

XXIV.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part I. *Rhynia Gwynne-Vaughani*, Kidston and Lang. By R. Kidston, LL.D., F.R.S., and W. H. Lang, D.Sc., F.R.S., Barker Professor of Cryptogamic Botany in the University of Manchester. (With Ten Plates.)

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INTRODUCTION.

The chert of the Muir of Rhynie, containing plant-remains, was discovered by Dr W. MACKIE of Elgin while investigating the sedimentary and volcanic rocks of Craigbeg and Ord Hill which occur in that area.\* The original discovery was made on loose specimens, built into the dykes or scattered over the fields, especially those lying to the north of the road which runs from Rhynie to Cabrach, and east and west of the right-of-way that here connects Windyfield Farm with the public road.

Our investigations have so far shown that only two vascular plants occur in the deposit. A transverse section of a stem of each of these was figured in Dr MACKIE'S paper, but the plants were neither named nor described. We have named the plant that occurs in greatest abundance *Rhynia Gwynne-Vaughani*,† after our late friend Professor D. T. GWYNNE-VAUGHAN, who, it had been hoped, would have been concerned with the investigation of these fossils. A full description of this plant is given in the present paper.

The second vascular plant has been named *Asteroxylon Mackiei*, after Dr MACKIE, the discoverer of the original specimens.‡ This plant has so far been found only in a few isolated patches among the remains of *Rhynia*. The description of *Asteroxylon Mackiei* and certain other vegetable remains is reserved for a later communication.

As it was uncertain whether the isolated plant-containing blocks of chert, some of which were 2 feet in diameter, were derived from the Old Red Sandstone or from another series of rocks, Mr D. TAIT, acting on instructions from Dr FLETT, dug three trenches in the lower field between Easaiche Bridge and Windyfield farmhouse.§ In one of these trenches the chert was found *in situ*. By some the section exposed was not thought to be conclusive as to the age of the chert bed, and to enable this to be determined beyond doubt, grants were received from the British Association and the Royal Society of London to defray the expense of having additional trenches dug on a more extended scale.

The work was again put under the supervision of Mr D. TAIT, when more com-

\* W. MACKIE, "The Rock Series of Craigbeg and Ord Hill, Rhynie, Aberdeenshire," *Trans. Edin. Geol. Soc.*, vol. x, pp. 205-236, pl. xxii.

† MACKIE, *l.c.*, pl. xxiii, fig. 5.

‡ MACKIE, *l.c.*, pl. xxiii, fig. 6.

§ MACKIE, *l.c.*, p. 223.

plete exposures were laid bare which showed that the chert bed was interbedded with the Dryden Shales and therefore referable to the Old Red Sandstone.\*

From the section exposed in trench No. 1 † in the lower field between Easaiche Bridge and Windyfield farmhouse the following measured section was taken :—

SECTION OF CHERT BAND IN TRENCH NO. 1, IN FIRST FIELD NORTH OF EASAICHE BRIDGE, ON SOUTH-EAST SIDE OF PATH AND DITCH SEPARATING TWO FIELDS, AND 178 FEET NORTH-EAST OF THE ROAD, MUIR OF RHYNIE, ABERDEENSHIRE.

			DRYDEN SHALES.
{ O	ft. in.	22	Bedded silicious sandstone in very thin layers with carbonaceous remains.
		0 5 21	
{ N	0 6	20 {	Silicious sandstone with sandy layer and lenticular masses of silicified peat formed of <i>Rhynia</i> . Silicious sandstone with irregular beds of chert full of <i>Rhynia</i> . Sandstone formed of very thin layers separated by black lines, irregularly bedded, and full of carbonised plant-remains.
		19 {	
{ M	0 9	18a {	Silicified peat mixed with sandy matter. Vegetable remains much broken up. Layer of silicious sandstone at top and at base, the latter about 1 inch thick. Intermediate portion formed of silicified peat composed of <i>Rhynia</i> . Vegetable remains in lower part of bed much broken up. Upper part contains stems little or not compressed.
		18b {	
{ L	1 0	17 {	Bedded silicified peat composed of <i>Rhynia</i> , in part much decomposed, with occasionally some sandy material. Bed of silicious sandstone with intercalated lenticular patches of peat formed of <i>Rhynia</i> .
		16 {	
K	0 3	15	Silicified peat with much broken-up vegetable remains. Thin sandy layer at top.
{ I	0 3	14 {	Bed of silicified peat with thin-bedded silicious sandstone at top about $\frac{1}{2}$ inch thick. <i>Rhynia</i> slightly compressed.
H	0 1	13	
{ G	0 3	12 {	Bed of silicified peat formed of <i>Rhynia</i> , a good deal decomposed and broken up, with thin layer of very fine-bedded silicious sandstone at top and base.
{ F	0 5	11a {	
		11b {	Irregular thin beds of silicious sandstone. Silicified peat formed of broken-up and decomposed <i>Rhynia</i> . Bedded silicified peat formed of <i>Rhynia</i> with layer of fine-bedded silicious sandstone, about $\frac{1}{2}$ inch thick at top, with another of about the same thickness at base.
{ E	1 1	10 {	
		9	

\* The exact horizon of the Rhynie Old Red Sandstone has not yet been definitely determined, but it cannot be younger than the Middle Old Red Sandstone.

† The site of this trench is shown on the map (fig. 1) in the Report of the Committee on "The Plant-bearing Cherts at Rhynie, Aberdeenshire," *Brit. Assoc. Rep.*, 1916, Newcastle Meeting.

			<i>Continued.</i>
D	ft. in. 0 3	8	Silicious band with thin sandstone layer at top and base with plant remains.
C	0 3	7	Fine light grey silicious sandstone.
{ B	0 9	6 {	Band of bedded silicified peat formed of <i>Rhynia</i> , with stems usually much decayed. At top occurs a thin bed of silicious sandstone.
{ A'	0 6	5 4	Cherty sandstone with carbonaceous matter. " " " " "
{ A''	1 3	3 2 1*	Silicious sandstone with carbonaceous matter. Highly silicious sandstone with <i>Asteroxylon</i> . Thick bed of impure peat with <i>Rhynia</i> and <i>Asteroxylon</i> . Stems generally much decomposed.
	0 1 2 0 2 0		Grey clay. White plastic clay, greenish tint and rusty spots, bedding obscure but more distinct near bottom. Clay or clayey shale, not so light in colour as that above.

*Rhynia* extends throughout the whole section. *Asteroxylon* has only been observed up to the present in bed A''.

It is not our sphere to treat of the detailed geology of the Rhynie area ; that will be done by other and more competent writers. As intimately connected with the petrifications which have been placed in our hands for description, it is, however, necessary to make some remarks on the nature of the chert band in which they occur.

Our material has consisted of a complete set of specimens taken from the chert band, lettered and numbered as noted in the first and third columns of the section given above. In addition, some of the loose specimens have yielded most valuable information. The chert is much jointed and fissured, and when fresh is of a blackish or dark grey colour in which, when visible, the plants are only indicated by darker spots or streaks. Specimens naturally weathered sometimes assume a light buff colour, and the plant-remains are clearly exhibited (Pl. II, fig. 2). When blocks are treated with a weak solution of hydrofluoric acid, which etches the surface and brings out more or less distinctly the structure of the chert, the plant-remains are also rendered more visible (Pl. I, fig. 1 ; Pl. II, fig. 5).

The blocks themselves and the numerous microscopical sections studied prove that the whole chert zone was originally formed of a series of peat beds which, during their formation, had been subject to periodic inundation, when thin layers of sand were spread over the surface. Each bed of peat appears to have a thin layer or bed of sand at its top.

Several of the isolated specimens have shown the plants growing vertically from

\* This column gives the original numbers of the specimens as collected.

the old land surface represented by the peat (Pl. II, figs. 2 and 5). One specimen (fig. 5) seems to contain a tuft of *Rhynia* which must have grown on the surface at the time the peat bed was brought to a final close by infiltration with silica. This example shows the upright stems for a length of 6 inches above the bed from which they grew. The uppermost parts of the stems are embedded in almost pure silica without any admixture of peaty substance, and with only a little fine, dust-like matter disseminated through the silica (Pl. V, fig. 20).

The whole history of the formation of the Rhynie Chert Zone, at least of that portion from which our specimens were taken, can be clearly read. One can in imagination see a land surface, subject at intervals to inundation, covered with a dense growth of *Rhynia Gwynne-Vaughani*. By the decay of the underground parts of *Rhynia* and the falling down of withered stems (for this plant had no leaves) a bed of peat was gradually formed varying from an inch to a foot in thickness. The peat was then flooded and a layer of sand deposited on its surface. Again the *Rhynia* covered the surface, and this process of the formation of beds of peat, with the deposition of thin layers of sand, went on till a total thickness of 8 feet had accumulated.

After the formation of 8 feet of alternating peat and sand local physical conditions must have altered, for water with silica in solution, possibly discharged from fumaroles and geysers, poured over the peat bed and sealed it up. Thus the whole was converted into a band of chert, the structure of the plants being preserved in many cases in great perfection. It may be mentioned that the presence of geysers or hot springs has been suggested by Dr MACKIE as an explanation of the occurrence of so many cherty developments in the rock series of Rhynie (*l.c.*, pp. 233-236).

### *Rhynia Gwynne-Vaughani*, Kidston and Lang.

#### MODE OF OCCURRENCE.

As mentioned in the introduction, the silicified peat is almost entirely formed of the prostrate stems and the rhizomes of *Rhynia*, while in one or two fortunate cases the closely crowded aerial stems were seen standing vertically (Pl. II, figs. 2 and 5). In these cases the ancient land surface with its vegetation is recorded in a manner very rarely met with.

The horizontal bedding of the silicified peat is distinctly seen in Pl. I. fig. 1, which represents a block from bed E 10 of the vertical section on page 762. In the lower parts of the individual peat beds the plant-remains can be seen to become more compressed than above. This is also seen in the microscopical section shown in Pl. III, fig. 9, where the stems in the upper part are round and separated by a considerable amount of amorphous peaty matrix, while in the lower part they are crowded and compressed. In fig. 10, from the lower part of another bed the



stratification of the silicified peat layers in different degrees of decay is still more clearly visible; two thin bands *a* and *b* occur in which the stems are much more decayed and crushed together. These two photographs give an idea of the abundance of the stems of *Rhynia* in the peat. From the fact that they are practically all cut transversely in these sections, it can be inferred that for some reason or other the stems lay horizontally and more or less parallel.

A horizontal surface of a block, on which the closely crowded and flattened stems of the plant show that the whole growth had been laid down and compressed, is represented in Pl. II, fig. 3. The small portion of this, enlarged two diameters, in fig. 4 shows at *a* a median line on the flattened stem. This will be seen below to indicate the position of a central vascular strand.\*

In contrast to this mode of preservation, the unaltered cylindrical stems of the free aerial portion of the plant can be exposed by fracturing the chert. Examples of such stems, which have preserved their shape perfectly in the almost pure silicious matrix, are shown enlarged fourteen times in Pl. III, figs. 6-8.

#### EXTERNAL MORPHOLOGY.

Owing to the favourable nature of the material, it has been possible to arrive at a clear conception of the morphology of the plant as a whole. It will assist the reader if we deal briefly with the general organisation of *Rhynia* before entering into the details of its structure.

The plant formed a practically pure growth, and its erect cylindrical stems stood closely crowded. These stems probably attained a height of 8 inches or more,† and range from 6 mm. to under 1 mm. in diameter. The plant was rootless and had no leaves, being composed entirely of a system of cylindrical axes or stems. Its lower portion consisted of branched underground rhizomes attached to the peaty soil by numerous rhizoids. Branches of the rhizome turned gradually or abruptly up and assumed the characters of the aerial stems. The latter were occasionally branched dichotomously and tapered gradually upwards. They bore small hemispherical projections which were more or less closely placed without apparent regularity. On some of these bulges tufts of rhizoid-like hairs were borne, while in other cases the projections developed into adventitious branches, usually attached by a narrow base. Some of these branches appear to have been readily detached, and their occurrence free in the peat suggests that they served to propagate the plant vegetatively.

Even in the most complete specimens, preserved as they grew from the peat, the terminal parts of the aerial stems are wanting. The reproductive organs have not been observed attached to the complete plants, and it is impossible to say

\* Such impressions, with or without an evident midrib, according to their preservation, might easily be described as linear leaves or even algae.

† The stems in Pl. II, fig. 5, measured 6 inches, but were incomplete.

whether the sporangia terminated the main axes or some of the lateral branches. It is, however, certain from detached specimens found in the silicified peat that some aerial axes ended in large, elongate-pointed sporangia.

That the rhizomes, aerial stems, and sporangia were portions of the same plant might have been inferred from their association in a bed composed of one type of plant only. Their continuity has, however, been directly traced, and is established by anatomical evidence.

Quite apart from any question of affinity, the build of *Rhynia*, with its rootless rhizomes of delicate structure sending up xerophytic aerial stems, finds its closest parallel among existing plants in the general morphology of *Psilotum*.

#### ANATOMY OF THE VEGETATIVE ORGANS.

The plant consists throughout of cylindrical axes with an epidermis, a relatively wide cortex, and a simple central cylinder. The latter has a solid strand of tracheides surrounded by a zone of phloem. It will be convenient to describe the rhizomes in the first place and then to deal with the aerial stems.

##### *Rhizome.*

The rhizomes seem to have been formed of more delicate tissue than the stems arising from them, so that the peat often consists entirely of the latter, the rhizomes having decayed. In other portions of the peat, however, well-preserved rhizomes have been found; thus Pl. IV, fig. 13, shows a small portion of a section through the peat in which rhizomes are seen in their natural position. The section passes through three pieces of the rhizome. The uppermost is cut transversely, and shows the broad cortex and the single stele. The lowest section is also transverse, but goes through a rhizome where dichotomous branching is about to take place, the stele having already divided. The middle section passes longitudinally through a rhizome, just missing the xylem of the stele except on the extreme right. The lower side of this rhizome shows two large hemispherical bulges of the outer cortical tissues. Portions of these bulges, more highly magnified, are represented in figs. 11 and 12 on Pl. III. The greater development of the cortex on the lower side of the two transverse sections in fig. 13 is due to the plane of section passing through similar bulges. From the downwardly directed surfaces of all three rhizomes, and especially from the hemispherical bulges of the middle piece, numerous rhizoids extend into the peat.\*

Sections through other rhizomes are shown on Pl. IV. In fig. 17 two rhizomes of different sizes are seen in transverse section. The stele of the larger one has divided preparatory to dichotomous branching. From the epidermal cells of its

\* The peculiar oval bodies in the cortex of the two lowest rhizomes in fig. 13 are the reproductive organs of saprophytic fungi. The detailed description of the numerous fungi which occur in the deposit is reserved for a future communication, but the reader must allow for their presence in many of the illustrations to this paper.

lower side rhizoids are given off without the cortex forming a very definite projection. On the other side of this rhizome a distinction is evident between the narrow zone of outer cortex and the broad inner cortex. The smaller section in this figure has a single stele, and its outer tissues continue on the lower side into a marked bulge which would doubtless later have borne rhizoids.

The position and general appearance of the rhizoids in all the examples examined show that the rhizomes were growing naturally in the peat when preserved. In fig. 18 a portion of the rhizoid-bearing surface of another rhizome is more highly magnified, and shows very clearly the relation of the rhizoids to the peaty soil. The rhizoids are seen to be non-septate, and do not appear to have been divided off from the epidermal cells bearing them. In fig. 14 the rather large rhizome seen in transverse section is attached by numerous rhizoids below, while from the opposite side an aerial branch ascends vertically.

The small rhizome shown rather more highly magnified in fig. 15 is preparing to branch. The slender, transversely extended strand of tracheides is cut somewhat obliquely. Another rhizome in transverse section is shown still more highly magnified in fig. 19. Around the central strand of xylem (*x.*) comes the thin-walled phloem (*ph.*), passing without a sharp limit into the inner cortex (*i.c.*). The two or three outermost layers of the cortex (*o.c.*) contrast with the inner cortex in their appearance. The epidermis (*ep.*) of the rhizome has its outer cell walls thin as compared with the aerial stems to be described below, and the cuticle is less developed. Stomata have not been observed in the epidermis of the rhizome, the cells composing which are four- to six-sided in surface view and almost isodiametric (fig. 16). On the vertical branch in fig. 14, which was presumably the base of an aerial stem, the epidermal cells assume a more elongated form and a stoma occurred near to the base of the branch.

The histological details of the various regions will be described more fully in connection with the aerial stems. It is sufficient to recognise here, as shown in the sections of rhizomes on Pl. IV :—1. The epidermis, the cells of which can grow out as rhizoids; 2. The narrow zone of outer cortex; 3. The broad inner cortex; 4. The phloem; 5. The slender strand of tracheides forming the xylem. These tissues are often less sharply defined than in the aerial stems, but, except for the differences in the epidermal layer, there is no fundamental distinction between the anatomy of the rhizome and that of the aerial stem.

The epidermis, the outer cell walls of which are thin as compared with those of the aerial stem, is seen to be fairly well defined in fig. 19 and on the upper side of the rhizomes in figs. 15 and 17. On the lower side, where numerous rhizoids are borne, no cuticle is recognisable, and the epidermis itself is less sharply distinguished from the cortex on account of periclinal divisions having taken place in the superficial cells. In other cases, as is best seen in fig. 13, this cell division in the epidermis and outer cortical layers has led to the formation of large hemi-

spherical protuberances. As figs. 11 and 12 on Pl. III show, this has involved a large number of the superficial cells, but only affects the epidermis and outer cortex. The result of this is that the large bulges, like the smaller bulges on the aerial stems to be described below, are growths from the superficial tissues only, and have no vascular supply from the stele of the rhizome.

The cell contents have disappeared or are unrecognisable, but no evidence of the presence of a fungus forming a mycorrhiza has been found, although the saprophytic fungi in the peat are well preserved.

#### *Aerial Stem.*

The aerial stems, as already shown (Pl. II, fig. 5), tapered gradually upwards, and slight modifications of the structure will have to be taken into account. Moreover, the lower portions of the stems must have been surrounded by the peat, and would constitute an ill-defined transition region. The range in diameter of stems can be seen at a glance in figs. 21–25 on Pl. V. These transverse sections are all of the same magnification ( $\times 20$ ), but the largest (fig. 21) is of a stem of only medium size, a little under 3 mm. in diameter, while stems of 6 mm. diameter have been observed. The smallest (figs. 24–25) are under 1 mm. in diameter.

Fig. 20, Pl. V, shows a number of stems from the upper region of the plant embedded in an almost pure silicious matrix. As the portions isolated in the round show (Pl. III, figs. 6–8), the stem had a well-marked epidermis, was destitute of leaves, but bore small hemispherical projections which were irregularly distributed.

The sections of stems in figs. 21–25 do not pass through any of these small projections, but the transverse section in fig. 27, and the longitudinal section in fig. 26, show them. The bulges of similar size shown in figs. 28–29 differ by bearing rhizoid-like hairs. It is a reasonable supposition, though we have no direct evidence for it, that these rhizoids were mainly developed in the transition region. In one case, however, a rhizoid was observed on a bulge in the upper region of a stem.

Fig. 30 shows an aerial stem preparing for dichotomous branching. The stele is already divided.

A characteristic aerial stem of good size is shown in transverse section in fig. 21. It exhibits the well-marked epidermis (*ep.*) with a thick outer wall and cuticle. The two or three succeeding layers of clear cells form the narrow outer cortex or hypoderma (*o.c.*). The broad inner cortex (*i.c.*) is composed of smaller rounded cells with intercellular spaces. The phloem (*ph.*) contrasts with the cells of the surrounding cortex by the smaller diameter of its thin-walled elements. In the centre is the solid strand of xylem (*x.*). The corresponding arrangement of the tissues is seen in longitudinal section in fig. 26, and even more clearly on Pl. VIII, fig. 59.

The several tissues may now be considered in order from without inwards.

*Epidermis and Stomata.*—The appearance of the epidermis in transverse section is well shown in Pl. VI, fig. 35, which includes portions of the outer surface of two

adjacent stems. Its cells are smaller than the underlying cortical cells. Their outer wall is thick, and in favourable cases exhibits a distinction into several layers, the outermost layer being the strongly developed cuticle. More usually, as in this figure, it is so preserved as to appear thick and uniform. The lateral and inner walls are thin. The epidermal cells are longer than broad, and, viewed from the outside, either on the surface of exposed stems (Pl. III, figs. 6-8) or in tangential sections (Pl. VI, figs. 31-32) are seen to be broadly fusiform. They are often characterised by a peculiar dark median line (fig. 31). Suitable transverse sections show that this line is the expression of a sharp cuticular ridge springing from the middle of the slightly convex surface of each epidermal cell. This ridge is shown in fig. 36, where, however, a slight obliquity exaggerates the thickness of the outer cell wall. In other cases this ridge is wanting, sometimes at least as the result of imperfect preservation, but in some regions of the stem the epidermal cells were wider and normally lacked the central ridge (Pl. III, fig. 6; Pl. VI, fig. 32). This has been verified from the study of outer surfaces of stems by reflected light as well as from sections.

Stomata occurred in the epidermis, but in no region do they seem to have been at all numerous. They have not been observed on the rhizome, but in the case of the stem springing from a rhizome in Pl. IV, fig. 14, a stoma was present on the base of the branch at *st*. They were thus present in the epidermis of the transition region, though doubtless more abundant on the upper portions of the aerial stems.

A stoma is shown in surface view in Pl. VI, fig. 32, and figs. 33 and 34 are of stomata in transverse section. Fig. 37 passes longitudinally through a stoma at *st*. As these figures show, there is nothing peculiar about the shape of the guard cells, and they are not depressed below the general surface, though, the sparseness of the stomata and the thickness of the cuticle indicate the xerophytic construction of the plant.

*Cortex*.—The outer cortex (Pl. VI, fig. 35, *o.c.*) consists of one to four layers of cells which are large relatively to the cells of the epidermis and of the inner cortex. It is best marked in the lower and thicker portions of the aerial stems. The cells of the outer cortex generally appear clear and empty-looking, and are slightly longer than broad.

The cells of the inner cortex are round in transverse section and were separated by fairly large intercellular spaces (Pl. VI, figs. 38 and 40). They are longer than broad, this being more marked on passing from above downwards in the stems (*cf.* Pl. VII, fig. 42, with fig. 43). As preserved, the inner cortex often has a darker brown colour which is specially marked in the cells immediately below the outer cortex (Pl. V, figs. 21, 22, and 24). In a few cases the cells of the inner cortex were filled with closely crowded bodies suggestive of chloroplasts or possibly starch (Pl. VI, fig. 39). The inner cortex was especially liable to decay, and stems are often found in which it had wholly disappeared while the stele and outer cortex remained.

That the inner cortex in the aerial stems probably constituted the assimilating

tissue while the outer cortex is to be regarded as a hypodermal layer, is shown not merely by the characters of their respective cells, but by their relations to each other in the neighbourhood of a stoma. This is seen in the transverse section on Pl. VI, fig. 34. The hypoderma, which in this case was clearly marked and consisted of two layers of large cells (fig. 34, *o.c.*), is not developed beneath the stoma (*st.*), but the inner cortex (*i.c.*) here extends to the surface. Thus the well-developed system of intercellular spaces in the inner cortex was placed in communication with the external atmosphere. In the longitudinal section shown in fig. 37 the inner cortex had disappeared, but the interruption in the hypoderma beneath the stoma is beautifully shown. This, as fig. 34 showed, was originally filled by cells of the inner cortex.

While there is no doubt as to the hypodermal nature of the outer cortex in the aerial stems, it must be borne in mind that a distinction of this narrow zone of cells from the inner cortex is traceable throughout the plant. This holds even for regions which there is no reason to think had a specialised hypoderma or assimilating inner tissue. Thus it has been seen in the rhizomes (Pl. IV, figs. 15 and 19), and even in small axes without a stele (Pl. X, fig. 73).

The stem shown on Pl. X, fig. 74, is peculiar in having one sector of the transverse section composed of cells of larger size. This applies both to the hypoderma and the inner cortex.

*Stele.*—The stele throughout the plant is composed of a central strand of tracheides surrounded by a zone of phloem. It is not delimited from the inner cortex by any layers which can be interpreted as endodermis or pericycle. The stele exhibits a considerable range in size, partly in relation to the region of the plant, and partly in relation to the stoutness of the individual stems (Pl. V, figs. 21–25; Pl. VII, figs. 44–46). Thus the stele represented in Pl. VII, fig. 45, is a fairly large one, and has a strand of xylem composed of numerous tracheides; while that in fig. 46, which belongs to the slender stem represented in fig. 25, had only two tracheides. Slender axes are also met with in which no vascular tissues have been differentiated (Pl. VIII, fig. 60; Pl. X, fig. 73).

The phloem in transverse section (Pl. VII, figs. 41 and 44) is composed of thin-walled elements, four- to six-sided, and fitted closely together. No distinction can be made between the various elements in this zone, which is about four or five cells in depth. In longitudinal section (Pl. VII, fig. 42) the elements composing the phloem are much longer than the cells of the inner cortex. They further differ from the cortical cells in their end walls being oblique instead of transverse. As comparison of figs. 42 and 43 will show, the elements forming the phloem become shorter and less characteristic in the stele of the more slender upper region of the stem. Although sieve plates have not been found, the position of this zone, its clear appearance, and the form of its component elements seem to justify its recognition as true phloem.

The xylem strand, whether composed of few or many tracheides, is always solid, no parenchyma being mixed with the tracheides. No distinction between protoxylem and metaxylem can be drawn, all the tracheides being alike. The thickening of the tracheides was annular (Pl. VII, figs. 47 and 48). It had the form of rather broad rings, which give the tracheides the appearance of being transversely barred. Occasionally two of the bars converge and, uniting at one end, take the shape of a Y or V, but neither definite spiral thickening nor the passage to a scalariform type of thickening has been seen.

*Hemispherical Projections.*—In Pl. III, fig. 7, a number of the definite little bulges which occur on the stems are seen in the round. Several of these projections are seen in the transverse section of a stem on Pl. V, fig. 27. Their structure is illustrated in greater detail in figs. 49–51 on Pl. VII. In fig. 49 a small bulge is seen from the outside on an obliquely viewed epidermal surface. In this view the surface cells of the projection are isodiametric. They fit closely together without intercellular spaces. They contrast in form with the surrounding epidermal cells and have a much thinner outer wall than these, but we have satisfied ourselves that there is unbroken continuity between the two. Two bulges in longitudinal vertical section are represented in figs. 50 and 51. As is especially clearly shown in fig. 51, the bulge is due to periclinal division in the epidermis and outer cortical cells. The thick outer wall and the cuticle cease to be marked over the projection; this often exhibits a brown discoloration of its outer cells, which are sometimes broken down.

Though much smaller, these projections agree in their relation to the tissues with the large bulges on the rhizome (Pl. III, fig. 11). In connection with this it is interesting to find that the superficial cells of some of the small projections grow out as rhizoids similar to those on the rhizome. Examples of these rhizoid-bearing projections will be found on Pl. V, figs. 25 and 29, and more highly magnified on Pl. VIII, figs. 52–54.

*Lateral Branches.*—Many of the small projections were the seat of a further development of considerable interest, adventitious lateral branches being produced from them. This is illustrated in figs. 55–61 on Pl. VIII. The tissues at the base of the branch are continuous with the epidermis and outer cortex of the parent axis. The branch in fig. 57 has its own vascular strand, but this does not exhibit any connection with the stele of the parent axis. Such transverse sections through the main axis and branch did not, however, exclude the possibility that the stele of the branch might have continued obliquely downwards as a trace through the cortex of the main axis to join with the stele of the latter. Where, however, as in fig. 61, we see the bases of two fairly large branches in a longitudinal section that includes the stele of the parent axis throughout, and there is no indication of traces passing out, it seems safe to conclude that these lateral branches had no vascular connection with the main axis.

In fig. 55 several small bulges are present around the stem, only one of which has given rise to a branch. The branch in fig. 56 is itself branching. These adventitious branches appear to have arisen from all regions of the stem.

The particular example shown in fig. 58 is from a stem about 4 inches above the ground, in the block shown on Pl. II, fig. 5.

Some of the branches had a fairly wide base of attachment (Pl. VIII, figs. 56-59, 61), while others widen out from a very narrow attachment (fig. 60). All intermediate forms are found. The adventitious branches appear to have been readily detached. In fig. 55 this separation of the branch has almost taken place. Specimens with a very narrow stalk-like base of attachment have been met with free in the peat, a good example being shown on Pl. X, fig. 72. This branch widens rapidly but has not developed a stele. The distribution in the peat of such detached branches suggests that new plants started from them, and that this was an important method of vegetatively propagating the plant.

Doubtless, as the branch grew on, a stele was differentiated in it, but small cylindrical stems of various diameters without any indication of a stele have been frequently met with (Pl. X, fig. 73). Another example is shown in fig. 60, lying beside the attached branch, which itself has no indication of a stele.

The scar left by the separation of a branch often became the seat of degenerative changes. Its position is then marked by a small black patch of dead tissue. The adjoining cells had frequently elongated at right angles to this, the wound-reaction showing that the separation of the branch had occurred during the life of the plant.

The foregoing description of the vegetative organs of *Rhynia Gwynne-Vaughani* has been based upon the best-preserved specimens. We may add a remark on some results of less perfect preservation in producing a different structural appearance, especially in the region of the stele. The fairly large stem represented in Pl. X, fig. 75, shows the commencement of the decay of the epidermis and of the inner cortex. When this is more advanced it leads to the complete disappearance of the inner cortex, only the stele and the thin cylinder of the outer cortex being preserved. A further change affecting the stele has been observed in numerous examples of partially decayed stems of various sizes. It is illustrated in the large steles shown in figs. 76-78, Pl. X. The markings on the xylem disappear, while dark material is deposited throughout the stele (fig. 76). This leads to a dark core representing the xylem surrounded by a dark zone in the position of the phloem. A somewhat similar condition is represented in fig. 77, where, however, the inner portion of the phloem has broken down, leaving a clear space between a dark central mass and a surrounding dark ring. In fig. 78, though decay is less advanced, the xylem (*x.*) actually appears lighter in tint than the phloem (*ph.*), and has lost all its thickening, while the zone of phloem appears to consist of elongated and very dark pointed elements.

This condition of preservation will be referred to further in the concluding remarks.



## SPORANGIUM.

The aerial stems of *Rhynia Gwynne-Vaughani* have been traced for at least 6 inches from the surface of the soil, but the block shown in Pl. II, fig. 5, unfortunately did not contain the terminal portions of the stems. Both dichotomous and lateral branching were occasionally observed in the upper regions. No reproductive organs have, however, been seen attached to these stems, though presumably they would occur on the higher portions. It is impossible therefore to say whether the main axis terminated in a sporangium or whether sporangia were borne on special lateral branches, though, judging from the size of the sporangium, the latter supposition appears less probable.

A number of specimens of sporangia have, however, been met with in the substance of the silicified peat (Pl. IX), while free spores were disseminated throughout the matrix.

It might have been inferred with reasonable certainty from the purity of the vegetation that these sporangia were the reproductive organs of *Rhynia*. The small specimen shown in figs. 63 and 63A fortunately places the matter beyond doubt, for the sporangium is here borne terminally on a slender axis with the characteristic vascular strand and tracheides described above.

Another and larger sporangium was cut in a series of transverse sections (slides Nos. 2417-2422), and following the series down, the basal region of the sporangium was found to be continuous with a badly preserved but characteristic axis of *Rhynia* (cf. Pl. IX, fig. 69).

The sporangium attained a length of at least 12 mm. and a breadth of 2.5 mm., and the axis it terminated was about 1.5 mm. in diameter. More precise measurements cannot be given, as the sporangia varied considerably in size. It was cylindrical in form, though as enclosed in the peat it is generally slightly flattened (figs. 64 and 65). The form of the base of the sporangium and its junction with the stalk is best shown in fig. 62. The apical region of this specimen appears somewhat more rounded than was actually the case, owing to the section being slightly tangential. As fig. 64 shows, the sporangium was more pointed.

In several cases a pair of sporangia have been met with lying side by side in the silicified peat (figs. 65, 69). This is suggestive of a possible junction of their stalks, but proof of this is wanting.

The wall of the sporangium is  $\frac{1}{3}$  mm. thick, and is differentiated into several layers (figs. 66-67). In fig. 66, which represents more highly magnified a portion of the wall of the sporangium shown in fig. 65, the wall is seen in true transverse section. The cells of the epidermal layer are narrow, and greatly extended at right angles to the surface. They have thick walls, and are covered by a well-marked cuticle. In this specimen the middle layers of the wall had wholly decayed, their position being represented by the clear space which separates the epidermal layer

(*ep.*) from what we interpret as a persistent tapetal layer (*tap.*). The cells of the latter appear rounded, have thin walls, and vary in size. For the most part the tapetum consists of a single layer with a rather irregular surface towards the cavity of the sporangium, but at places it is two cells thick.

The tissue intervening between the epidermis and the tapetum was evidently more delicate and is not well preserved in any of our specimens. It is best shown in fig. 68, Pl. IX, and consisted of a considerable number of layers of small, thin-walled cells.

The corresponding layers are recognisable in the sporangial wall when cut longitudinally (fig. 67). The tapetal cells were seen to be longer than broad. In this view the epidermal cells appear almost square. This difference from their appearance in transverse sections (fig. 66) is explained by the actual form of these cells as seen from the outside, being narrowly fusiform, like the epidermis of the stem, though on a smaller scale.

The thick-walled epidermal layer appears to have been uniformly continuous over the surface of the sporangium. No satisfactory indication of any lines of dehiscence has been detected in any of the sections, though specially looked for.

The sporangium contained an enormous number of spores. In some cases these were still united in tetrads (Pl. X, fig. 70), each spore showing a convex outer wall and a three-sided inner face where it adjoined its sister cells. In other sporangia the spores were separate. They exhibit some variation in form and size but on an average measure about  $65 \mu$  in diameter.

The spores found scattered through the peat (Pl. X, fig. 71) resemble those in the sporangia, but had increased slightly in size. Only the cuticularised wall is preserved. One of the spores in fig. 71 shows the triradiate marking on its inner face.

No stages in the germination of the spore have been seen, nor has the gametophyte been found.

#### SUMMARY.

1. The plants grew in a gregarious fashion in a peaty soil practically composed of the decaying remains of the same species. This land surface was probably in the neighbourhood of water, and liable to periodic inundations.

2. The plant had no roots and no leaves. It was entirely composed of branched cylindrical stems.

3. The branched underground rhizomes were attached to the peat by numerous rhizoids, most abundant on large, downwardly directed bulges of the outer cortex.

4. Some of the branches grew upwards as tapering aerial stems.

5. The aerial stems bore small lateral projections irregularly scattered over the surface.

6. Some of the projections, possibly in the lower region, developed rhizoids.

7. Some of the projections at various levels on the stem gave rise to adventitious lateral branches.

8. Some of the lateral branches, attached by a narrow base, were readily detachable and probably served for vegetative propagation.

9. Dichotomous branching of the stem occurred sparingly.

10. In the rhizomes and stems, epidermis, outer cortex, inner cortex, and stele can be distinguished.

11. The epidermis in the aerial stems had a thick outer wall and stomata were sparingly present.

12. The cortex consisted of a narrow outer zone, which in the aerial stems had the character of a hypoderma, and a broader inner cortex. The more delicate tissue of the inner cortex had intercellular spaces and was in relation with the stomata. It possibly represented the assimilating tissue.

13. The vascular system consisted throughout of a simple cylindrical stele composed of a slender solid strand of tracheides with broad annular thickenings and no distinction of protoxylem and metaxylem. Surrounding the xylem was a zone of phloem consisting of elongated thin-walled elements.

14. No vascular strands were given off to the small projections on the stem.

15. No vascular connection existed between the stele of a lateral branch and the stele of the parent axis.

16. In the dichotomous branching of the stem the stele divided to supply the two branches.

17. The plant bore large cylindrical sporangia. The sporangium had a thick wall, and terminated a stout stalk which corresponded to a small stem.

18. The sporangium contained numerous spores which were all of one kind.

#### CONCLUDING REMARKS.

The plant which has been described (whatever the precise age of the Old Red Sandstone Beds in which it is found may prove to be) is the most ancient land plant of which the structure is at all fully known. By a fortunate circumstance of its preservation in large quantity as it grew, its external form, structure, and sporangia are known almost as well as if we were dealing with an existing species.

It will be evident that the simplicity of the general organisation and of the anatomy of *Rhynia* has important bearings on the origin of the sporophyte and its differentiation into stem, root, and leaf in the Pteridophyta. While fully alive to the interest of this, we do not propose in the present paper to consider the bearing of the new facts here brought forward on these speculative questions. We hope to consider them later.

In attempting to indicate the position of *Rhynia Gwynne-Vaughani* in the vegetable kingdom, it will be sufficient to briefly compare it on the one hand with

the existing group of the Psilotales, and on the other hand with one less perfectly preserved Devonian plant, *Psilophyton princeps*, Dawson. Even these comparisons will not be developed fully until *Asteroxylon* has been described in the next paper of this series.

The Psilotales, with the two existing genera *Psilotum* and *Tmesipteris*, have always presented difficult morphological problems. They are rootless, the underground parts consisting of rhizomes bearing rhizoids. The leaves are small and without vascular system in *Psilotum*, larger and with a vascular supply in *Tmesipteris*. Their reproductive organs consist of bi- or tri-ocular synangia, subtended by a pair of leaf-like lobes. This fertile structure has been variously interpreted as a bifid sporophyll subtending an adaxial synangium or sporangiophore, or as a lateral branch bearing a pair of leaves and terminating in a synangium.

The Psilotaceæ agree with *Rhynia* and differ from all other Pteridophyta in the absence of roots and (if the second interpretation be accepted) in the position of the synangia terminating a short branch. There is, further, a striking general agreement between *Psilotum* and *Rhynia* in the plant consisting of more or less delicate subterranean rhizomes, bearing a system of xerophytic stems, and in the occurrence of both dichotomous and lateral branching. We also find in the rhizome or in the ultimate branches of *Psilotum* a parallel to the simplicity of the stele of *Rhynia*.

The Psilotaceæ exhibit, however, some important points of difference from *Rhynia*, such as the presence of leaves, the specialisation of the fertile branches or sporophylls, the more complicated anatomy, the synangia, and the shape of the spores.

The comparison will not be carried further at present, but it may be noted in passing that it would lead us to regard the Psilotaceæ as having preserved many primitive characters and not as reduced. On this view the Psilotaceæ would be the little modified survivors in the existing flora of a type of plant that existed in early geological times, the most fully known example of which is now *Rhynia Gwynne-Vaughani*. It does not, however, follow that a direct line of descent is to be drawn between *Rhynia* and the Psilotaceæ as we know them.\*

With regard to the comparison of *Rhynia* with extinct plants, it is only necessary at present to consider *Psilophyton princeps*, Dawson, including under this the variety *ornatum*, which probably merely represents the lower portions of the stems. We take the description of this species as given by DAWSON in the "Fossil Plants of the Devonian and Upper Silurian Formations of Canada," † though the plant has been described by him in several of his other works. The main characters

\* The primitive nature of the general organisation of the Psilotaceæ is clearly held on other grounds by C. Eg. BERTRAND in his *Recherches sur les Tmesipteridées*, Lille, 1883, pp. 313-316; and by LIGNIER in his "Equisétales et Sphénophyllales leur origine filicinéenne commune," p. 95, *Bull. Soc. Linn. de Normandie*, 5<sup>e</sup> sér., vol. vii, 1903, p. 93, Caen.

† *Geological Survey Canada*, Montreal, 1871.

of *Psilophyton princeps*, as we understand it, are shown on pl. ix, figs. 97–110; pl. x, figs. 112–114, 118–120; pl. xi, figs. 127, 128, 133*a*, *b*, *c*, and 134, 134*a*, *b*, *c* of the memoir cited above.\*

*Psilophyton princeps* as thus limited † consisted of upright stems which frequently dichotomised, the weaker branches often appearing as if borne laterally. The stouter stems bore numerous spiny outgrowths but no definite leaves. The growing regions of the stem were circinate coiled. The stems were marked by longitudinal ridges. The finer branches appear to have been destitute of spines. They dichotomised repeatedly, and their ultimate branches terminated in oval sporangia which were borne singly or in pairs.

The material of *Psilophyton princeps* is mainly in the form of impressions. DAWSON has, however, figured a few specimens in which the structure was imperfectly preserved, ‡ and has based a reconstruction § on such remains. The most interesting of these is the axis given natural size in his fig. 133*c*, and magnified in fig. 134. This had a wide cortex and a single central cylinder. Little of the structure of the cortex was preserved, but the central cylinder is figured and described || as consisting of “an axis of scalariform vessels surrounded by a cylinder of parenchymatous cells and by an outer cylinder of elongated woody cells.” DAWSON’S figures are of such interest that they are reproduced in the accompanying text-figs. 1 and 2, together with his description of the figures.

The description of the central bundle of *Psilophyton princeps* as composed of “scalariform vessels” surrounded by “woody fibres” is at first sight difficult to understand, but seems to become intelligible in the light of the imperfectly preserved examples of *Rhynia* described above on page 772.

While we have not seen DAWSON’S original specimens, we venture to interpret his published figures as exhibiting a stem with a stele consisting of a solid strand of tracheides surrounded by a zone of phloem which had become partially decayed and discoloured much as in the specimens of *Rhynia* shown in our Pl. X, figs. 76–78. In particular, DAWSON’S fig. 134 (see text-fig. 2) may be compared with our fig. 77, and his reconstructed fig. 127 (see text-fig. 1) with our fig. 78. DAWSON’S fig. 134*a* suggests that the tracheides in his specimens were annular rather than scalariform.

What DAWSON speaks of as “the outer fibrous cylinder” or “bark fibres” would correspond to the persistent outer cortex of *Rhynia*. The “cellular cylinder” in text-fig. 1 would correspond to the inner cortex; this has almost completely dis-

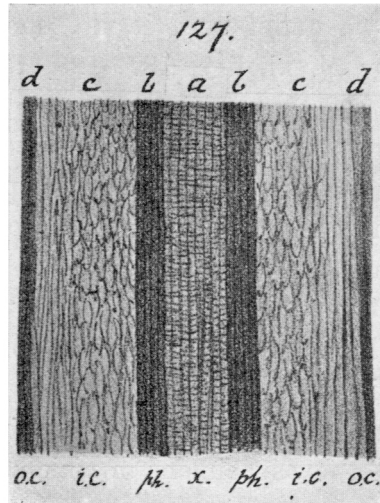
\* It will be observed that we exclude from *Psilophyton princeps* DAWSON’S figures of “rhizomes,” pl. x, figs. 111, 115, 116, and 117. We also exclude at present from *Psilophyton* all the other species which have been referred to it by DAWSON and other writers, as they do not seem to show the characters necessary for their definite reference to this genus.

† The course we adopt is in general agreement with the views of SOLM-LAUBACH, *Fossil Botany*, pp. 189–192, and more recently of P. BERTRAND in “Note préliminaire sur les Psilophytens des grès de Matringhen,” *Ann. Soc. géol. du Nord*, vol. xlii, p. 157, 1913.

‡ *L.c.*, pl. xi, figs. 133 and 134.

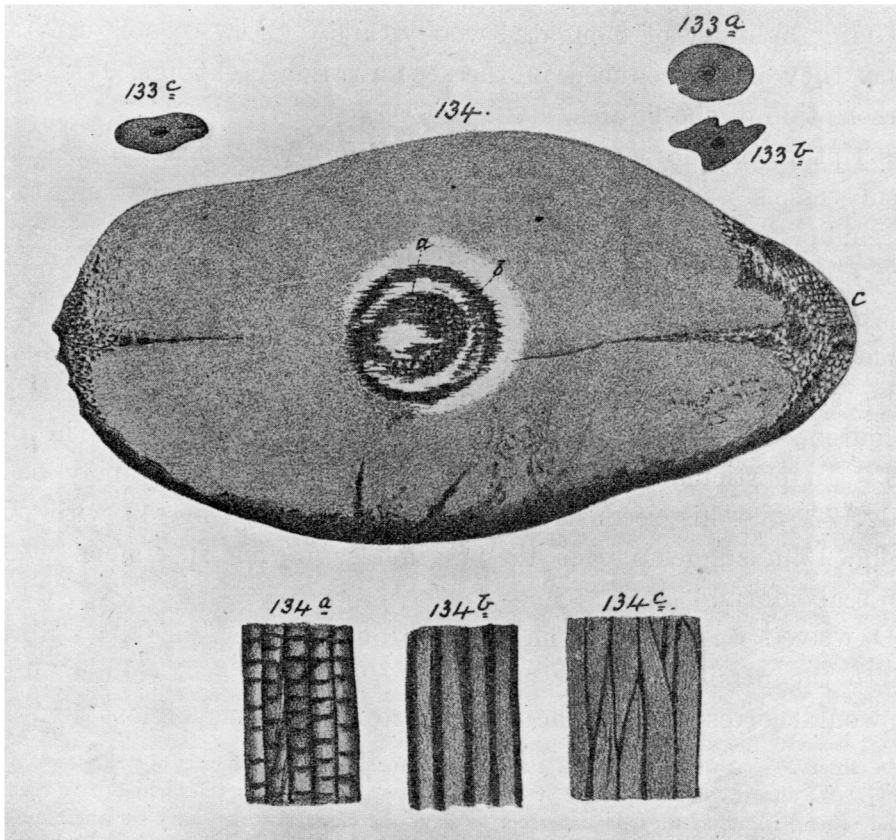
§ *L.c.*, pl. xi, fig. 127.

|| *L.c.*, p. 37.



TEXT-FIG. 1.—*Psilophyton princeps*, Dawson.

“Restored section of magnified stem, showing (a) scalariform axis, (b) woody cylinder, (c) cellular cylinder, (d) outer fibrous cylinder.” (DAWSON, *l.c.*, p. 90, pl. xi, fig. 127 )  
 The letters placed below the figure indicate our interpretation of DAWSON’S reconstruction. *o.c.*, outer cortex ; *i.c.*, inner cortex ; *ph.*, phloem ; *x.*, xylem.



TEXT-FIG. 2.—*Psilophyton princeps*, Dawson.

“FIG. 133.—Rhizoma, transverse sections showing axis. Natural size.  
 “FIG. 134.—The same magnified. 134a, scalariform tissue ; 134b, woody fibres ; 134c, bark fibres. 100 diams.”

appeared in text-fig. 2. The "woody cylinder" or "woody fibres" (*b* in text-figs. 1 and 2) would correspond to the phloem of *Rhynia*, while the "scalariform axis" (*a*, text-figs. 1 and 2) is the equivalent of the central strand of xylem. To make this interpretation clear, we have added letters below text-fig. 1 corresponding to the lettering used throughout our plates. This text-figure may further be compared with the longitudinal sections shown in figs. 26, 42, and 59 of this paper.

If this interpretation be correct, there would be a substantial agreement in structure between *Psilophyton princeps* and *Rhynia Gwynne-Vaughani*. The two plants further agree in bearing large oval sporangia on the ends of ultimate branches of the stem. *Psilophyton princeps* differs from *Rhynia*, however, in the presence of spines, in the more profuse dichotomous branching, in the subordination of some of the branches to a sympodial main axis, and in the absence, so far as we know, of lateral adventitious branches.

On these grounds we regard *Psilophyton* as exhibiting characters which ally it with the more fully known *Rhynia*, and separate these two genera from all other vascular plants. The differences between *Rhynia* and *Psilophyton*, however, warrant their being treated as distinct genera.

It will be clear that *Rhynia* and *Psilophyton* belong to the Vascular Cryptogams or Pteridophyta, but they cannot be placed in any of the Classes of this great group as at present known and defined. These Classes are the *Filicales*, *Equisetales*, *Sphenophyllales*, *Psilotales*, and *Lycopodiales*.

It is therefore necessary to recognise another group of Pteridophyta, of equivalent value to those mentioned, to include *Rhynia Gwynne-Vaughani* and certain of the specimens described under the name of *Psilophyton princeps*. *This Class is characterised by the sporangia being borne at the ends of certain branches of the stem without any relation to leaves or leaf-like organs. For this Class we propose the name Psilophytales.* This name is derived from that of the earlier described though less perfectly known genus *Psilophyton*, and further suggests the resemblance between the plants of this class and the existing *Psilotales*. Whether the other characters in which *Rhynia* and *Psilophyton* seem to agree will prove to be common characters of the whole group, must be left open for the present, but they are not essential for its definition.

## CLASSIFICATION AND DIAGNOSIS.

PSILOPHYTALES: A Class of *Pteridophyta* characterised by the sporangia being borne at the ends of certain branches of the stem without any relation to leaves or leaf-like organs.

*Rhynia Gwynne-Vaughani*, Kidston and Lang, n.g. and n. sp.

*Psilophyton princeps*, Dawson (*pars*).

"Fossil Plants of the Devonian and Upper Silurian Formation of Canada," *Geol. Survey Canada*, 1871, p. 37, pl. ix, figs. 97-110; pl. x, figs. 112-114, 118-120; pl. xi, figs. 127, 128, 133, 134.

## RHYNIA, Kidston and Lang, n.g.

*Diagnosis*.—Aerial stems without leaves or spines but bearing small protuberances; sporangium large, cylindrical, terminal on ultimate branches.

*Rhynia Gwynne-Vaughani*, Kidston and Lang, n. sp.

*Diagnosis*.—Plant gregarious, rootless and leafless. Underground rhizomes with rhizoids, generally situated on large, downwardly directed protuberances of the cortex. Aerial stems cylindrical, tapering upwards, about 8 inches in height, bearing small hemispherical protuberances. Stems sparingly dichotomous and also bearing lateral adventitious branches.

Sporangium large, cylindrical, and terminating an aerial stem. Sporangial wall thick, of many layers of cells. Homosporous, spores developed in tetrads about 65  $\mu$  in diameter.

Stele throughout the plant small, cylindrical, consisting of a solid strand of annular tracheides, surrounded by a zone of thin-walled phloem. Cortex consisting of an inner and outer zone. Epidermis of aerial stems with cuticularised outer wall and stomata.

*Locality*.—Muir of Rhynie, Aberdeenshire.

*Horizon*.—Old Red Sandstone (not younger than the Middle Division of the Old Red Sandstone of Scotland).

In conclusion, we wish to express our thanks to Dr W. MACKIE, Elgin, for placing his slides in our hands for description as well as supplying us with material; to Dr J. S. FLETT, F.R.S., Director of the Geological Survey of Scotland, for kind assistance; and to Mr D. TAIT for much help given when examining the chert band at Rhynie.

We also gratefully acknowledge our indebtedness to the Executive Committee of the Carnegie Trust for a grant towards defraying the expense of the plates illustrating this memoir.



## EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

*Rhynia Gwynne-Vaughani*, Kidston and Lang.

## PLATE I.

Fig. 1. Vertical surface of a block from the chert band (E 10 of section on page 762), etched with hydrofluoric acid to render the plant-remains more distinct. The dark layers *s, s* and *s', s'* are silicious sandstone with carbonaceous matter. From *s, s* to the base of the block and between *s, s* and *s', s'* are two layers of the silicified peat (P 1, P 2) composed of the remains of *Rhynia Gwynne-Vaughani*. The structure of some of the larger stems is clearly shown, especially in the lower layer of peat. Natural size. (No. 5282.)

## PLATE II.

Fig. 2. Portion of the vertical surface of a block of the Rhynie chert which had been weathered naturally. The rounded stems of *Rhynia* stand in low relief from the surface. Up to the level *a-a*, which marks an original land surface, the stems lie horizontally in the silicified peat, but above this level they are seen to become vertical. Natural size.

Fig. 3. Portion of the horizontal surface of another block of the Rhynie chert showing the crowded stems of *Rhynia* flattened down and compressed. Natural size. (No. 5283.)

Fig. 4. A small portion of fig. 3 enlarged. At *a* and at other places the narrow ribbon-shaped compressed stems show a raised median line marking the position of the stele.  $\times 2$ . (No. 5283.)

Fig. 5. A loose block of the Rhynie chert, etched with hydrofluoric acid and viewed from the side. The lower portion up to the level of the old land surface *a, a* shows remains of *Rhynia* lying in all directions in the silicified peat. From this level to the summit of the block the tapering aerial stems can be followed bending over to the right. Natural size.

## PLATE III.

Fig. 6. Small stem exposed on a fractured surface of the chert showing the rounded form of the stem and the epidermal cells which in this case have no median line.  $\times 14$ . (No. 5286.)

Fig. 7. Similar specimen showing a number of the small projections or bulges. The epidermal cells in this and the following figure have the median ridge.  $\times 14$ . (No. 5284.)

Fig. 8. Hollow impression from which the stem has been removed showing the epidermis and three of the small projections.  $\times 14$ . (No. 5285.)

Fig. 9. Portion of a vertical section through the peat. The stems in the lower part are more compressed and decayed, while those above are uncompressed and separated more widely by interstitial matter.  $\times 5\frac{1}{2}$ . (Slide No. 2410.)

Fig. 10. Portion of a similar vertical section through the silicified peat showing still more marked decay and crushing of the stems at *a* and *b*.  $\times 5\frac{1}{2}$ . (Slide No. 2388.)

Figs. 11-12. Enlargements of portions of fig. 13, Pl. IV. For description see explanation to fig. 13.

## PLATE IV.

Fig. 13. Portion of section through peat composed of much decayed stems in which three rhizomes are shown in their natural position. On the downwardly directed sides of all the rhizomes the epidermis and outer cortex show increased development, which in the case of the longitudinal section is seen to have resulted in the formation of two definite rhizoid-bearing bulges, *a* and *b*. A portion of the bulge *a* is more highly magnified in fig. 11, Pl. III, and of the bulge *b* in fig. 12. These figures, and especially fig. 11, show the origin of the bulge by increased growth and division of cells of the epidermis and outer cortex. *a.c.*, outer cortex; *i.c.*, inner cortex. Fig. 13,  $\times 14$ . Figs. 11-12,  $\times 60$ . (Slide No. 2412.)

Fig. 14. Transverse section of a rhizome attached to the peat by rhizoids (*rh.*), and sending up an aerial stem. Close to the base of the latter at *st.* a stoma was recognised.  $\times 20$ . (Slide No. 2396.)

Fig. 15. Small rhizome preparing to branch, the xylem of the stele having divided.  $\times 20$ . (Slide No. 2396.)

Fig. 16. Tangential section showing the isodiametric epidermal cells of a rhizome in surface view. *rh.*, rhizoids.  $\times 60$ . (Slide No. 2396.)

Fig. 17. Two rhizomes in the peat in transverse section. Further description in text.  $\times 14$ . (Slide No. 2396.)

Fig. 18. Section through a rhizoid-bearing bulge of another rhizome showing the long non-septate rhizoids extending downward into the peat. *rh.*, rhizoids.  $\times 28$ . (Slide No. 2411.)

Fig. 19. Transverse section of rhizome.  $\times 60$ . *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem. (Slide No. 2396.)

#### PLATE V.

Fig. 20. Section through chert showing cylindrical aerial stems in an almost pure silicious matrix free from foreign vegetable matter.  $\times 9$ . (Slide No. 2408.)

Figs. 21-25. Transverse sections of aerial stems of different diameters.  $\times 20$ . The various regions of the stem distinguished by lettering in figs. 21 and 23 can also be recognised in the other figures. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem. Fig. 21 (Slide No. 2398). Fig. 22 (Slide No. 2398). Fig. 23 (Slide No. 2397). Fig. 24 (Slide No. 2399). Fig. 25 (Slide No. 2416).

Fig. 26. Portion of a longitudinal section of an aerial stem. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem; *pr.*, small projection.  $\times 20$ . (Slide No. 2390.)

Fig. 27. Transverse section of an aerial stem showing three projections. *pr.*, projections.  $\times 20$ . (Slide No. 2406.)

Figs. 28-29. Transverse sections of two stems showing small projections bearing rhizoids. *pr.*, projections; *rh.*, rhizoids.  $\times 20$ . (Slide No. 2389.)

Fig. 30. Transverse section of an aerial stem showing the stele dividing preparatory to dichotomous branching.  $\times 20$ . (Slide No. 2392.)

#### PLATE VI.

Fig. 31. Epidermis in surface view showing the form of the cells and the dark median line.  $\times 60$ . (Slide No. 2390.)

Fig. 32. Stoma with surrounding epidermal cells in surface view; median line absent. *Cf.* fig. 31.  $\times 160$ . (Slide No. 2394.)

Fig. 33. Stoma in transverse section showing the two guard cells and the pore.  $\times 160$ . (Slide No. 2408.)

Fig. 34. Transverse section of the epidermis and the underlying tissues in the neighbourhood of a stoma. *st.*, stoma; *ep.*, epidermis; *o.c.*, outer cortex interrupted beneath stoma; *i.c.*, inner cortex extending outwards to beneath stoma.  $\times 160$ . (Slide No. 2405.)

Fig. 35. Epidermis and underlying tissues in two adjacent stems. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex.  $\times 60$ . (Slide No. 2405.)

Fig. 36. Transverse section showing the cuticular ridges of the epidermal cells. *Cf.* fig. 31.  $\times 60$ . (Slide No. 2389.)

Fig. 37. Longitudinal section through the epidermis and outer cortex in the region of a stoma (*st.*). The inner cortex which filled the interruption in the outer cortex has decayed.  $\times 60$ . (Slide No. 2395.)

Fig. 38. Transverse section showing the rounded cells and intercellular spaces of the inner cortex.  $\times 60$ . (Slide No. 2398.)

Fig. 39. Transverse section of inner cortex showing the cell contents partially preserved.  $\times 160$ . (Slide No. 2395.)

Fig. 40. Transverse section of an aerial stem. *ep.*, epidermis; *o.c.*, outer cortex, not well marked; *i.c.*, inner cortex with large intercellular spaces; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2397.)

#### PLATE VII.

Fig. 41. Transverse section of stem with well-marked stele. *ph.*, phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2392.)

Fig. 42. Portion of longitudinal section of stem shown in fig. 26 more highly magnified. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2390.)

Fig. 43. Longitudinal section of stele of the upper region of an aerial stem. *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem.  $\times 60$ . (Slide No. 2415.)

Fig. 44. Transverse section of small stele to show the phloem. *ph.*, phloem; *x.*, xylem.  $\times 160$ . (Slide No. 2391.)

Fig. 45. Transverse section of xylem of stele represented in fig. 41. *ph.*, phloem; *x.*, xylem.  $\times 160$ . (Slide No. 2391.)

Fig. 46. Transverse section of the stele of the small stem shown in fig. 25. *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem consisting of two tracheides.  $\times 160$ . (Slide No. 2416.)

Figs. 47 and 48. Longitudinal sections of the xylem showing the broad annular thickening of the walls of the tracheides.  $\times 250$ . Fig. 47 (Slide No. 2403). Fig. 48 (Slide No. 2400).

Fig. 49. Part of an oblique section of an aerial stem showing the epidermis (*ep.*) in surface view, and also a surface view of one of the small projections (*pr.*).  $\times 60$ . (Slide No. 2390.)

Figs. 50 and 51. Two longitudinal sections passing through small projections. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex.  $\times 60$ . Fig. 50 (Slide No. 2390). Fig. 51 (Slide No. 2415).

#### PLATE VIII.

Figs. 52, 53, and 54. Examples of small projections (*pr.*) bearing rhizoids (*rh.*) shown in transverse sections of stems. Figs. 52-53,  $\times 60$ . Fig. 54,  $\times 160$ . (Slide No. 2389.)

Fig. 55. Transverse section of a stem showing two projections (*pr.*) and a partially separated branch (*br.*) which is leaving a scar (*sc.*).  $\times 60$ . (Slide No. 2413.)

Fig. 56. Obliquely transverse section of a stem bearing a lateral branch (*br.*) attached by a fairly broad base. The adventitious branch appears to be itself branching. *x.*, xylem of parent stem; *x'*, xylem of branch.  $\times 20$ . (Slide No. 2409.)

Fig. 57. Transverse section of stem with an adventitious branch (*br.*) attached by a fairly narrow base. *x.*, xylem of parent stem; *x'*, xylem of branch.  $\times 20$ . (Slide No. 2402.)

Fig. 58. Longitudinal section from the higher region of the stem showing on the right a branch (*br.*) with a fairly wide base, while on the left the base of another branch is cut obliquely.  $\times 20$ . (Slide No. 2414.)

Fig. 59. Longitudinal section, becoming oblique on the left, of a stem with well-marked tissues. The branch (*br.*) is attached by a broad base. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem of parent stem; *x'*, xylem of branch.  $\times 20$ . (Slide No. 2401.)

Fig. 60. Transverse section of a stem with a small projection (*pr.*) and a branch (*br.*) attached by a very narrow base. The branch has no stele, and a transverse section of another small axis without a stele lies beside it.  $\times 60$ . (Slide No. 2413.)

Fig. 61. Median longitudinal section of a stem showing at *br'* and *br''* the bases of two lateral branches. No vascular connection exists between these and the parent axis. *x.*, xylem of parent axis; *x'*, xylem of one of the branches.  $\times 20$ . (Slide No. 2404.)

#### PLATE IX.

Fig. 62. Slightly tangential longitudinal section of a sporangium terminating a fairly stout stem. The sporangium, which is filled with an enormous number of spores, is lying in the peat.  $\times 5\frac{1}{2}$ . (Slide No. 2393.)

Fig. 63. Small empty sporangium (*sp.*) borne on a slender stem (*ax.*) and lying in the peat.  $\times 5\frac{1}{2}$ . (Slide No. 2392.)

Fig. 63A. The sporangium shown in fig. 63 more highly magnified. *ep.*, thick-walled epidermis; *tap.*, tapetal layer; *x.*, xylem of axis; *a*, accidentally contracted junction of axis and base of sporangium.  $\times 20$ . (Slide No. 2392.)

Fig. 64. Longitudinal section of another sporangium showing the pointed apex.  $\times 7$ . (Slide No. 2396.)

Fig. 65. Two sporangia (*s.* and *s'*) cut transversely as they lay side by side in the peat.  $\times 14$ . (Slide No. 2411.)

Fig. 66. Portion of the sporangium *s.* in fig. 65 more highly magnified. *ep.*, thick-walled epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum; *sp.*, spores.  $\times 60$ . (Slide No. 2411.)

Fig. 67. Portion of the wall of the sporangium in fig. 62 more highly magnified. *ep.*, thick-walled epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum; *sp.*, spores.  $\times 60$ . (Slide No. 2393.)

Fig. 68. Transverse section of another sporangium. *ep.*, thick-walled epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *sp.*, spores.  $\times 14$ . (Slide No. 2395.)

Fig. 69. Section through the silicified peat passing transversely a sporangium (*s.*) and an axis which bore another sporangium. The axis is shrivelled and altered, but in a manner characteristic of *Rhynia*. *c.*, cortex of axis; *v.s.*, vascular strand.  $\times 11$ . (Slide No. 2421.)

PLATE X.

Fig. 70. Spores, some still united in tetrads, from the sporangium shown in fig. 68.  $\times 160$ . (Slide No. 2395.)

Fig. 71. Spores free in the silicified peat, one showing the triradiate marking.  $\times 160$ . (Slide No. 2395.)

Fig. 72. Adventitious branch widening out from very narrow base and occurring free in the silicified peat.  $\times 33$ . (Slide No. 2406.)

Fig. 73. Transverse section of small stem without any stele.  $\times 60$ . (Slide No. 2391.)

Fig. 74. Transverse section of stem, the cortical cells of which are of larger size in one sector than elsewhere.  $\times 20$ . (Slide No. 2392.)

Fig. 75. Transverse section of large stem showing commencing decay of the inner and persistence of the outer cortex.  $\times 20$ . (Slide No. 2387.)

Fig. 76. Transverse section of a partially decayed stem. *o.c.*, remains of outer cortex; *ph.*, phloem; *x.*, xylem. The space marked *i.c.* was originally occupied by inner cortex.  $\times 60$ . (Slide No. 2393.)

Fig. 77. Transverse section of a similar stem to that in fig. 76, but with the inner portion of the phloem broken down. Lettering as in fig. 76.  $\times 60$ . (Slide No. 2393.)

Fig. 78. Longitudinal section of the stele of a partially decayed stem; the xylem (*x.*) has lost its thickenings, while the phloem (*ph.*) has assumed a dark colour.  $\times 60$ . (Slide No. 2395.)

(All the figured specimens are in the collection of Dr R. KIRSTON.)





1.





*a.*

2.



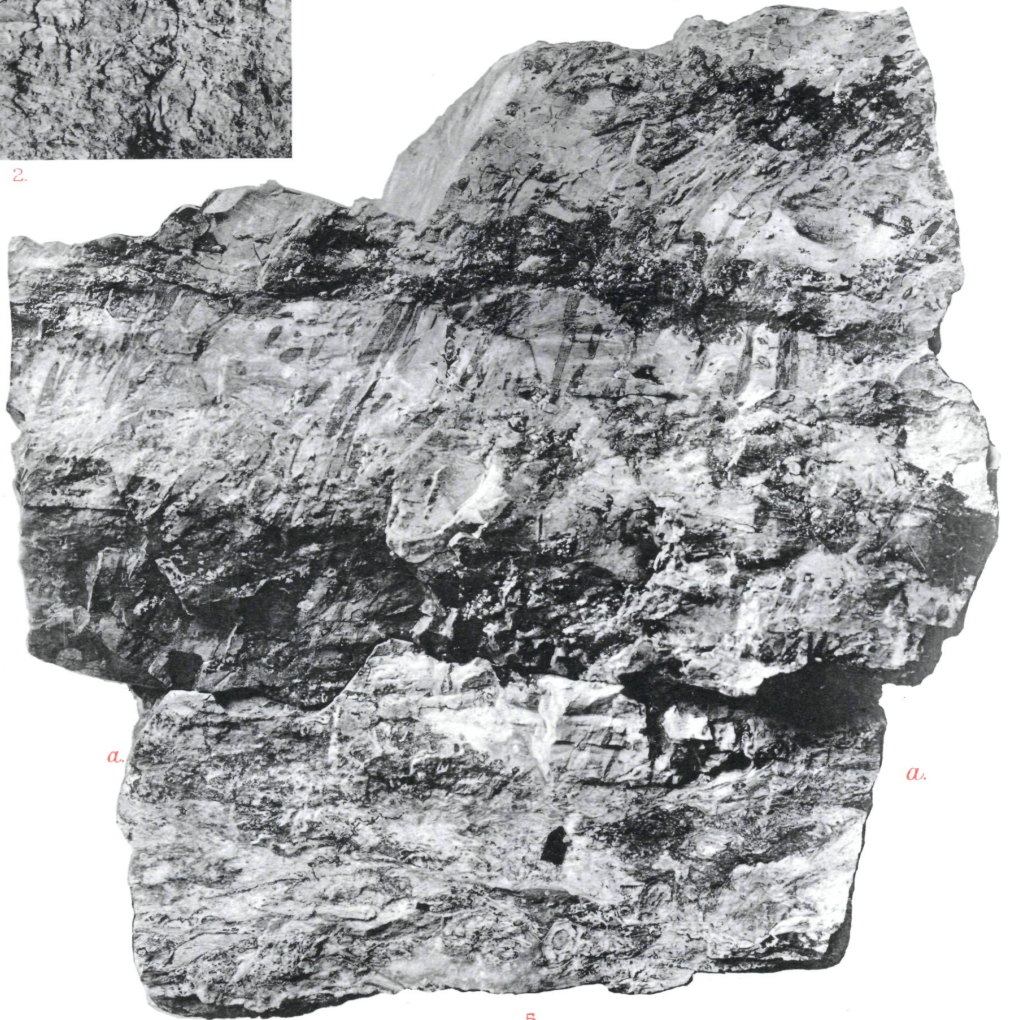
*a.*

3.



*a.*

4.

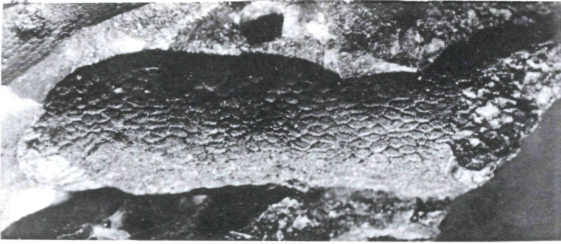


*a.*

*a.*

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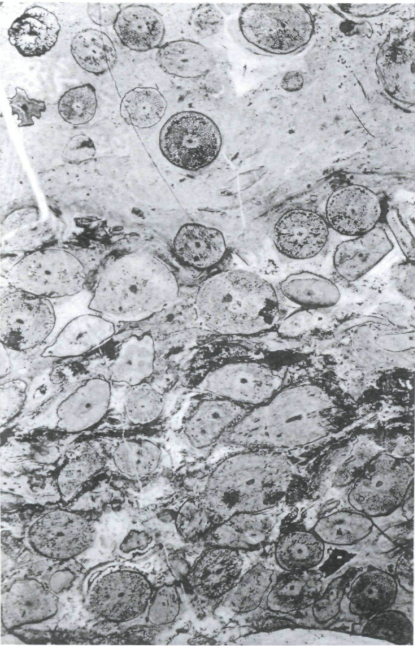




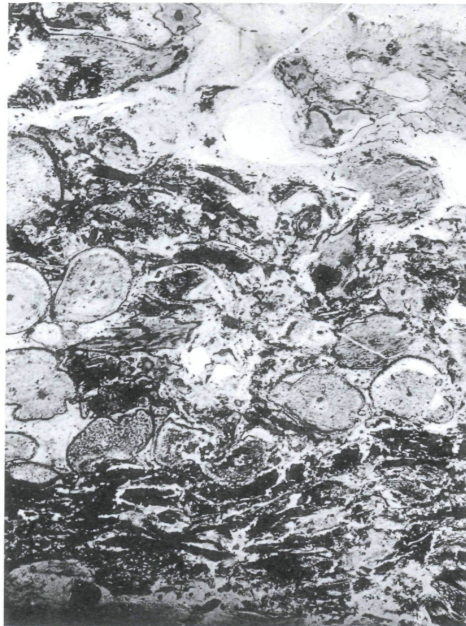
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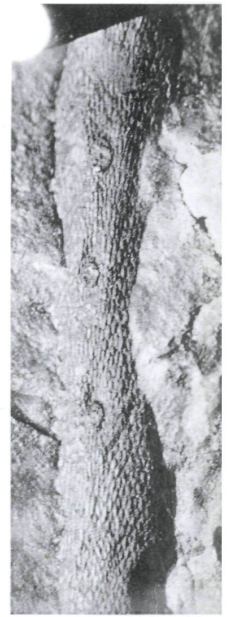
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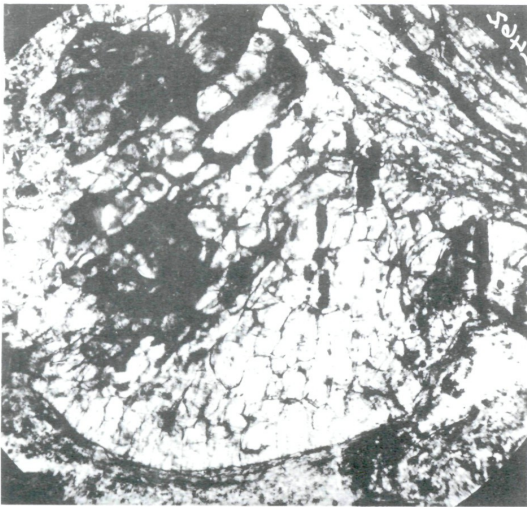
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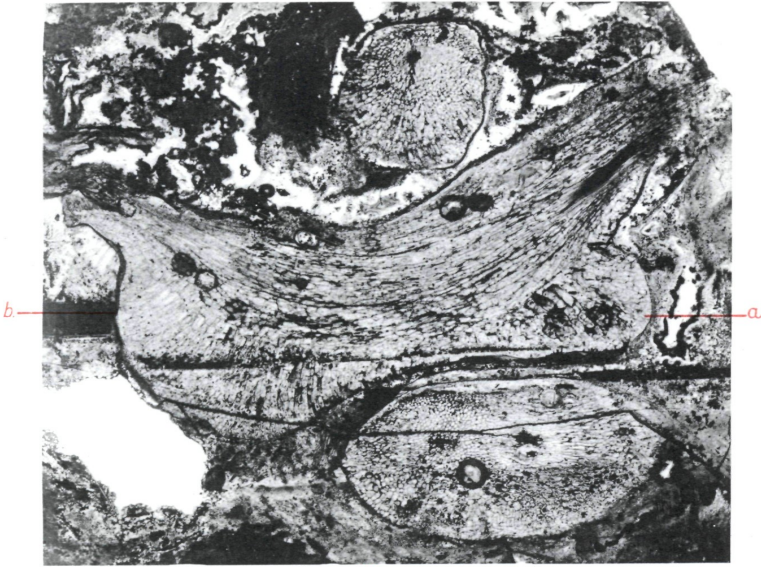


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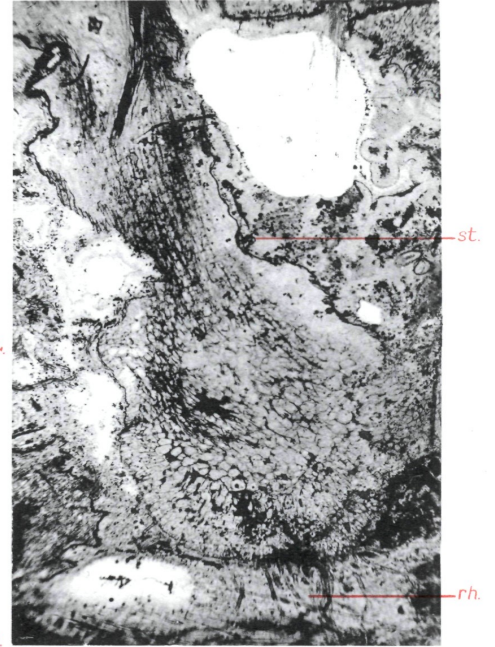
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Bemrose, Colln., Derby.

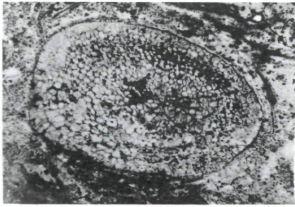




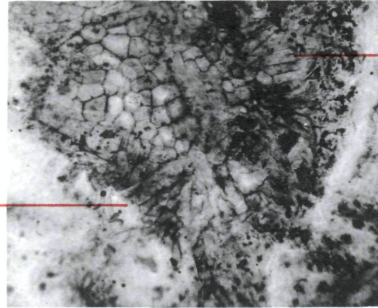
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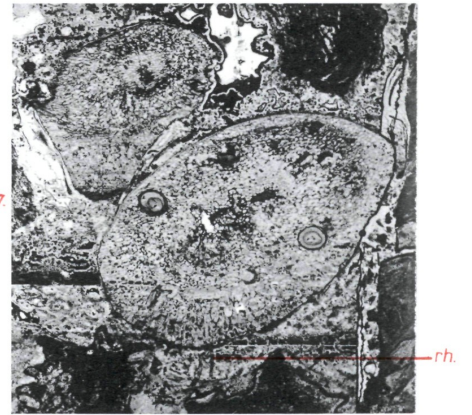
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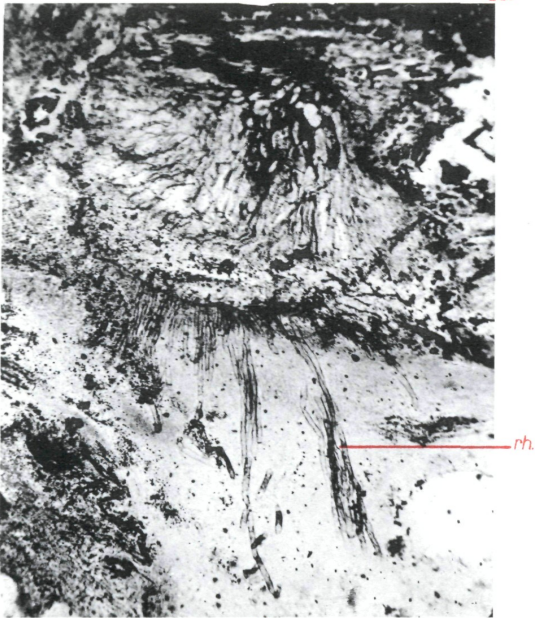
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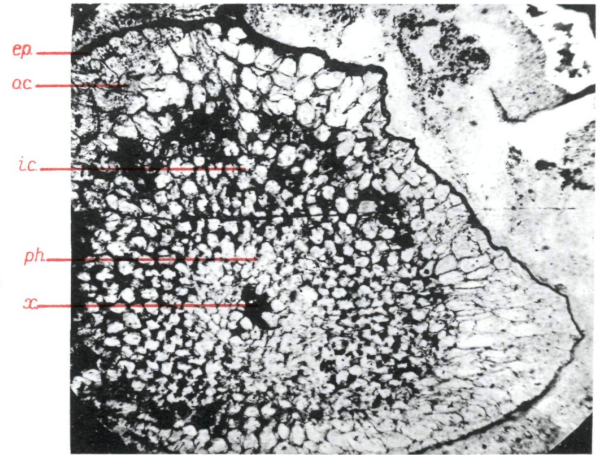
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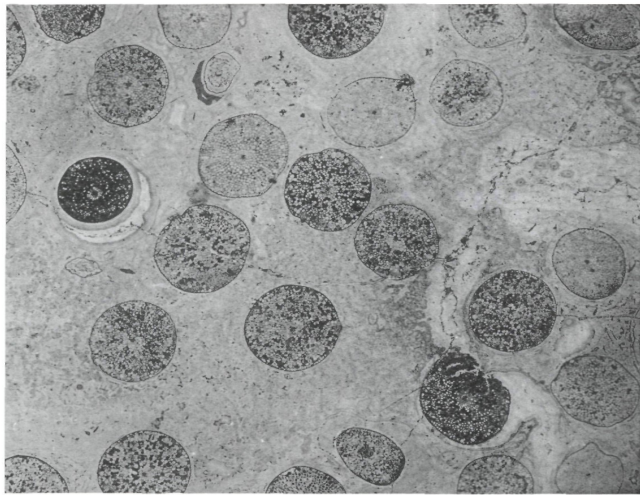


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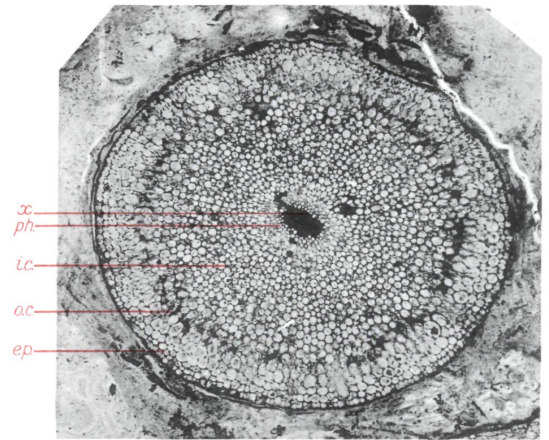


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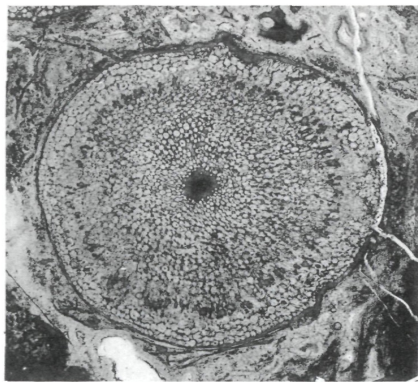




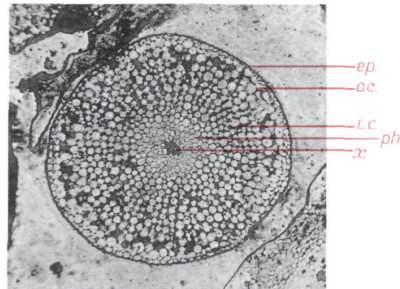
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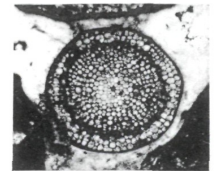
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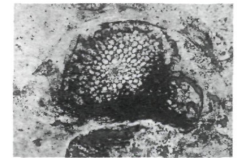
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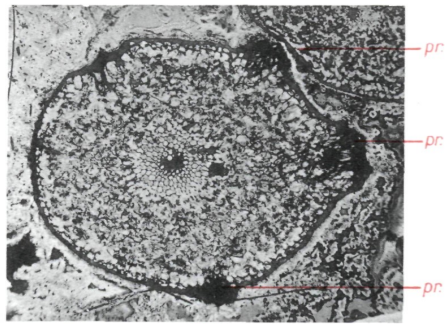
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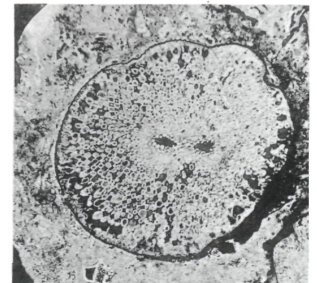
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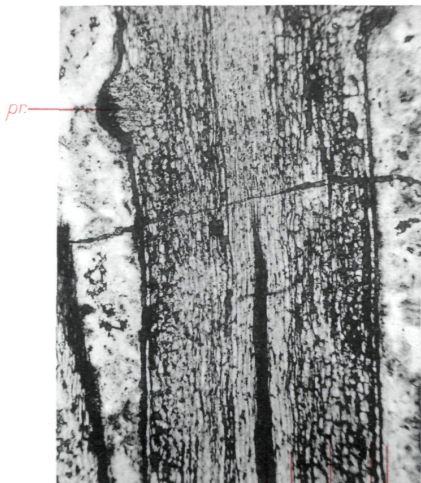
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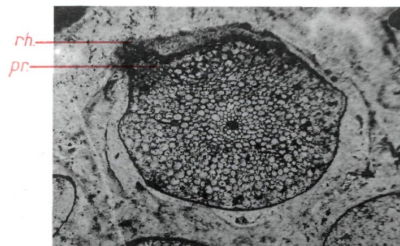
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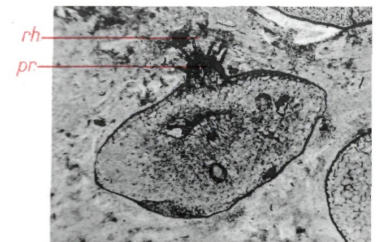
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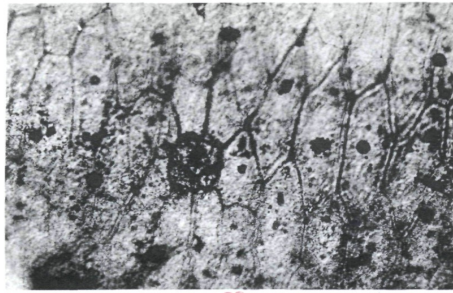
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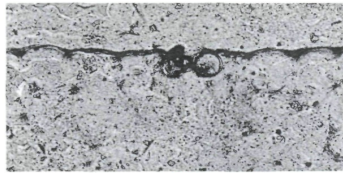




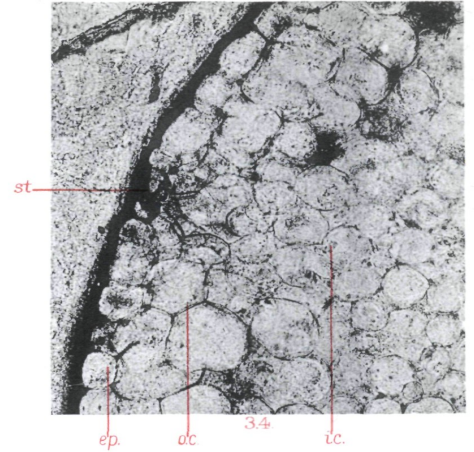
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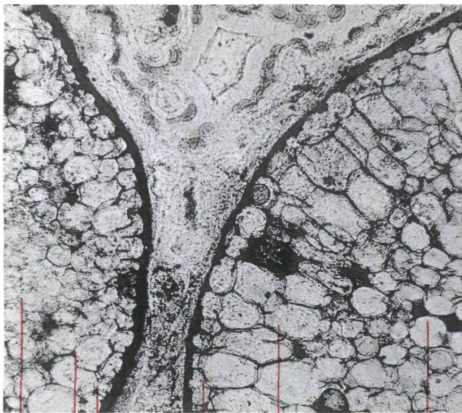
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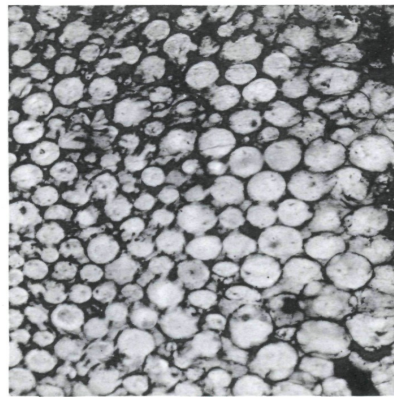
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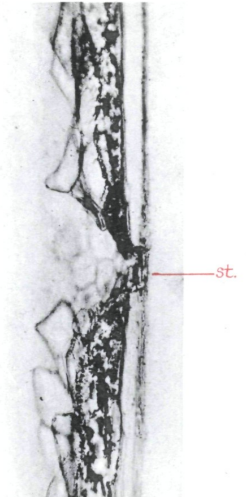
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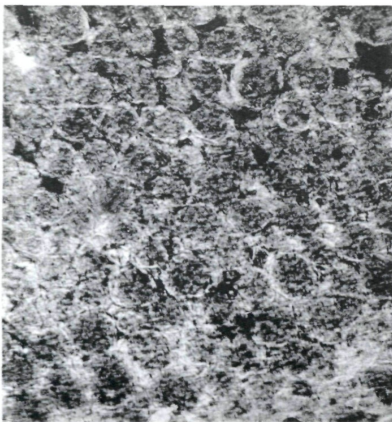


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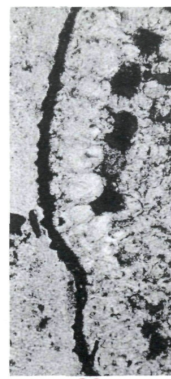


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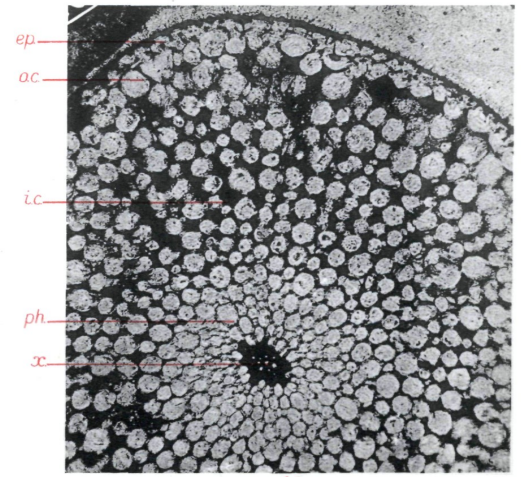
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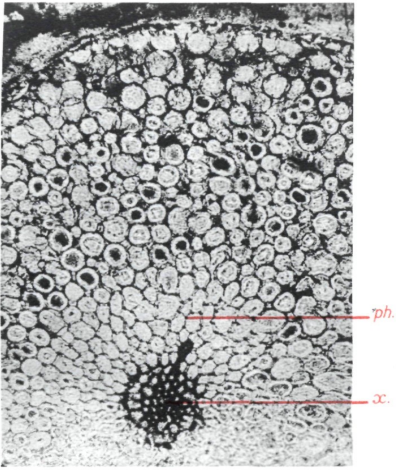
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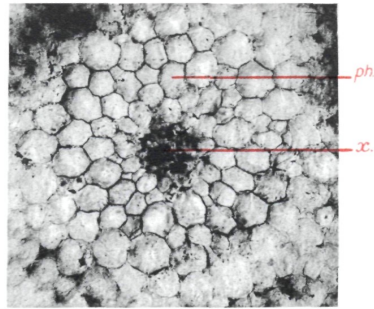
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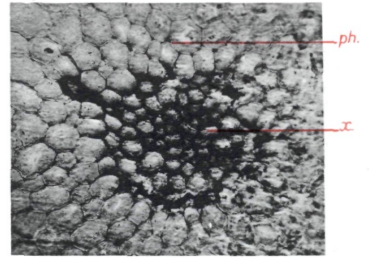




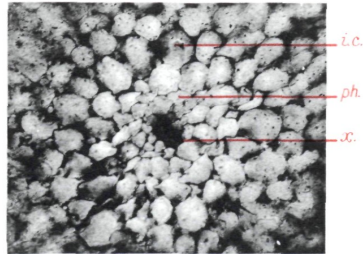
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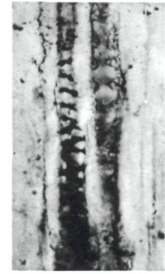
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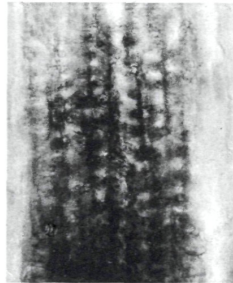
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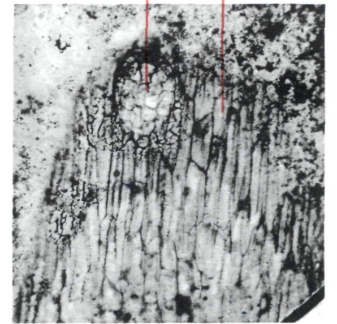
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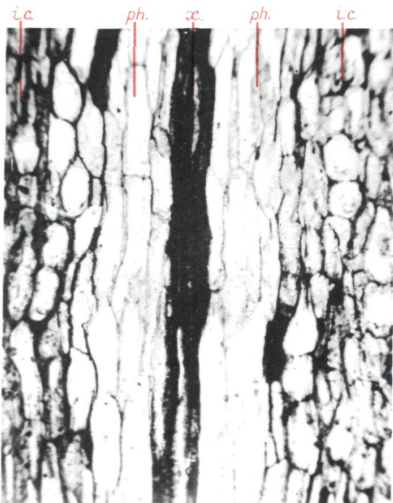
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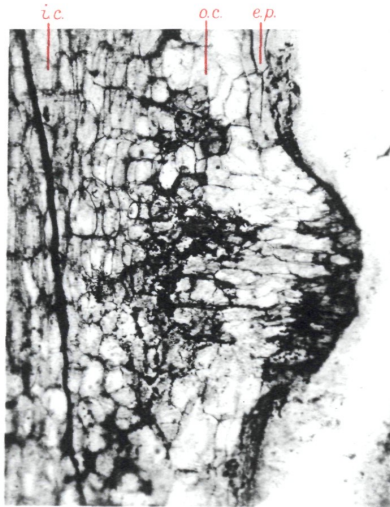
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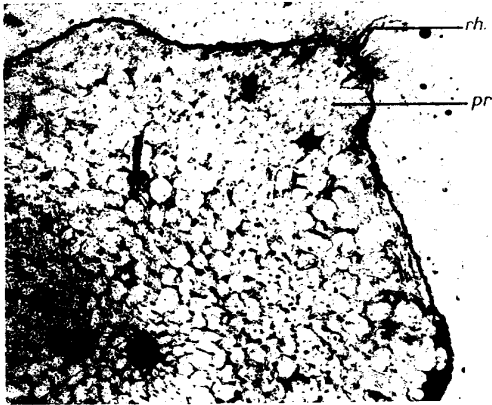
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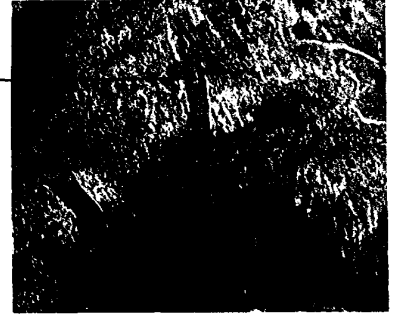
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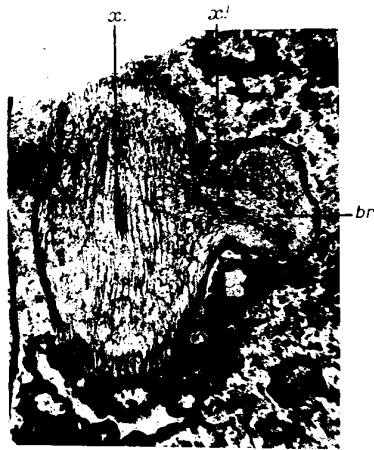
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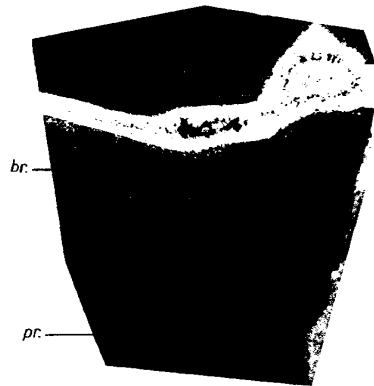
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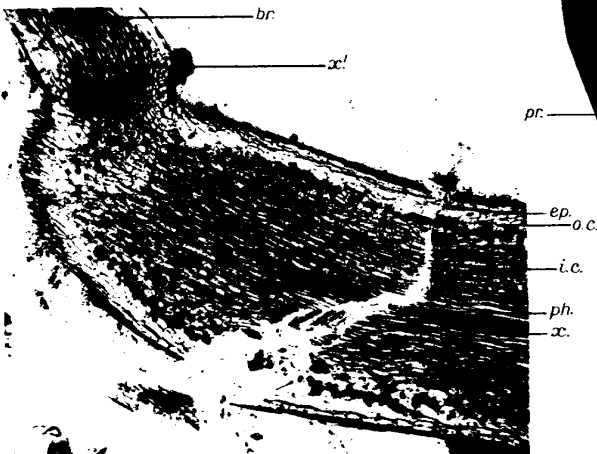
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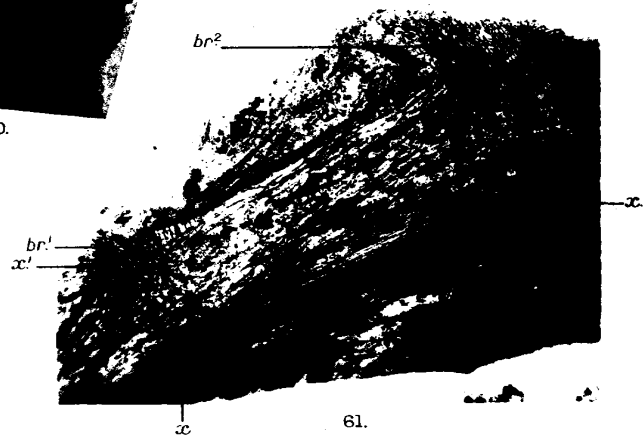
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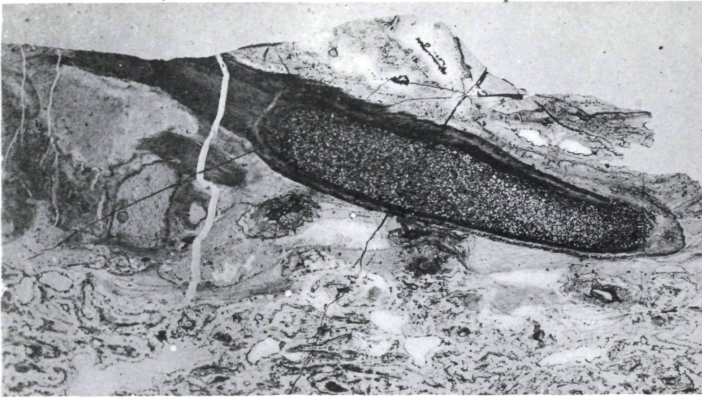


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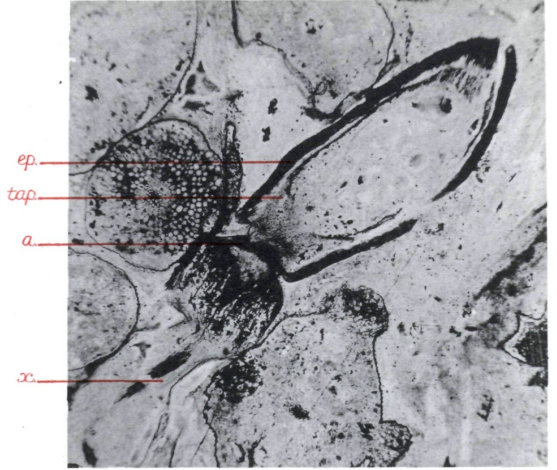
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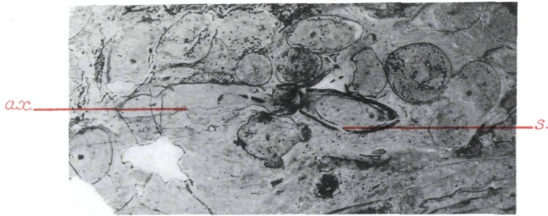




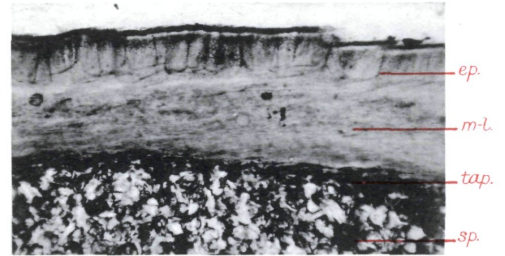
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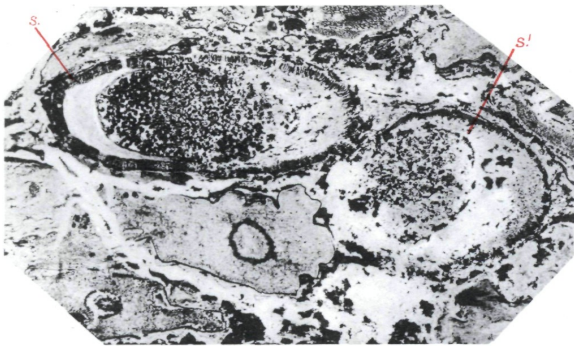
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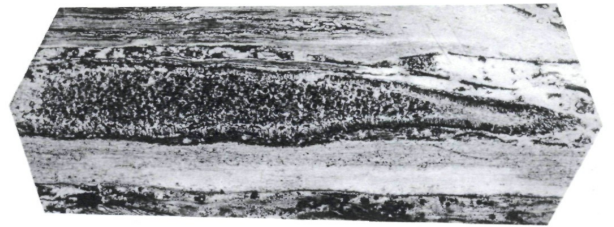
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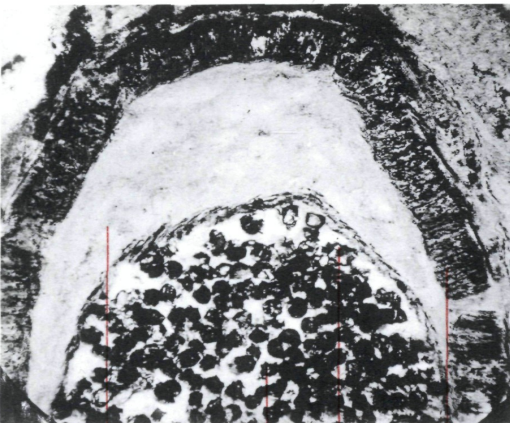
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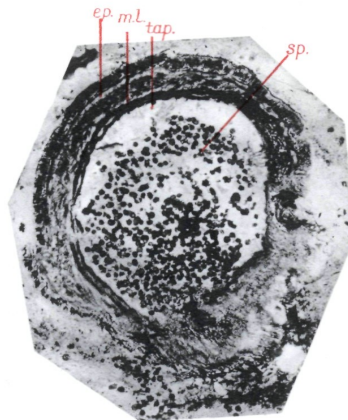
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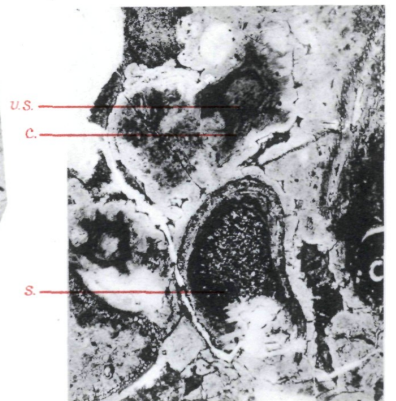
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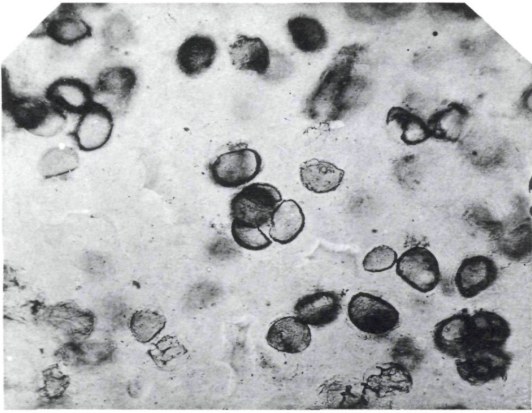


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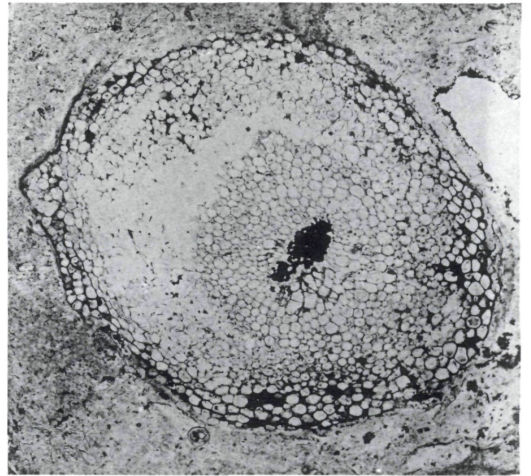
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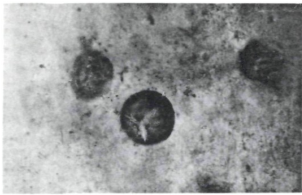




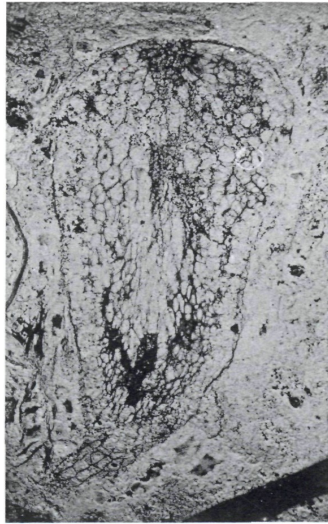
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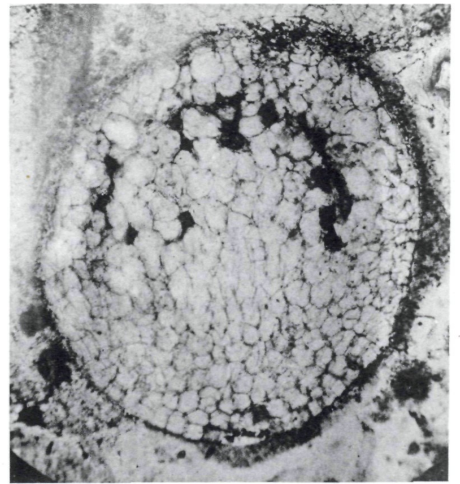
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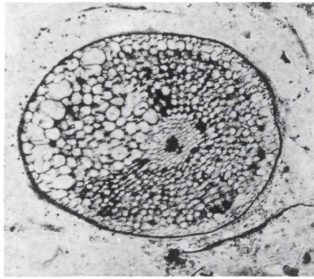
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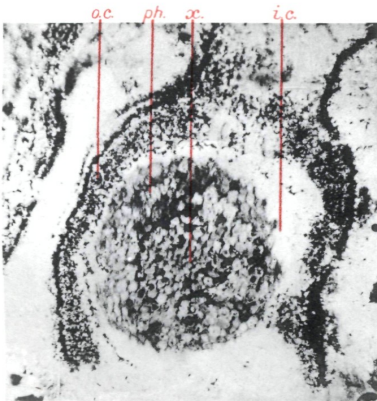
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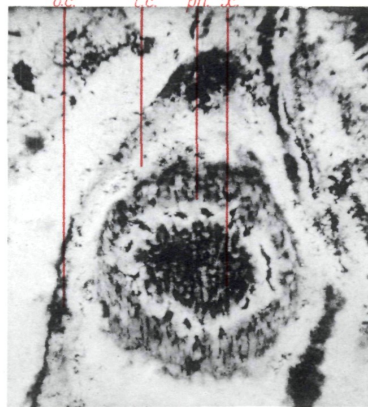
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R. Kidston, Photo.

Bamrose Collis Derby