certainty the presence of *S. bacupensis* among a coal-ball flora in which the main axis is absent.

The identity of *S. bacupensis* being established, it is necessary to draw attention to the wrong determinations met with in the Scott collection.

It has been said in Introduction to this study that two preparations of Scott's collection have been chosen to figure as type specimens in this paper. Among the numerous specimens identified as *S. bacupensis* in the British Museum, some of them are doubtful. The preparations number 1085, 6 and 7 represent transverse and tangential sections through a specimen of which the following characteristic features are: centripetal primary wood ill developed, consisting of elements closely joined to one another; secondary wood well developed, few medullary rays, few appendages showing in transverse section a somewhat mesarch structure. Cortex unhappily not preserved. Both structure of primary and secondary wood show a striking difference from the same tissues in *S. bacupensis.* In these latter, as we know, the primary wood consists of very small elements developed in no apparent direction. The secondary wood is abundantly divided in rather narrow bundles by numerous medullary rays and rootlet bundle. The monarch appendage bundle has an edged-shaped transversal section.

The structure of the specimens enclosed in the preparations number 1085, 6 and 7 is much more like *S. weissiana*, Lecl. However, as special attention has not been drawn to them, the analogy between the two plants cannot be determined here with certainty. It was, however, necessary to rectify the error of determination. The true morphological nature of Stigmarian axes is still unknown. If they belong to plants which have attained their highest development in later palaeozoic times they have proved to be more primitive in their anatomical structure than most of their recent allies. They suggest a relationship corresponding with existing Lycopods (*Lycopodium* and *Selaginella*) and *Isoetes*, but of course no strict homology with any of them may be assumed.

In the present state of our knowledge it is also fruitless to try to determine with certainty if the appendages represent modified leaves or rootlets. As Professor Lang (5, p. 104) clearly notes, until information as to the structure of the apical region of a Stigmarian axis and the mode of production of the root is known, close comparison with other plants cannot be profitably established. Yet the investigation of Professor Lang on the rootlets of *Stigmaria* demonstrating the possibility of their endogenous origin brings forward a new and weighty argument in favour of the appendages being of the nature of roots.

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EXPLANATION OF PLATES I–VII.

Illustrating Dr. S. Leclercq's paper on *Stigmaria bacupensis*, Scott et Lang.

All the photographs have been taken by the author by means of 'La chambre micro-photographic' camera of Zeiss, except Pl. II, Fig. 9, in which the apparatus of Eddinger was employed, and the re-figured figures Pl. I, Figs. 3 and 5, Pl. IV, Fig. 29, and Pl. VI, Fig 53 in which the fluorescent screens of Tall were used.

PLATE I.

Fig. 1. Stele of a young branchial axis; *x.*, primary xylem; x_2, secondary xylem (transverse section). Prep. 950, D. H. Scott, British Museum. × 25.

Fig. 2. Main axis of *S. bacupensis* cut obliquely, surrounded by numerous appendages cut transversally and longitudinally. Prep. 1773, D. H. Scott, British Museum. × 2.

Fig. 3. Repeated figure of a decorticated *S. bacupensis* rootlet attributed by Williamson to a young *S. ficoides* appendage; *par.*, destroyed patch of large-celled parenchyma of outer cortex. (1881, Pl. LIII, Fig. 16.) × 80.

Fig. 4. Decorticated *S. bacupensis* appendage. The outer zone of the outer cortex is peeled off; *par.*, destroyed patch of large-celled parenchyma of outer cortex. Prep. 2/1. × 90.

Fig. 5. Repeated figure of an undetermined rootlet investigated by Prof. F. E. Weiss. A comparison with *S. bacupensis* type specimen rootlet establishes the identity of the two appendages (Pl. VI, Figs. 46 and 47), Weiss (1902), Pl. XXVI, Fig. 3. × 30.

Fig. 6. Main axis cut transversally, surrounded by some of its numerous appendages: *st.*, stele; *c.*, cortex; *r.*, rootlet. Prep. 21/2. × 6½.

Fig. 7. Transverse section of a main axis, surrounded by the outer tissues. Lettering as in Fig. 6. Prep. 624/1. × 2½.

Fig. 8. Transverse section of a somewhat more developed main axis, surrounded by the outer tissues. Lettering as in Fig. 6. Prep. 678/1. × 2.

Fig. 12. Tracheides of secondary wood; x_2, joined by a row of primary wood elements of various size. Preparation made by means of the celluloid method of J. Walton. Prep. 624 1/7. × 140.

PLATE II.

Fig. 9. General transverse section of the axis showing: *x.*, primary xylem; x_2, secondary wood; *r.ba.*, rootlet base; *rb.*, rootlet bundle; *pr.*, periderm; *gs.*, glandular strand; z_3, third zone of the outer cortex. Prep. 624/1. × 40.

Fig. 10. Transverse section of the primary xylem formed by elements of various dimensions: *x.*, primary xylem; x_2, secondary xylem. Prep. 624/1. × 150.

Fig. 11. Wide element (*w.e.*) situated in the centre of the axis (see Pl. II, Fig. 10), surrounded by several smaller elements. Prep. 624/1. × 250.

Fig. 12. See Plate I.

Fig. 13. Reticulate tracheides cut transversally. Prep. 624/1. × 270.

PLATE III.

Fig. 14. Radial section through the solid primary xylem showing annular and barred elements of various size: *my.*, mycelium; x_2, secondary tracheide. Prep. 624 1/6. × 140.

Fig. 15. Radial section through a stele showing (x) primary and (x_2) secondary wood in contact. Prep. 624 1/6. × 75.

Fig. 16. Radial section through the primary wood showing spiral and barred elements found in its centre. Prep. 624 1/6. × 420.

Fig. 17. Radial section through the primary wood showing barred elements mixed with thick bearded mycelium: *my.* Prep. 624 1/6. × 140.

Fig. 18. Tangential section through secondary wood showing (*s.tr.*) scalariform tracheides; (*mr.*) medullary rays; (*rb.*) outgoing rootlet bundle. Prep. 802 1/4. × 14.

Fig. 19. Radial section of an axis showing: $x.$, primary wood; x_2, secondary xylem; *my.*, mycelium. Prep. 624 1/6. × 14.

Fig. 20. Transverse section through irregular periderm: *pr.*, files of prosenchymatous cells; *ch.*, chambered-cells; *gs.*, glandular strand; z_3, zone III of the outer cortex. Prep. 678 1/1. × 14.

PLATE IV.

Fig. 21. A portion of periderm enlarged: *pr.*, files of prosenchyma; *ch.*, chambered-cells showing numerous secondary septa, *sp.*; *ph.*, tangentially elongated prosenchymatous cells. Prep. 678 1/1. × 40.

Fig. 22. Tangential section through periderm showing the definite vertical files of chambered-cells, *ch.*, among the prosenchymatous cells, *pr.* Prep. 678 2/4. × 14.

Fig. 23. Tangential section through the periderm showing the chambered-cells with their numerous daughter-cells, *dg.*, and the parallel sides and pointed end prosenchymatous cells, *pr.* Prep. 678 2/4. × 40.

Fig. 24. Radial section through the outer cortex; *pr.*, prosenchymatous cells of periderm; *gs.*, glandular strand; z_3, parenchymatous cells of the zone III. Prep. 678 1/2. × 14.

Fig. 25. Radial section through the outer cortex showing the conspicuous parenchymatous strand; *ch.* formed among the prosenchyma by numerous daughter-cells of chambered-cells. Other lettering as in Fig. 24. Prep. 678 1/2. × 25.

Fig. 26. Glandular strand cut transversally filled by product of secretion. The wide-celled parenchyma, elongated tangentially and radially is well seen. Prep. 624 1/2. × 75.

Fig. 27. Two glandular strands cut transversally; the right one shows a central passage; *pr.*, periderm; z_3, third zone of the outer cortex. Prep. 624 1/2. × 75.

Fig. 28. A glandular strand in formation. Prep. 950. Scott collection, British Museum. × 180.

Fig. 29. Repeated figure of Prof. W. H. Lang's paper, showing in a very young axis two glandular strands in formation: *gs.*, glandular strand. (Lang, 1923, Pl. II, Fig. 5.) × 50.

PLATE V.

Fig. 30. Part of tangential section through the secondary zone of the main axis cortex to show glandular strands (*gs.*) and an outgoing appendage. Prep. 624 1/6. × 36.

Fig. 31. Group of three glandular strands cut tangentially. Prep. 678 2/2. × 40.

Fig. 32. One glandular strand of the above figure enlarged: *c.*, central passage filled by dark bodies; *l.*, peripheric layers of cells; *pa.*, wide-celled parenchyma tangentially elongated. Prep. 678 2/2. × 70.

Fig. 33. Glandular strand cut tangentially: *c.*, central canal; *l.*, disorganized peripheric layers; *pa.*, tangentially elongated parenchyma. Prep. 678 2/2. × 75.

Fig. 34. Glandular strand cut radially. *pr.*, prosenchymatous cells of periderm; *tc.*, thick wall cells. Other lettering as in Fig. 33. Prep. 678 1/2. × 75.

Fig. 35. Transverse section through the third zone of the cortex. On the right group of cells showing indications of tangential divisions. Prep. 950, Scott collection, British Museum. × 70.

Fig. 36. Cortex of a young axis in transverse section showing the outermost zone: z_4. Prep. 2 1/2. × 20.

Fig. 37. Radially cut axis showing a bundle appendage running horizontally through secondary xylem; *x.*, crushing primary xylem; x_2, secondary tracheides; *r.*, rootlet bundle. Prep. 678 1/2. × 40.

PLATE VI.

Fig. 38. Part of radial section to show rootlet bundle incurved bluntly when leaving off the secondary wood, x_2; *mc.*, disorganized middle cortex. Preparation obtained by means of new celluloid method of J. Walton. Prep. 624 1/5. × 36.

Fig. 39. Part of radial section to show the very oblique course taken by rootlet bundle through middle cortex region: *x.*, primary wood; x_2, secondary wood. Prep. 624 1/6. × 14.

Fig. 40 and 40 *bis*. Part of tangential section through wood, showing an outgoing rootlet bundle: *tr.*, tracheide scalariform; *mr.*, medullary rays; *px.*, protoxylem of rootlet bundle. Prep. 802 1. × 36. Prep. 802 1/4. × 40.

Fig. 41. Transverse section of a rootlet bundle (*rb.*); passing through periderm (*pr.*). Prep. 678 2/4. × 70.

Fig. 42. Transverse section of a rootlet bundle (*rb.*) passing through the second zone of the main axis cortex. The first zone of the rootlet cortex is formed. Prep. 624 1/6. × 36.

Fig. 43. Transverse section of a rootlet bundle running through the third zone of the main axis cortex. The second zone of the rootlet bundle is formed. On the right of the figure, some cells show indications of tangential divisions. Prep. 678 2/2. × 36.

Fig. 44. Part of transverse section to show two bases of rootlet: *rt.*, rootlet bundle; *ic.*, inner cortex; *mc.*, remains of middle cortex; *oc.*, outer cortex; z_4, outermost zone of the main axis cortex crushed between the two rootlets. The continuity of the second and third zones of the outer cortex of the main axis with the two zones of the rootlet cortex is well seen. Prep. 624 1/2. × 25.

Fig. 45. Transverse section of rootlet bundle passing through the middle cortex region of the main axis: *px.*, protoxylem; *tr.*, tracheides scalariform; *ic.*, remains of inner cortex. Prep. 624 1. × 70.

Fig. 46. Transverse section of a free rootlet; *rb.*, rootlet bundle; *ic.*, inner cortex; *w.*, remains of middle cortex cells-wall; *br.*, bridge of parenchyma; *vs.*, fine vascular strand; *iz.*, inner dark zone of the outer cortex; *oz.*, outer zone of the outer cortex considerably enlarged just opposite the protoxylem point of the bundle. Prep. 2 1/2. × 40.

Fig. 47. Transverse section of a group of rootlets. On the right of the figure a rootlet with remains of middle cortex. Prep. 2 1/2. × 20.

Fig. 48. Rootlet with (*mc.*) middle cortex preserved. Prep. 2 1/2. × 45.

PLATE VII.

Fig. 49. Oblique section through a *S. bacupensis* rootlet showing a delicate strand of tracheide (*vs.*) starting from the rootlet bundle (*rb.*). Prep. 624 2/3. × 25.

Fig. 49 *bis*. Part of the above section magnified; *vs.*, fine vascular strand; *ic.*, inner cortex; *rb.*, portion of rootlet bundle. Prep. 624 2/3. × 100.

Fig. 50. Radial section passing just through the large-celled portion, *lc.*, of the outermost zone of the outer cortex of a rootlet: *iz.*, inner dark zone; *oz.*, outer light zone; *rb.*, rootlet bundle. Prep. 624 *z.* × 15.

Fig. 51. Part of the above radial section magnified showing wide spirally marked cortical tracheides, *ct.* Other lettering as in Fig. 50. Prep. 624 *z.* × 100.

Fig. 52. Transverse section of a rootlet just escaped from the main axis: the outer cortex is thicker than in normal free rootlet. Prep. 1773, Scott collection, British Museum. × 36.

Fig. 53. Repeated figure of Koopmans new species of Stigmarian rootlet: *Stigmaria arachnoidea.* (Koopmans r. G. (1928), p. 18, Pl. XII, Fig. 92.) × 25.

Fig. 54. Part of transverse section to show three outgoing rootlets; remains of wide cells of rootlet middle cortex, *mc.*; projections of outermost zone of main axis outer cortex, z_4. Prep. 624 1/2. × 25.

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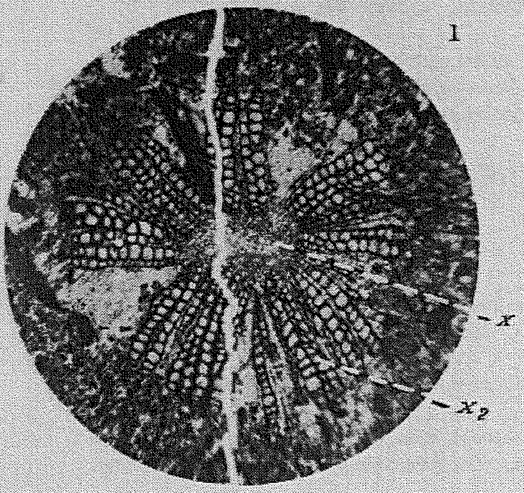

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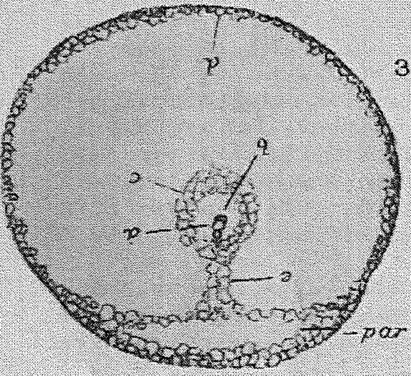

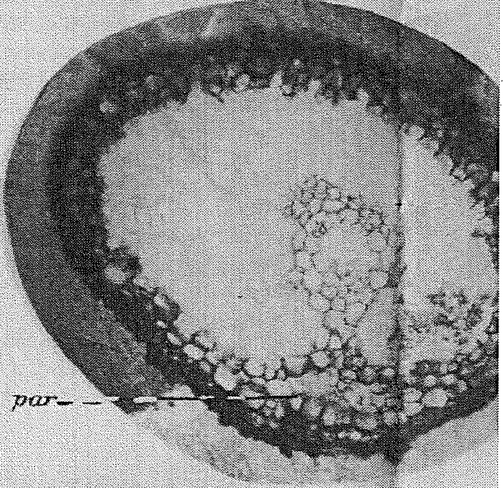

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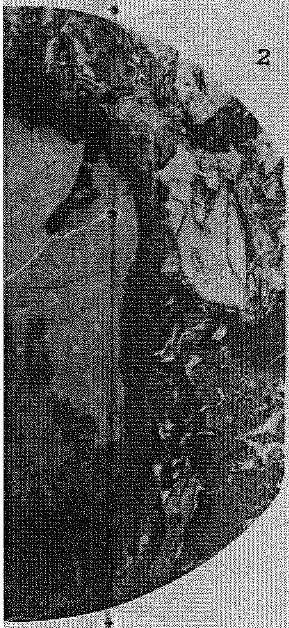

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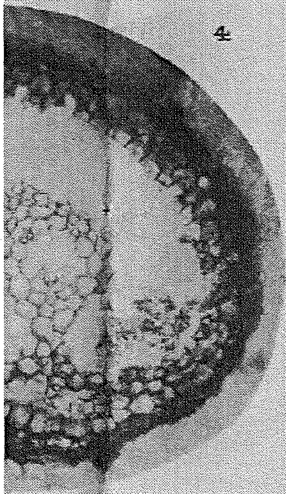

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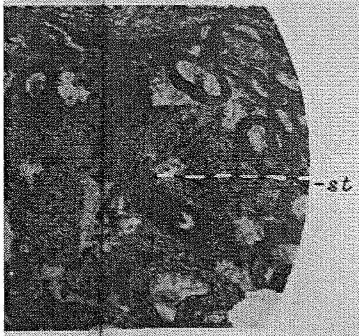

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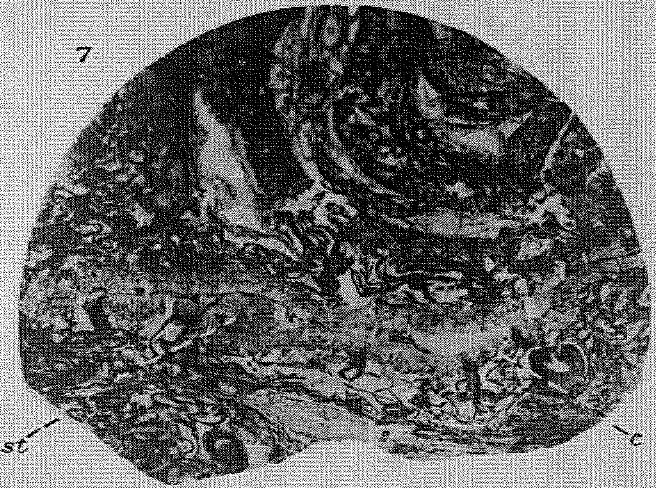

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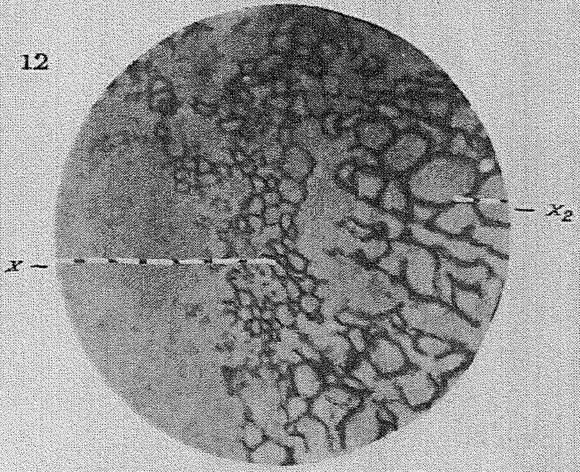

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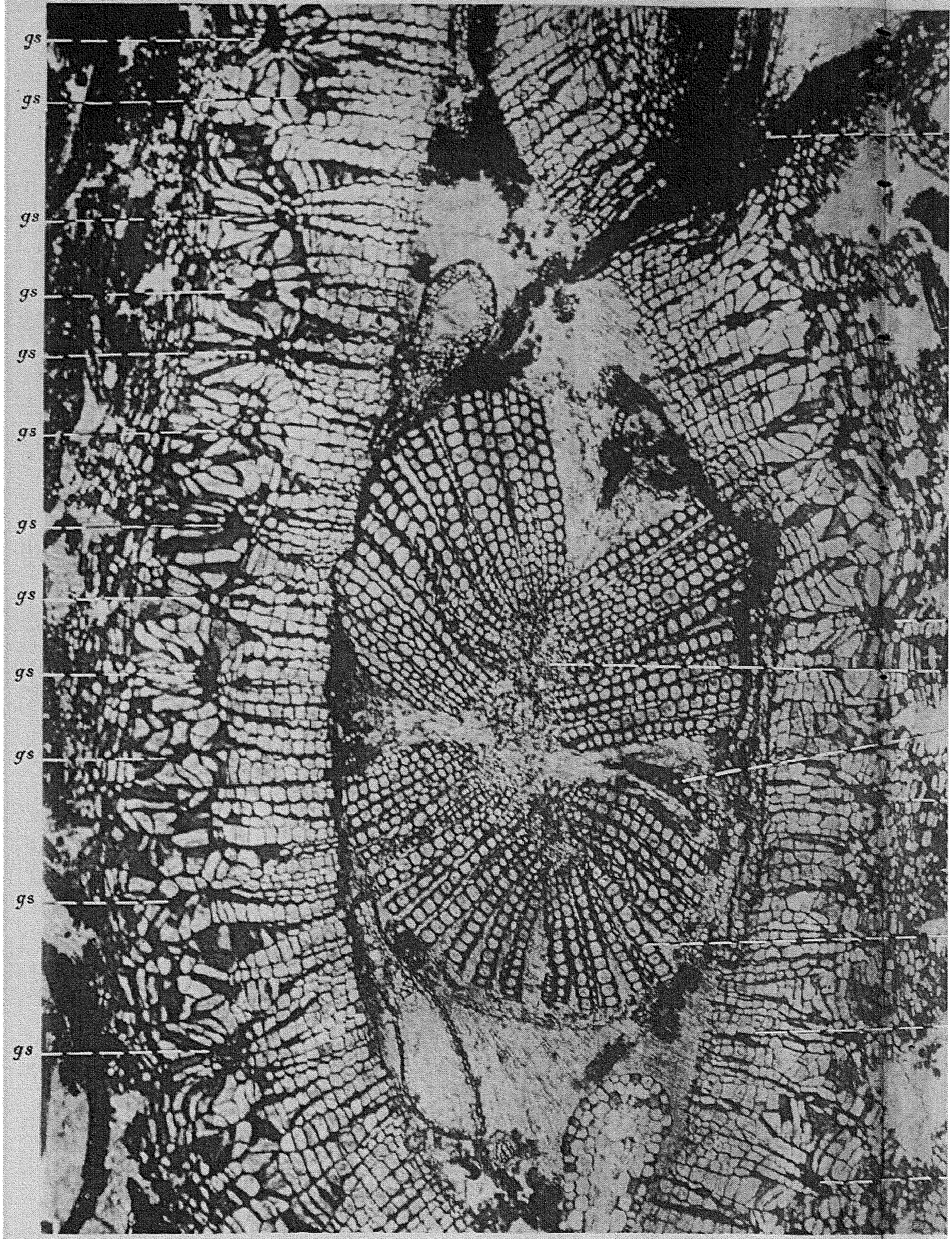

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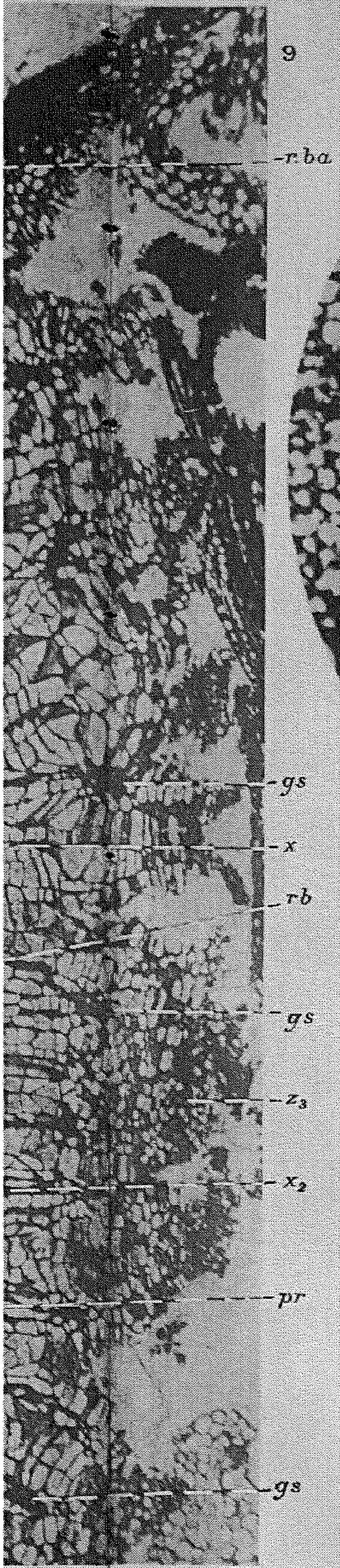

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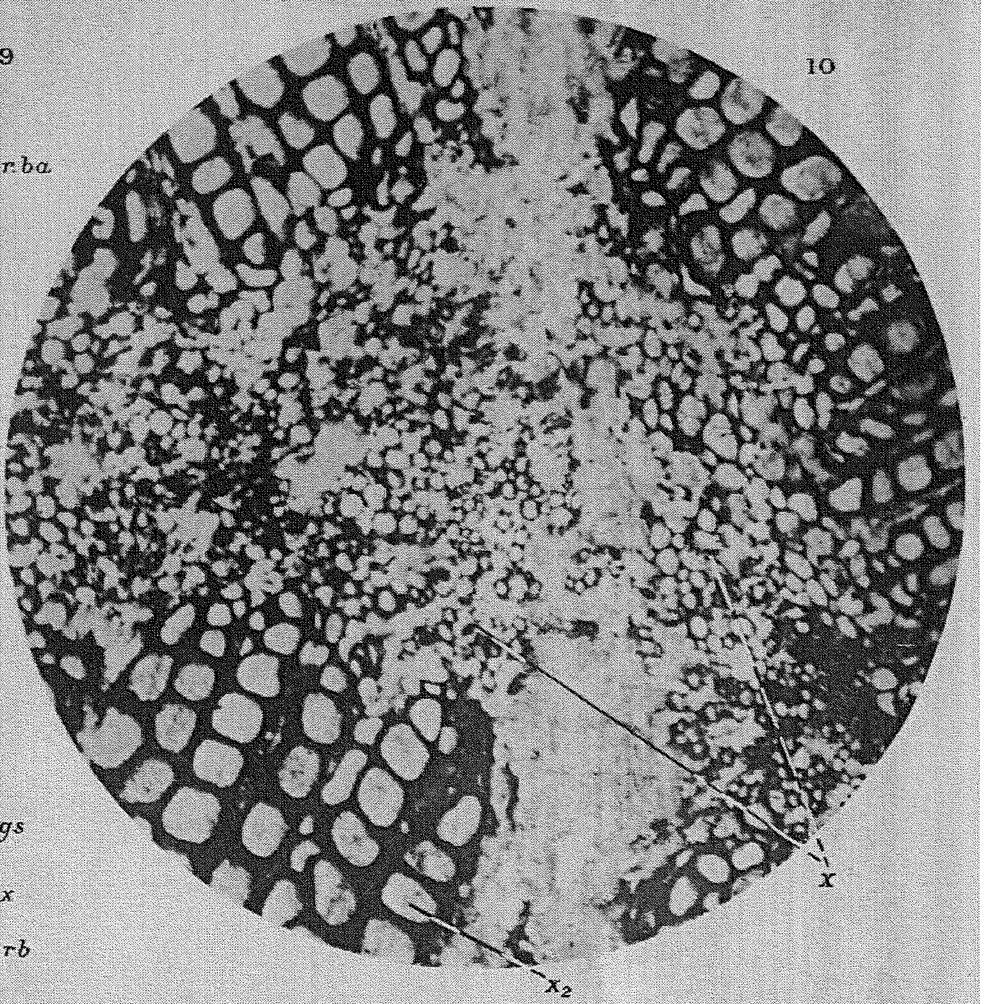

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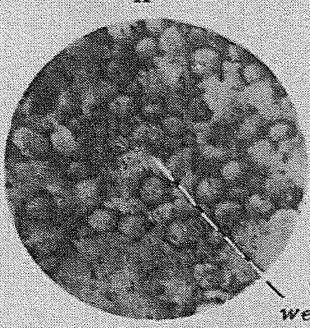

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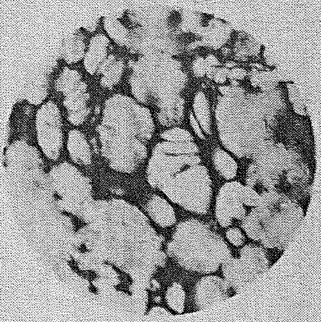

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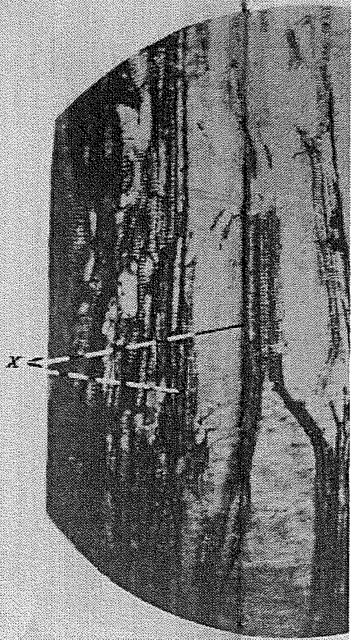

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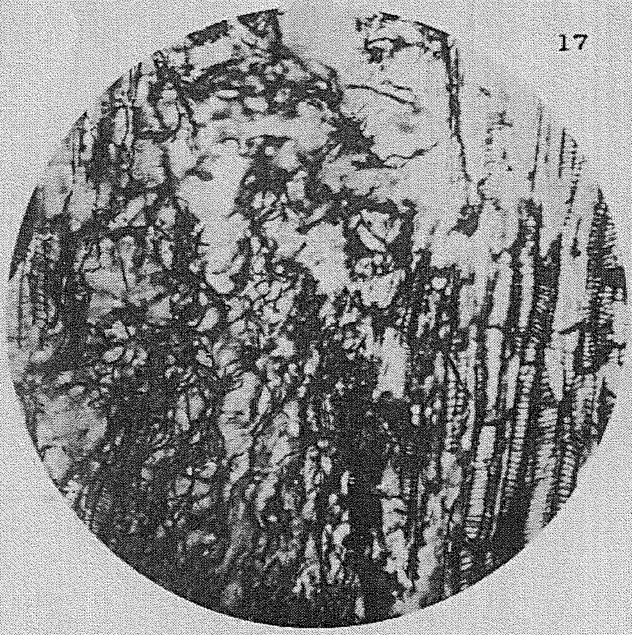

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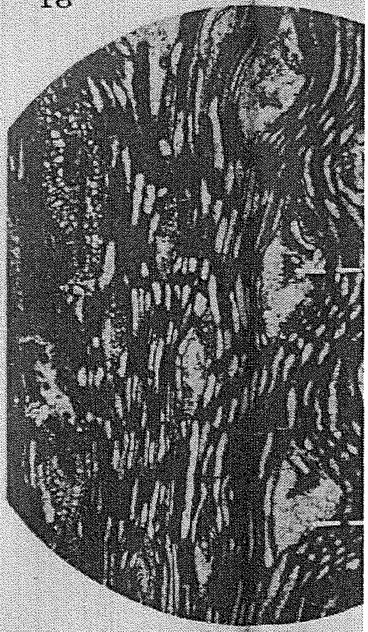

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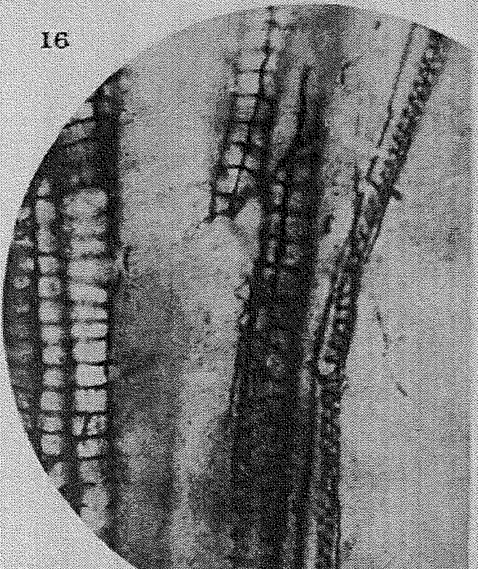

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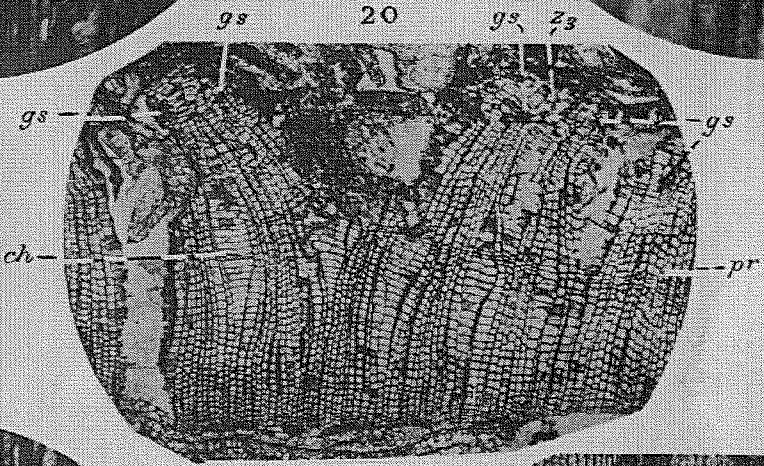

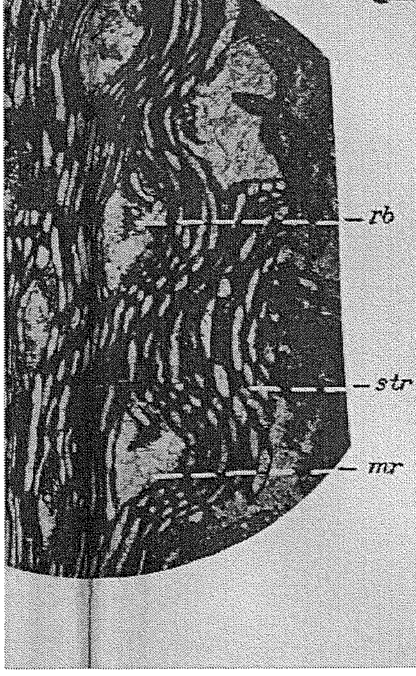

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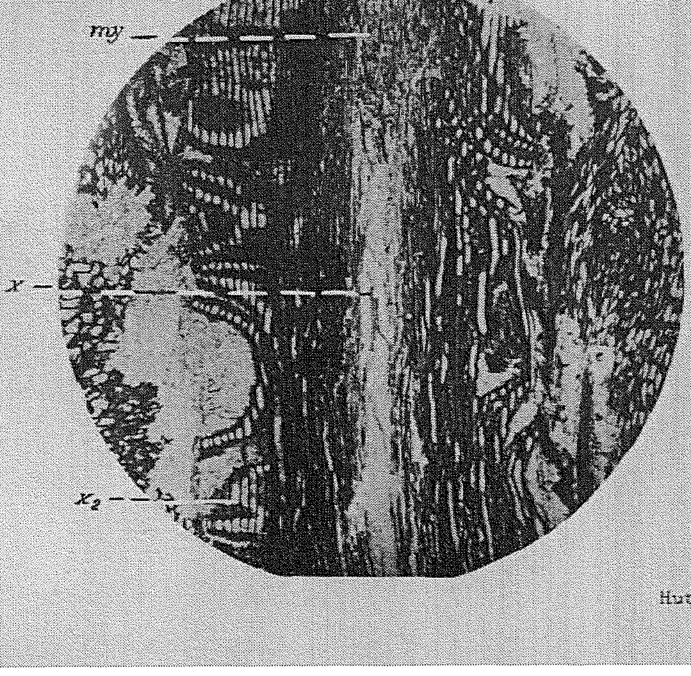

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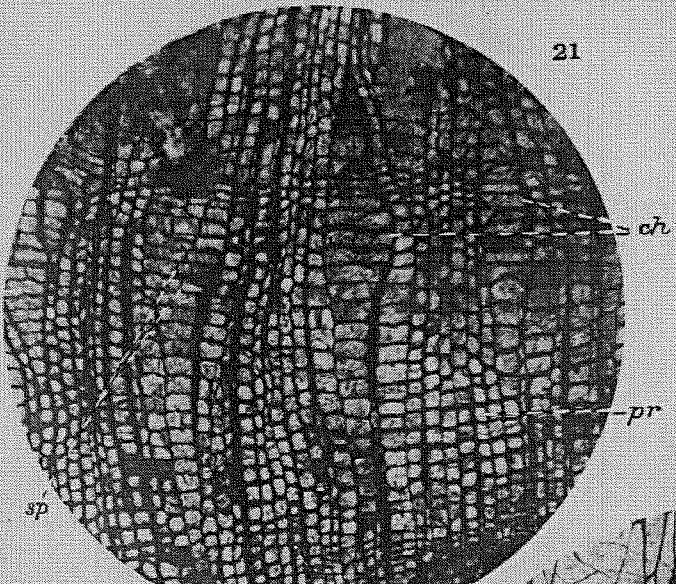

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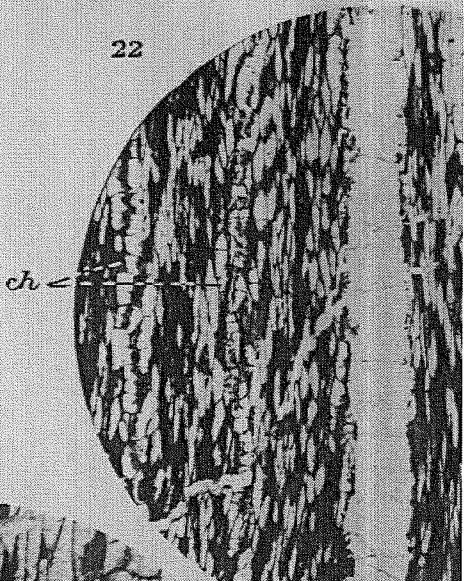

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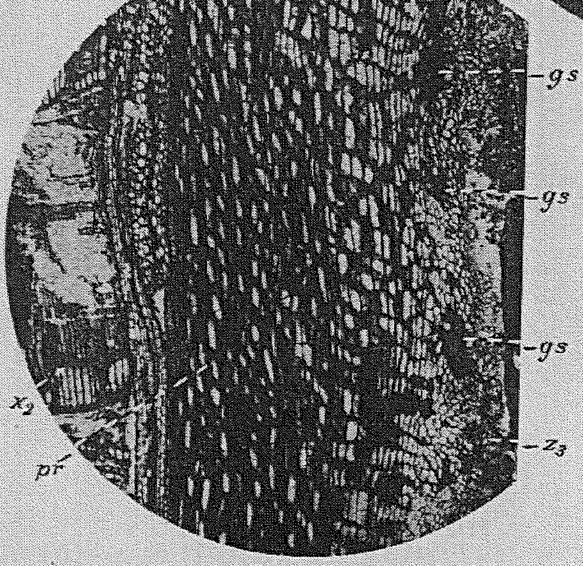

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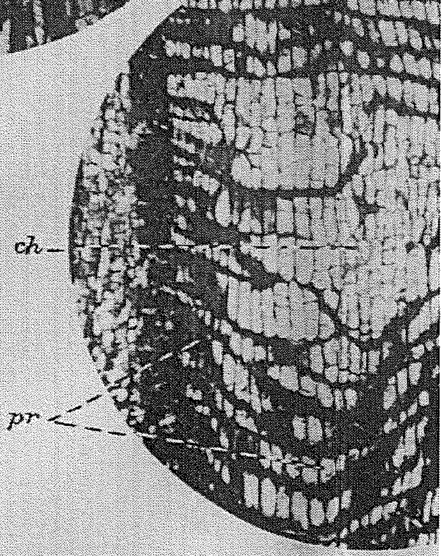

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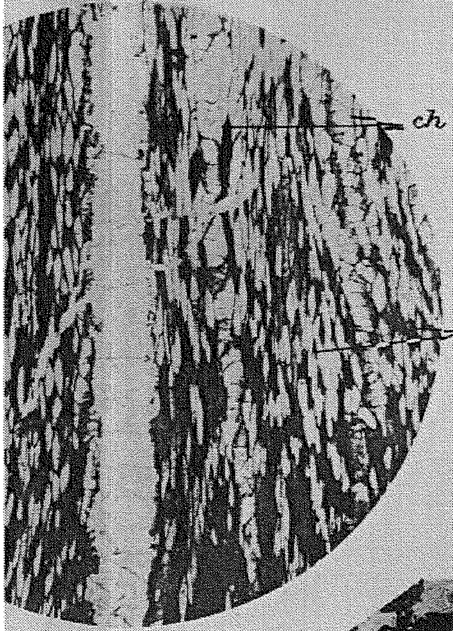

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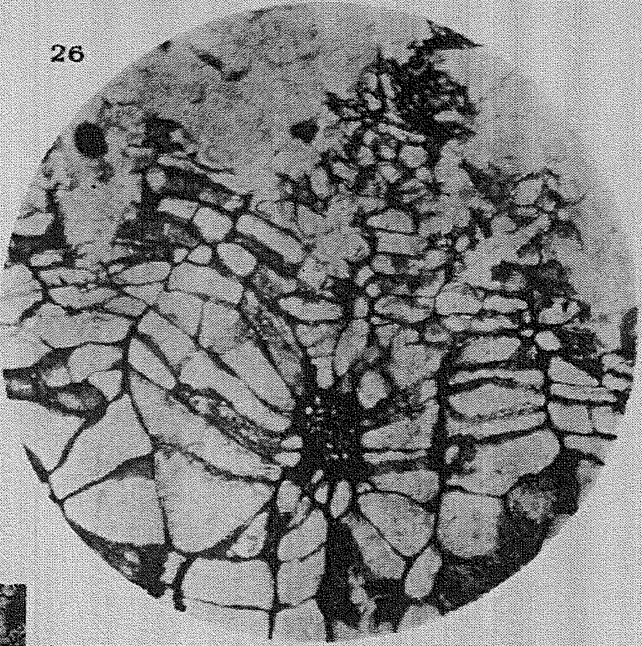

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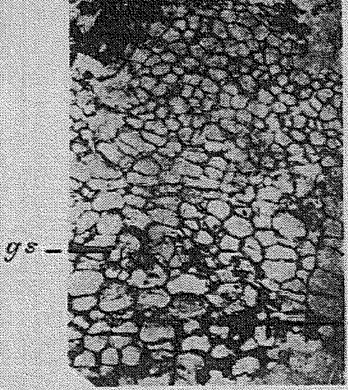

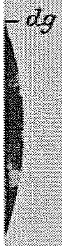

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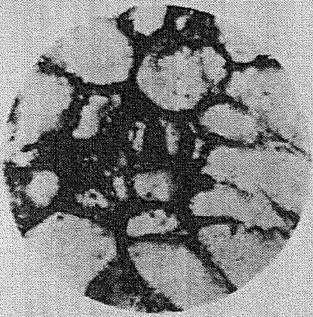

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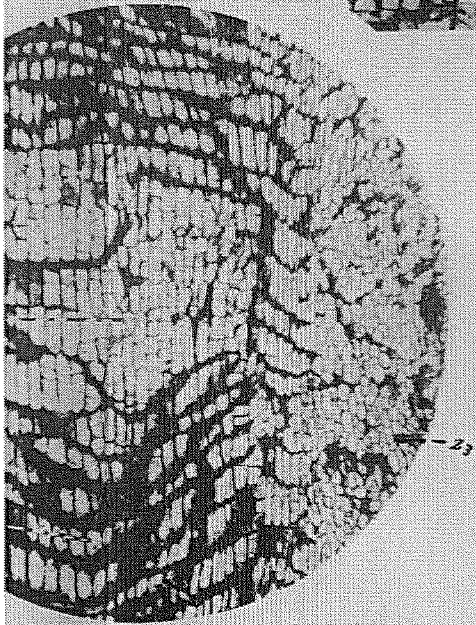

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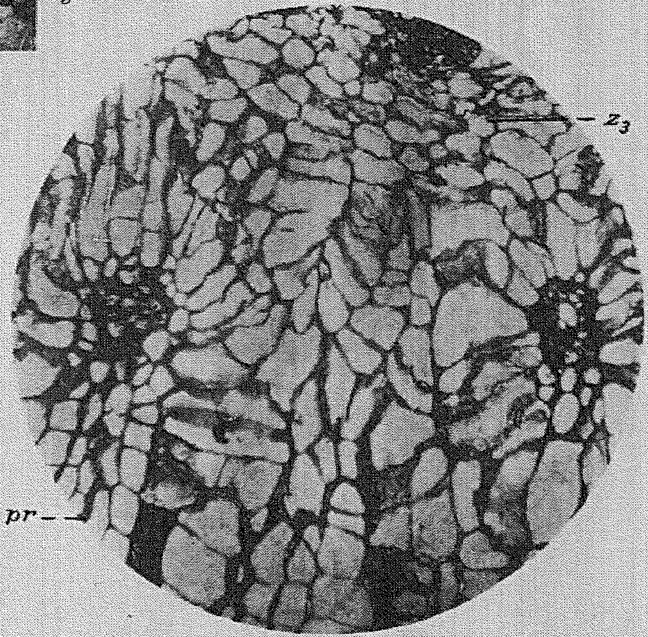

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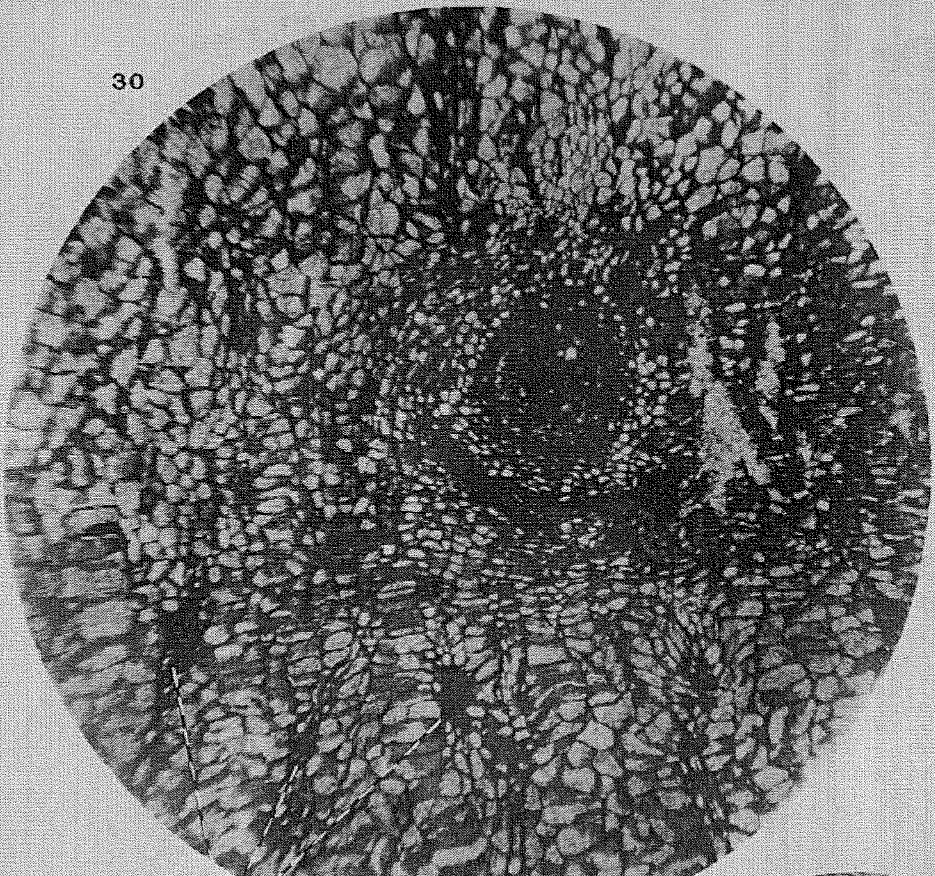

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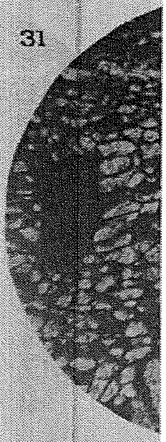

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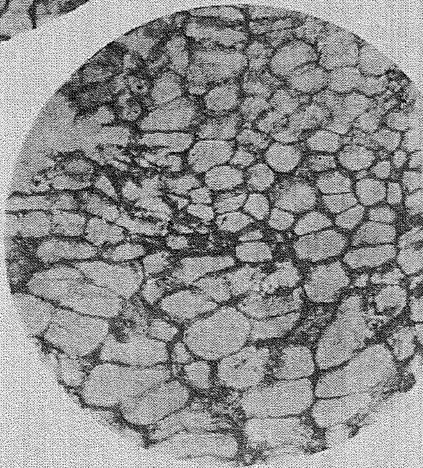

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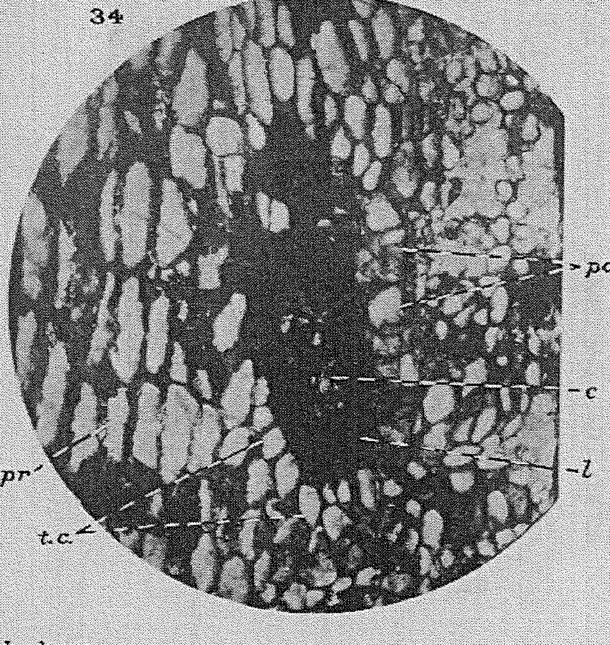

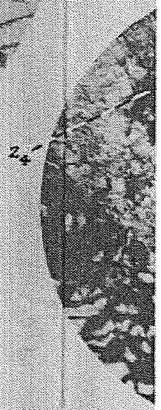

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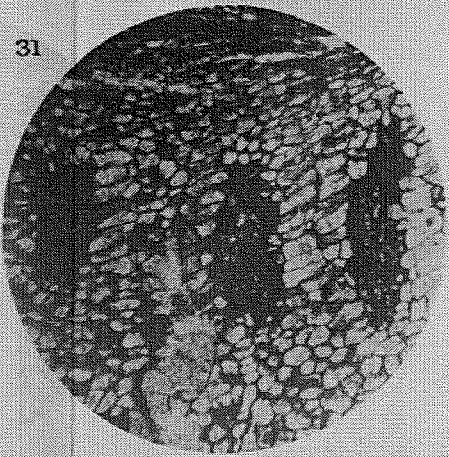

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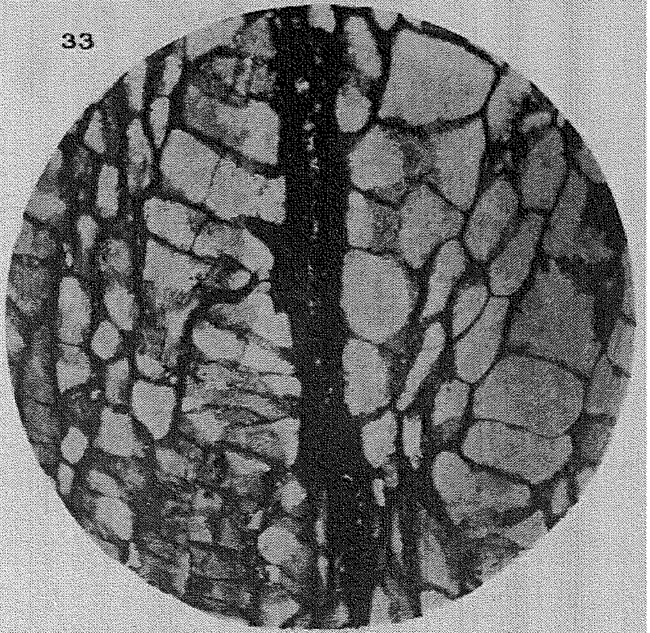

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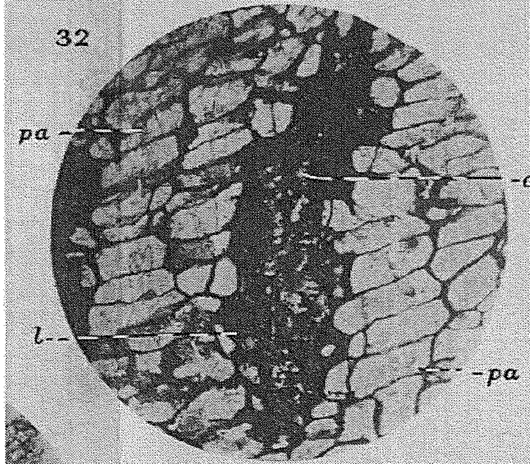

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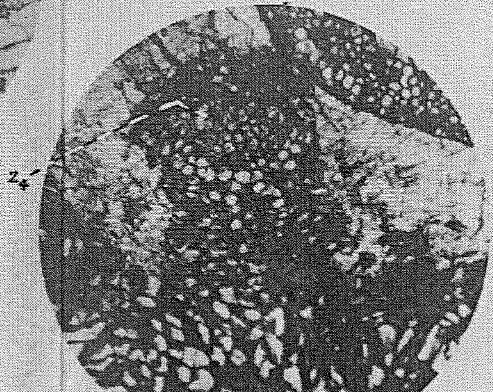

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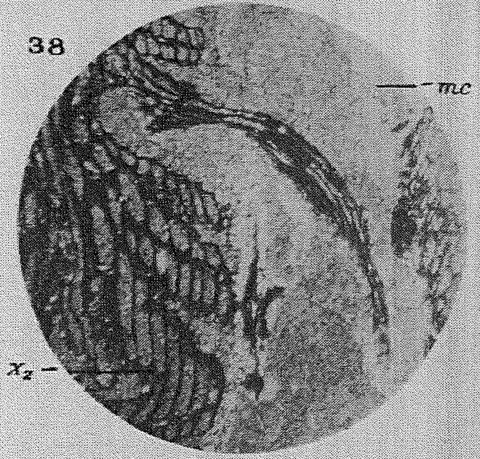

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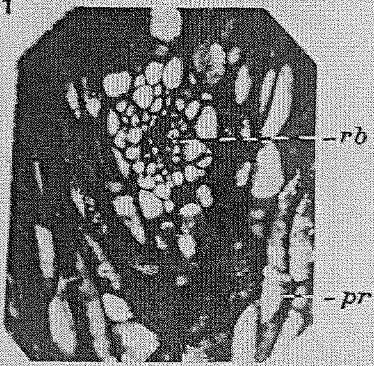

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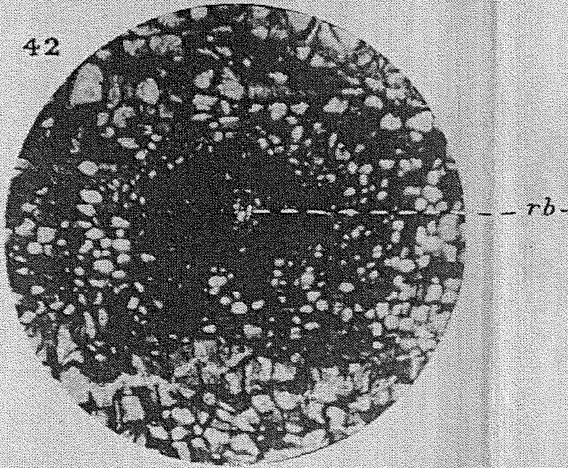

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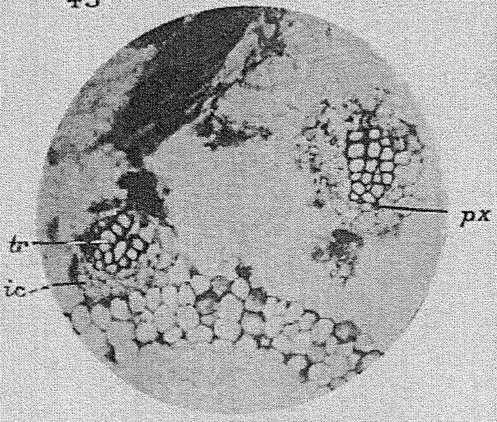

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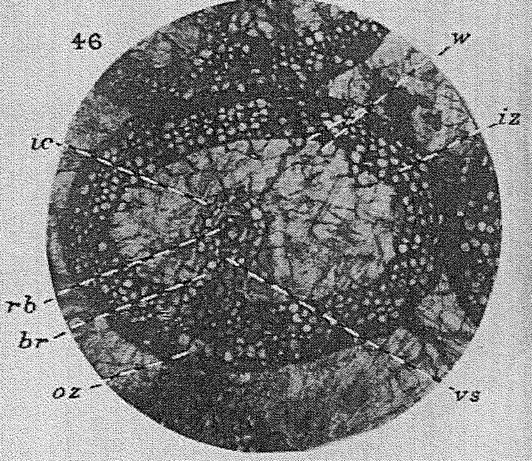

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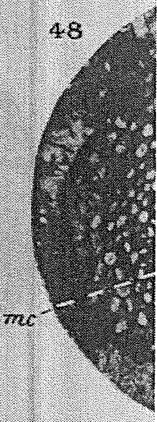

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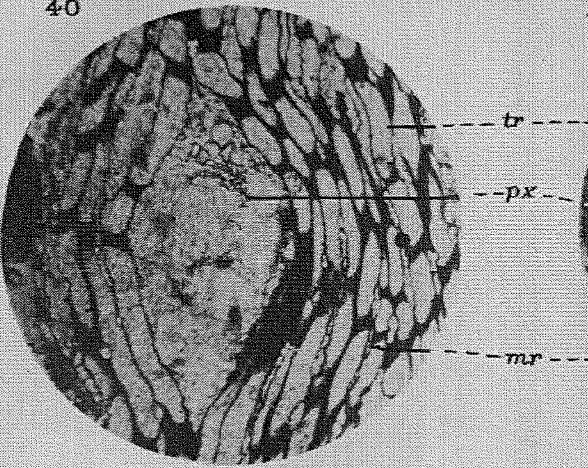

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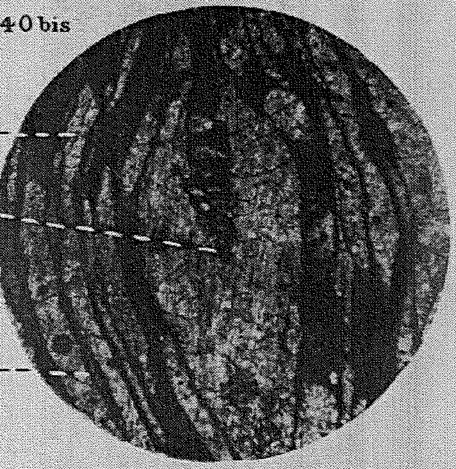

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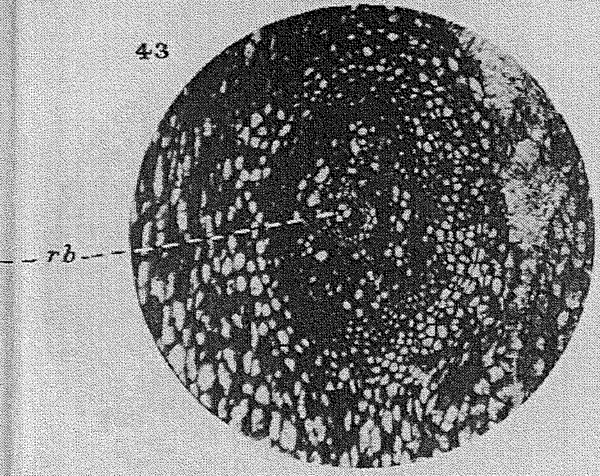

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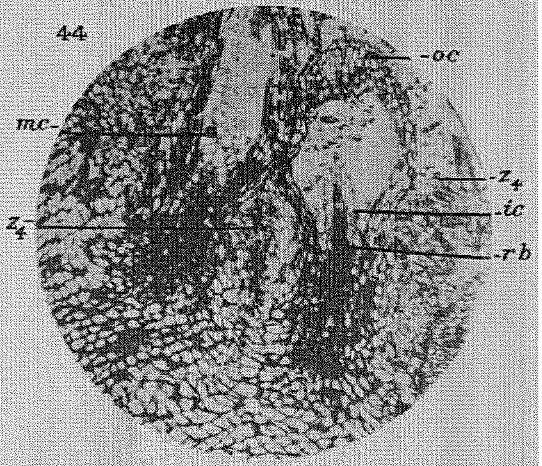

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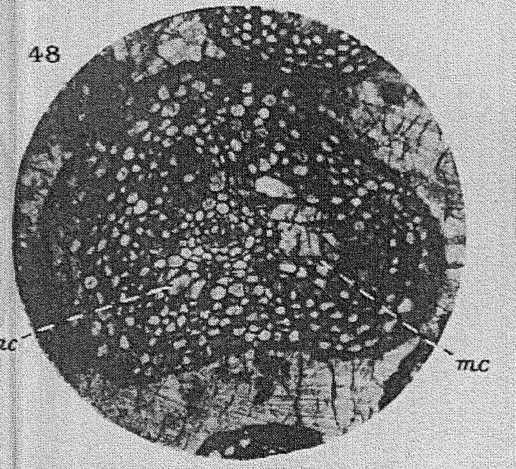

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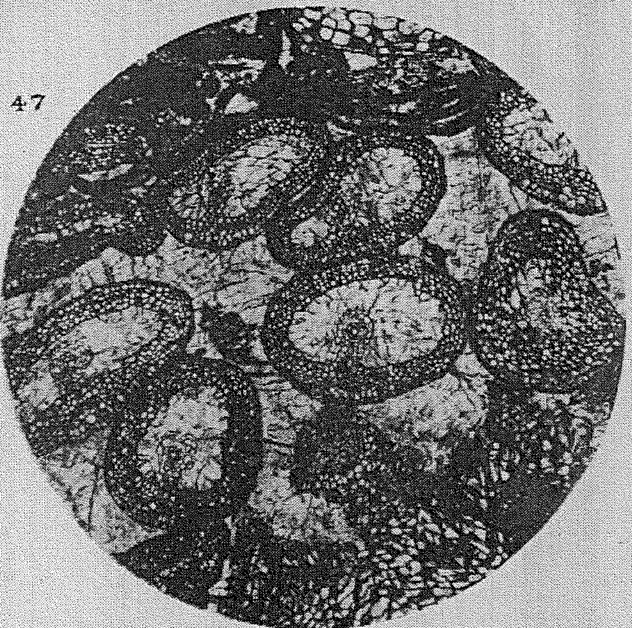

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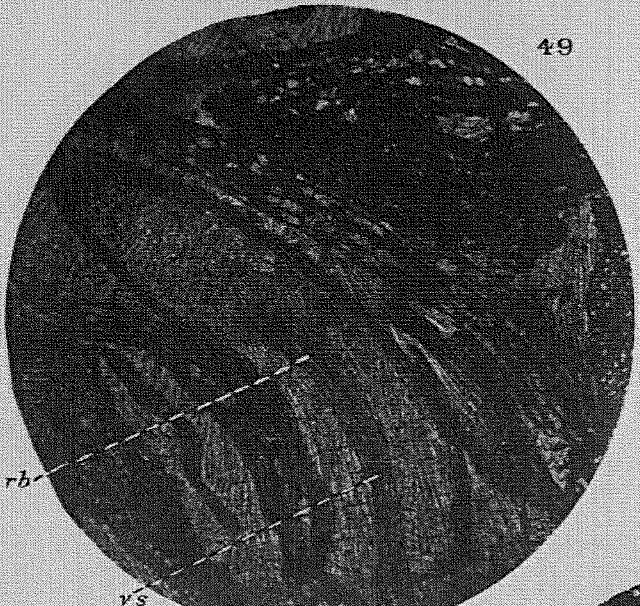

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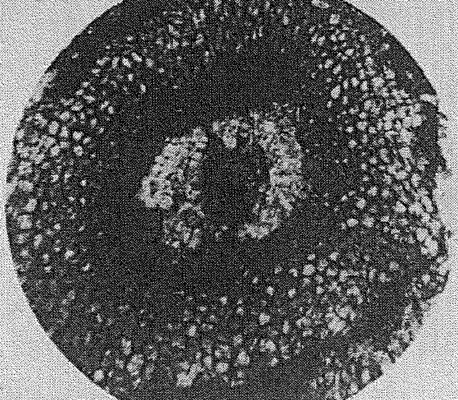

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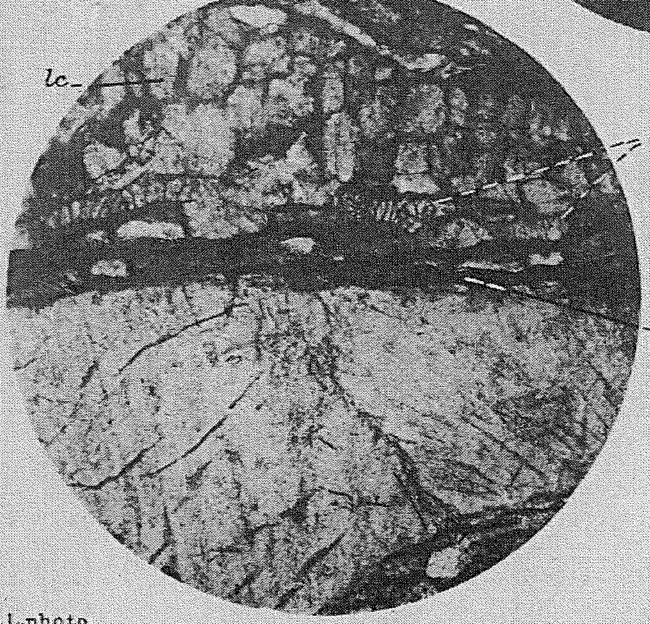

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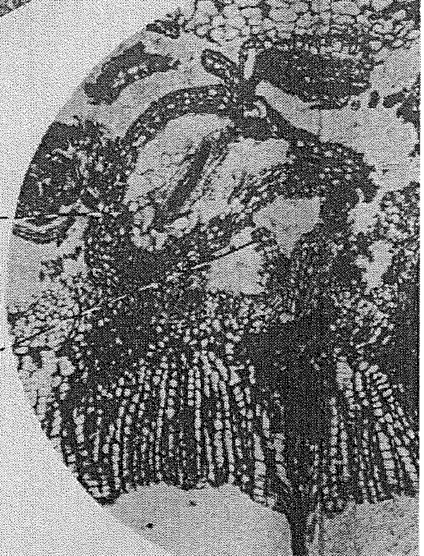

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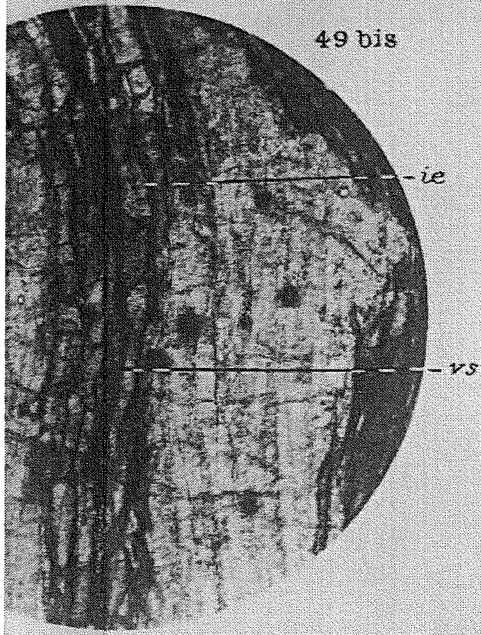

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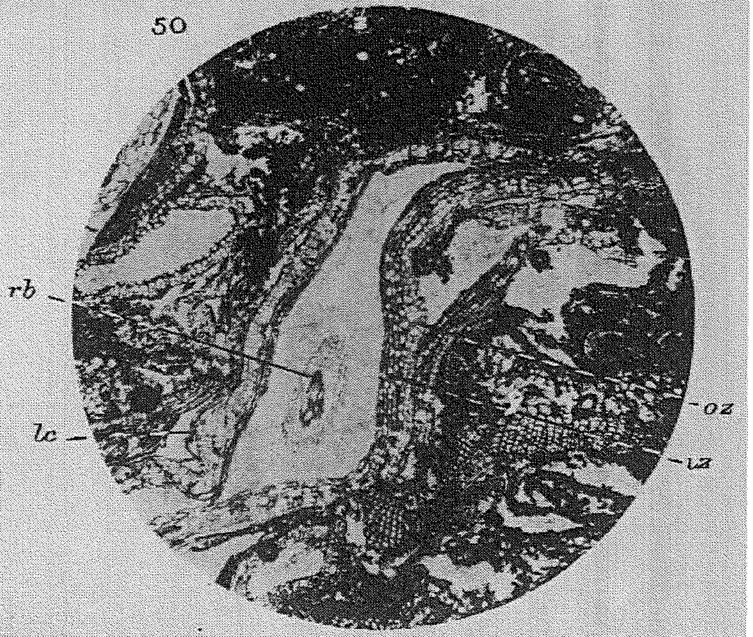

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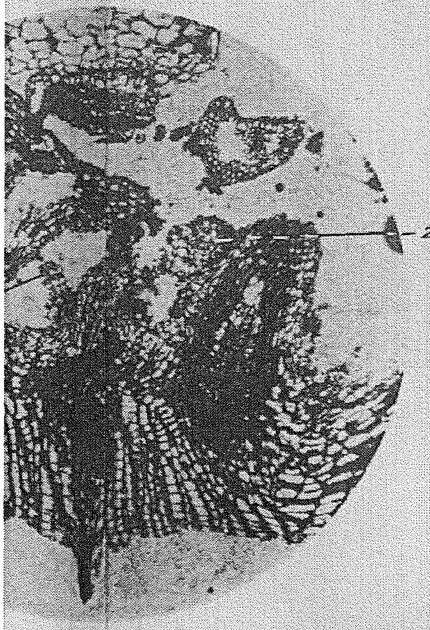
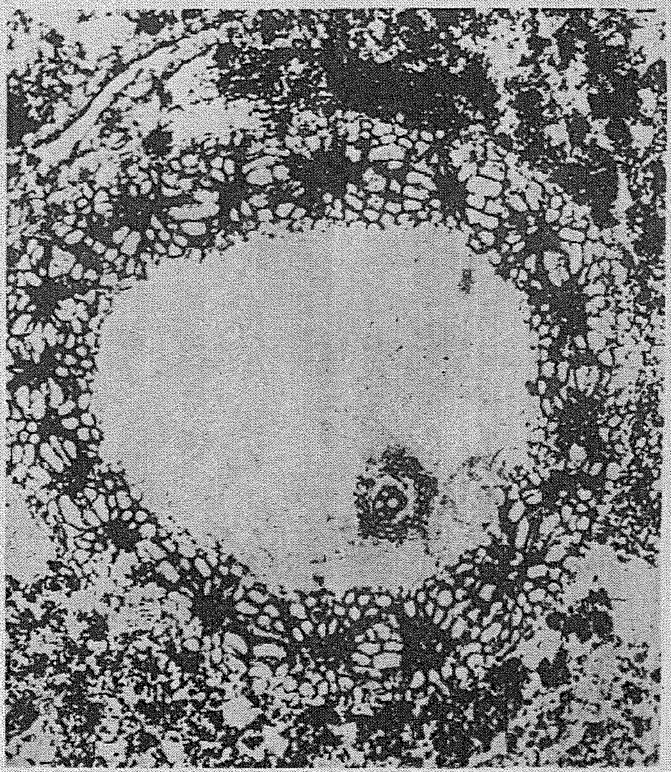


53



Huth coll.