XXIV.—On Old Red Sandstone Plants showing Structure, from the Rhynie Chert Bed, Aberdeenshire. Part II. Additional Notes on Rhynia Gwynne-Vaughani, Kidston and Lang; with Descriptions of Rhynia major, n.sp., and Hornea Lignieri, n.g., n.sp.

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Transactions of the Royal Society of Edinburgh / Volume 52 / Issue 03 / September 1920, pp 603 - 627
DOI: 10.1017/S0080456800004488, Published online: 06 July 2012

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(Read July 8, 1918. MS. received May 17, 1919. Issued separately January 20, 1920.)

Introduction.

In Part I* a general account was given of the silicified peat-bed found at Rhynie, and one vascular plant was described in detail under the name of *Rhynia Gwynne-Vaughani.* Further study has shown that there are two species of *Rhynia* which we now distinguish as *Rhynia Gwynne-Vaughani* and *Rhynia major.* The account in Part I applies to both these species. Along with them there occurs a plant of similar grade of organisation to *Rhynia,* though quite distinct from that genus: this we name *Hornea Lignieri. Asteroxylon Mackiei,* on the other hand, which will be described in the next part, was a plant of larger size and much more complex morphology.

We are thus now able to establish the existence and main features of four archaic Vascular Cryptogams from the Rhynie bed. In the present paper additional notes on *R. Gwynne-Vaughani* are given, and *R. major* and *Hornea Lignieri* described in detail. In conclusion, the morphological bearings of the facts will be briefly considered.

Our former paper was based mainly on sections prepared from loose blocks of the chert, and partly from specimens collected from the chert bed *in situ.* The material for the present paper was mostly obtained in position in the chert bed, though a few loose blocks have yielded valuable information.

Rhynia.

As mentioned above, two species of *Rhynia* have to be distinguished. Their similarity in organisation is so great that they are not always readily separated from one another, and in our former paper they were described together under the name *Rhynia Gwynne-Vaughani.* The second species, which we now separate as *Rhynia major,* is larger in all its parts, and differs from *R. Gwynne-Vaughani* in the absence of hemispherical projections and adventitious branches from the stems, in the greater size of the stele and xylem strand, and in the much larger size of the sporangia and spores.

* *Trans. Roy. Soc. Edin.,* vol. li, 1917, p. 761.

The difficulty of sharply distinguishing particular fragments of these two plants is in no way inconsistent with the opinion we have been led to form, that they are distinct but closely allied species. Their comparative study is assisted by certain beds or loose blocks containing the remains of only one or the other species. The difference in size of the two plants will be evident on comparing the block of chert represented of natural size in Pl. I, fig. 1, with the figs. 2 and 5 on Pl. II of our former paper. The peat in fig. 1 is composed of stems of *R. major*, many of which have a diameter of 5 mm., while the stems of *R. Gwynne-Vaughani* in figs. 2 and 5 are about 2 mm. in diameter.

Although we were dealing with mixed material of two species, which we now know separately, the description of the plant and its differentiation into rhizome, stems, and sporangia given in Part I holds good for both species of the genus *Rhynia*. It has only to be qualified by recognising the specific differences to be dealt with below. It will be convenient at this stage, however, to review the illustrations to our former paper and to indicate which belong to *R. Gwynne-Vaughani* and which to *R. major*.

All the figures on Pl. II are of *R. Gwynne-Vaughani*, as are also figs. 6–10 on Pl. III, fig. 20 and figs. 23–30 on Pl. V, all the figures on Pl. VI except fig. 37, and all the figures on Pls. VII and VIII. The sporangium in figs. 63 and 63A on Pl. IX is the only one figured that belongs to this species. Figs. 72–74 on Pl. X are small stems of this species. A survey of the figures named shows that the general habit and size of *R. Gwynne-Vaughani*, the external features of the stems, the details of structure of the stems, the hemispherical projections and the occurrence in their place of adventitious branches, and the sporangium were represented. The transverse section of a stem in Dr Mackie's paper,* which was the first figure of *Rhynia* published, also belongs to this species.

To *R. major*, on the other hand, we now refer fig. 1 on Pl. I, showing a block of the chert with the stems of natural size; all the figures of rhizomes on Pl. IV (figs. 13–19), with the details in figs. 11 and 12 of the preceding plate; the large stems in figs. 21 and 22 † of Pl. V; the outer cortex and stoma in fig. 37 on Pl. VI; the large sporangia in figs. 62 and 64–69 on Pl. IX; the spores in figs. 70 and 71 of Pl. X; and the partially decayed stems in figs. 76–78 of the same plate.‡ Consideration of these figures will show that the rhizomes, stems, and sporangia of *R. major* were represented, though the detailed account of the structure of the stem is based on *R. Gwynne-Vaughani*. On the other hand, all the rhizomes described and figured in Part I are of *R. major*, and the description of the sporangium is mainly based on this species.

The rhizomes figured on Pl. IV of Part I all occurred in one block of silicified

* *Trans. Edin. Geol. Soc.*, vol. x, 1913, pl. xxii, fig. 5.

† The magnification of figs. 21 and 22 on Pl. V of Pt. I was erroneously given as 20 diameters. These stems are magnified about 14 diameters.

‡ To complete this survey of the illustrations to Part I, it should be stated that the poorly preserved specimen in fig. 75 of Pl. X does not belong to *Rhynia*, but to *Asteroxylon*.

peat, composed of partly decayed stems of *R. major*, with sporangia of that species, and were evidently preserved as they grew at one level of the peaty mass. The presumption is that they belong to *R. major* and not to *R. Gwynne-Vaughani*, no stems of which are found in this block. This conclusion, though confirmed by some details, would be difficult without the evidence afforded by association. Rhizomes of *R. major* have, however, now been met with in other blocks, and rhizomes of similar type, though smaller, which undoubtedly belong to *R. Gwynne-Vaughani* will be described below.

Additional Notes on Rhynia Gwynne-Vaughani, Kidston and Lang. (Pl. I.)

1917. *Rhynia Gwynne-Vaughani*, Kidston and Lang (*pars*), *Trans. Roy. Soc. Edin.*, vol. li, p. 761, pl. ii, figs. 2–5; pl. iii, figs. 6–10; pl. v, figs. 20, 23–30; pl. vi, figs. 31–36, 38–40; pl. vii, figs. 41–51; pl. viii, figs. 52–61; pl. ix, figs. 63–63A; pl. x, figs. 72–74.

Many of the features of *R. Gwynne-Vaughani* were sufficiently described and illustrated in Part I, and only some supplementary notes are required.

Since there is reason to regard all the rhizomes described in Part I as of *R. major*, a rhizome belonging to *R. Gwynne-Vaughani* is figured here (Pl. I, fig. 1). The rhizome, which is cut transversely, has given off laterally an ascending stem. This rhizome has a thin-walled epidermis, a slight but evident distinction between outer and inner cortex, and a small stele, the xylem of which consists of about four tracheides. Rhizoids extend downwards into the peat from the epidermis of the lower side of the rhizome. The ascending branch shows epidermis, cortex, phloem, and xylem; it agrees in size and structure with the typical stems of *R. Gwynne-Vaughani* making up the peat of this region of the bed. Comparison with the rhizomes of *R. major* in Part I will show the essential similarity in structure of this region of the plant in the two species, and the difference in size.

We have little to add to the description of the stem in Part I, which was based almost entirely on this species. It may, however, be pointed out that, while the small strand of xylem is often uniform and composed of similar tracheides, this is not always the case. In larger strands a distinction of smaller central tracheides surrounded by outer tracheides of greater diameter is evident. This distinction can be seen in figs. 41 and 45 on Pl. VII of Part I. Attention is directed to this character in *R. Gwynne-Vaughani*, since it will be found to hold regularly and strikingly for the steles of *R. major* and *Hornea Lignieri*.

In the peat, composed of numerous stems of *R. Gwynne-Vaughani*, a number of cases have been noticed in which stems have been cut in the neighbourhood of their tips. The most striking example is shown in Pl. I, figs. 2–4, and demonstrates the appearance of the growing point. Fig. 2 shows at *a*, among a group of typical stems of this species, one with its tip cut longitudinally. This tip is more highly magnified in fig. 3. The meristematic tissue is composed of small cells filled with dense contents, which evidently represent the slightly contracted protoplasts. The elongation of the cells in the central region of the stem is apparent a short distance behind the actual apex. The cells of the growing point itself are isodiametric, and those of the outermost layers were evidently undergoing periclinal divisions. The whole appearance suggests a small celled meristem, but it is of course impossible to say whether an apical cell was present or not. The cuticle can be traced from the older contracted region of the branch over the growing point; it has become separated from the outermost layer of cells by a clear zone.

By the side of this undoubted apex, at *b* in fig. 2, is seen what we can only interpret as the extreme tip of another growing point which has been removed by a horizontal section and is thus viewed from above. The arrangement of the meristematic cells in this transverse section is shown more highly magnified in fig. 4. If this interpretation is correct, the specimen gives additional evidence as to the absence of any prominent initial cell.

In connection with the apical meristem, fig. 5 may be referred to. This longitudinal section, while not including the apex, shows a region situated close to it with the protoplasts almost filling the small cell cavities.

The only sporangium of *R. Gwynne-Vaughani* figured in Part I (Pl. IX, figs. 63, 63A) lay amongst characteristic stems of that species, and terminated a stem showing the distinctive vascular strand and tracheides. It contrasted with what we now know to be the sporangia of *R. major* by its much smaller size. It measured about 3 mm. in length by 1 mm. across. At the junction of stalk and sporangium in this specimen there is a constriction (Pl. I, fig. 6) to which we do not attach importance as indicating a natural feature. Above the constriction the epidermal cells assume the character of the sporangial wall. They are deeper than on the vegetative stem, but as seen in surface view at the top of the sporangium have the fusiform outline (Pl. I, fig. 7). The cell walls are moderately thickened and brown. Within the well-marked epidermis come some layers of thin-walled tissue, mostly perished, and only indicated towards the base of this sporangium. Bounding the empty cavity of the sporangium is the persistent layer which we have spoken of in Part I as the "tapetum." The nature of this layer in the sporangia of *Rhynia* will be further considered below under *R. major*.

A transverse section of a slightly larger sporangium is shown in fig. 8. The well-developed epidermal layer, the perished middle zone of the sporangial wall, and the persistent tapetal layer can be distinguished. The sporangial wall is about ·2 mm. in thickness, and the width of the sporangium must have been slightly over 1·5 mm. There were no spores remaining in this sporangium, but another of similar size, and with an equally well differentiated wall (fig. 9), was filled with well-preserved spores. The tapetal layer in this specimen appears a number of cells deep, but this is probably to be explained by the section being oblique.

The sporangium represented in fig. 10 is peculiar in that the epidermal layer of its wall is not sharply distinguished from that of the stalk. A firm tapetal layer seems to be completely wanting, though the soft tissues of the wall are well preserved. This peculiar sporangium widened out gradually from the stalk without any constriction at the base. The sporangial cavity is partly filled with mature spores.

Another small sporangium (fig. 11) was even more remarkable. The group of spores, still arranged in tetrads, is surrounded by a thick wall, which has neither a definite tapetal layer nor a characteristic thick-walled epidermis. The ill-preserved epidermis is bounded by a cuticle which is ridged like that of adjacent vegetative stems of *R. Gwynne-Vaughani* (*cf.* Part I, Pl. VI, figs. 31, 36, p. 769).

The two sporangia last described, which clearly belong to *R. Gwynne-Vaughani*, suggest a less differentiated condition in which spores were formed within the end of a stem without this being modified into a definite sporangiun. It is of interest to find this type of sporangium co-existing in the same species with a more specialised type, provided with a tapetal layer and a specially constructed and thickened epidermal layer. There is no evidence, however, that any of the sporangia of this plant had a definite dehiscence.

The spores of *R. Gwynne-Vaughani* in the sporangium in fig. 11 were still associated in tetrads (fig. 12). Other mature spores from the sporangium in fig. 9 are represented in fig. 13. The fully mature but not shed spores of this species measure about 40 μ in diameter.

Rhynia major, n.sp. (Pls. II and III.)

1917. *Rhynia Gwynne-Vaughani*, Kidston and Lang (*pars*), *Trans. Roy. Soc. Edin.*, vol. li, pl. i, fig. 1; pl. iii, figs. 11–12; pl. iv, figs. 13–19; pl. v, figs. 21–22; pl. vi, fig. 37; pl. ix, figs. 62, 64–69; pl. x, figs. 70, 71, 76–78.

The figures quoted above, and the descriptions in Part I based upon them, give the structure of all the regions of the plant—rhizomes, stems, sporangia—of *R. major*. It has been already pointed out that the differences distinguishing this species from *R. Gwynne-Vaughani* are mainly those of size and of minor details. It is necessary to consider the new species a little more fully, however, in order to bring out clearly the nature of these differences.

The remains of *R. major* so far found do not give any such picture of the habit of the plant as a whole as the specimen figured in Part I, Pl. II, fig. 5 did for *R. Gwynne-Vaughani*. The greater diameter of the stems, as shown in Pl. I of Part I, suggests that *R. major* was a larger plant throughout, and this is supported by the large size of the sporangia. We have, however, no direct evidence of the height this species attained.

We have nothing to add to the description of the rhizomes of *R. major* given in Part I, except to record the occurrence of similar though less perfect examples, also associated with the typical stems of this species, in some specimens of the silicified peat collected from the section exposed *in situ*.

The stems of *R. major* must be more fully described, since the description of the stem of *Rhynia* in Part I was almost entirely based on specimens of *R. Gwynne-Vaughani*.

As regards size, the examination of large numbers of sections of stems has shown that in *R. major* a diameter of 5–6 mm. was often attained (Pl. II, figs. 14, 19). Finer branches, probably from the upper region of the plant, are met with down to a diameter of 1·5 mm. or less (fig. 15). These measurements contrast with those of *R. Gwynne-Vaughani*, in which the usual diameter of larger stems is about 2 mm., though a thickness of over 3 mm. is sometimes attained, while the finer stems or branches may be less than 1 mm. in diameter.

On Pl. V of Part I two transverse sections of *R. major* were figured in figs. 21 and 22. Large as they appear in comparison with the other stems on the same plate, the difference is in reality greater, since their magnification should have been given as × 14 instead of × 20. A true comparison with the stems of *R. Gwynne-Vaughani*, magnified 20 diameters, in Part I, Pl. V, figs. 23–29, is afforded by the accompanying figs. 14, 19, 17, and 15 on Pl. II of this memoir.

A general view of a portion of the silicified peat composed of large stems and sporangia of *R. major* is given at a lower magnification (× 7) in Pl. III, fig. 25. The stems shown in figs. 18 and 21 are magnified 14 diameters.

All these figures show how closely the stem of *R. major* agrees in general construction with that of *R. Gwynne-Vaughani*.* As is best shown in the well-preserved stem in fig. 14, there is a clear differentiation into epidermis (*ep.*), outer cortex (*o.c.*), inner cortex (*i.c.*), phloem (*ph.*), and xylem (*x.*). A difference that may be at once emphasised is the absence of the hemispherical projections which are such a striking feature of many stems of *R. Gwynne-Vaughani*. In the large number of sections of *R. major* examined no trace either of hemispherical projections or of the adventitious branches corresponding in place of origin to them has been seen.

The epidermis had the outer walls thickened and covered with a well-marked cuticle. It appears smooth, and no ridges have been observed on the epidermal cells. Stomata were sparingly present as in *R. Gwynne-Vaughani*. The outer cortex, two or three cells deep, was evidently a mechanically important hypoderma in the larger stems. Within it came the wide inner cortex, the outer cells of which, when well preserved, often have the dark contents common in the same position in *R. Gwynne-Vaughani* (fig. 14). The outer cortex was interrupted beneath the stomata, as is shown in figs. 14 and 18 and in Part I, Pl. VI, fig. 37. In the large stems the outer cortex was very resistant to decay, while the wide inner cortex often broke down (figs. 25, 19, 18).

* This is also brought out in comparing figs. 21 and 22 with the other figures on Pl. V of Pt. I.

The stele, which is clearly marked off from the inner cortex, though no special boundary line is present, has a wide clear zone of phloem surrounding the central solid strand of xylem. Even in the smallest stems of *R. major* (fig. 15) the stele is relatively large as compared with *R. Gwynne-Vaughani.*

The cells of the phloem are thin-walled, and as seen in transverse section (fig. 16) fit closely together. The intercellular spaces present in the inner cortex, when this is well preserved, cease on passing to the phloem. In longitudinal sections (figs. 17 and 20) the cells of the phloem are seen to be thin-walled and elongated, resembling the same tissue in *R. Gwynne-Vaughani.*

The xylem consists of far more numerous tracheides than in most steles of *R. Gwynne-Vaughani.* A distinction, such as was occasionally found in the latter plant, is here regularly present between the central and peripheral tracheides. The inner tracheides are much smaller than the outer ones, and have thinner walls (figs. 22, 16A). Although the xylem appears beautifully clear in many transverse sections, no satisfactory indication of the thickening of the tracheide walls is shown in any of the longitudinal or oblique sections as yet examined. Everything points to the walls having been thickened, but the thickening seems to have readily perished, and practically all the material of the plant had undergone decay to this extent at least. There is sometimes an appearance of porose thickening, but this often fills up the cavity, and from the examination of many specimens we are convinced that this appearance is due to an alteration of the original thickening, and that it would not be wise at present to attach any weight to it.*

While, as stated above, no adventitious branches have been met with in *R. major*, the stems of this plant showed equal or dichotomous branching. An example is seen in Pl. III, fig. 21, at *a*, where two steles of the same size are present in the one cortex.

A number of sporangia of *R. major* were figured in our previous paper (Part I, Pl. IX, figs. 62, 64–69), and the description of the sporangium there given is based on them, and applies to this species. The figures on this plate show how much larger the sporangia of *R. major* were than those of *R. Gwynne-Vaughani.* There is some range in size of the sporangia of *R. major*, and still larger examples than any described in Part I have since been met with. Thus the sporangium on Pl. III, fig. 24, was nearly 4 mm. in diameter. Its wall was well preserved, and showed the vertically extended, thickened epidermal cells (*ep.*), the zone of thin-walled tissue (*m.l.*), and the "tapetal" layer (*tap.*) around the large cavity filled with spores.† The sporangium in Pl. III, fig. 23, may have been slightly larger, since the wall is broken and overlapped at *a*; only the epidermal layer enclosing the spores is preserved. It seems clear that the sporangia of *R. major* attained a length of more than 12 mm., a diameter of more than 4 mm., and a thickness of wall of ·3–·4 mm.

* The decayed steles in Pt. I (Pl. X, figs. 76–78) belong to *R. major*, and the comparison there made with DAWSON'S figure of *Psilophyton* must be modified in so far as the outer dark zone in our specimens is derived from the outer xylem and not as suggested from the altered phloem.

† *Cf.* Pt. I, Pl. IX, fig. 67.

The spores (Pl. III, fig. 26) were about 65 μ in diameter. The difference in size from the spores of *R. Gwynne-Vaughani* was constant in all the sporangia of the two species so far studied.

The remarkable and very persistent layer of cells which lines the cavity of the sporangium in both species of *Rhynia* has been referred to throughout as the "tapetum." Its position corresponds to that of a persistent tapetal layer, but it shows peculiarities which call for special remark. When best preserved it is seen to be a layer of somewhat flattened, elongated cells, the *walls* of which remain bounding the empty-looking cell cavities. It suggests to our minds a relatively rigid tissue, and is perhaps best compared with the sheath of tracheidal cells which has been described in some other fossil sporangia.* The appearance of the walls of these "tapetal" cells in *Rhynia* is quite consistent with their being of tracheidal nature, though the preservation does not allow of any special thickening being recognised.

DIAGNOSIS.

The recognition of two species of *Rhynia* necessitates some modification of the generic characters and a differential description of the species.

Rhynia.

Plant gregarious, rootless and leafless, consisting of subterranean rhizomes attached by unicellular rhizoids, and erect, dichotomously branched, cylindrical aerial stems. Stomata present. Stele consisting of a zone of phloem surrounding a strand of tracheides. Sporangia cylindrical, without columella, terminal on aerial stems. Homosporous. Spores with cuticularised wall, developed in tetrads.

Rhynia Gwynne-Vaughani.

Aerial stems tapering upwards, probably about 20 cm. high, and ranging in thickness from 3 mm. to under 1 mm. Small hemispherical protuberances of superficial tissues of the stem occur, and sometimes, in place of them, adventitious branches, the stele of the branch not being continuous with that of the main stem. Xylem strand of stele slender, only sometimes showing a distinction of smaller central and larger peripheral tracheides. Tracheides with broad annular thickening. Sporangia about 3 mm. long and 1·5 mm. in diameter. Sporangial wall about ·2 mm. thick. Spores about 40 μ in diameter.

Locality.—Muir of Rhynie, Aberdeenshire.

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

* F. W. OLIVER, "On a Vascular Sporangium from the Stephanian of Grand Croix," *New Phytologist*, vol. i, p. 60.

Rhynia major.

Plant larger in all its parts than *R. Gwynne-Vaughani.* Aerial stems tapering upwards, and ranging in thickness from 6 mm. to 1·5 mm. or less. No hemispherical projections or adventitious lateral branches. Stele large, xylem strand of numerous tracheides differentiated as smaller central and larger peripheral tracheides. Sporangia reaching a length of 12 mm. and a diameter of 4 mm. Sporangial wall about ·3–·4 mm. thick. Spores about 65 μ in diameter.

Locality.—Muir of Rhynie, Aberdeenshire.

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

HORNEA LIGNIERI, n.sp. (Plates IV–X.)

Another vascular plant from the Rhynie peat-bed agreed in general build with *Rhynia*, but differed in the sporangia having a columella of sterile tissue, around and above which the dome-shaped spore-sac extends. We regard it as a distinct, though allied, genus, and have named it after Dr Horne, to whose energy and interest the successful discovery of the Rhynie peat-bed *in situ* is largely due. The specific name has been given in reference to the acute morphological speculations of the late Professor LIGNIER, some of which gain confirmation and reality from the discovery of these simple types of Vascular Cryptogams.

The remains of *Hornea* occur in considerable quantity, at places forming an almost pure peat and elsewhere mixed with the other plants of the Rhynie deposit. The preservation is not quite so good as in the case of *Rhynia* and *Asteroxylon*, but shows all the essential structural features.

Hornea Lignieri resembled *Rhynia* in being a rootless and leafless plant, differentiated into rhizome, dichotomously branched cylindrical stems, and terminal sporangia. The continuity of these parts has been established. From the lobed tuberous rhizome, which was probably subterranean but might have been only partly embedded in the soil, a number of cylindrical stems arose separately. These bore no appendages, nor did they have hemispherical projections or lateral branches. They were from about 2 mm. to slightly under 1 mm. in diameter, and branched dichotomously. This occurs in the larger stems, but was probably more frequently repeated in the upper region of the plant, the stems diminishing in thickness as they subdivided. The sporangia terminated stems of various diameters, and show a corresponding range in size. The transformation of the end of a stem into a sporangium often affected a nascent dichotomy, the branching being then evident in the construction of the columellate sporangium.

The rhizome, stems, and sporangia may now be described in detail.

Rhizome. (Plates IV–VI.)

The rhizome of *Hornea* was of a different type from that of *Rhynia*, as will be evident from figs. 27 and 28 on Pl. IV. It had no vascular strand of its own, but was a lobed parenchymatous body of considerable size, from which arose stems, each provided with a central stele. The stele of each stem ended separately and blindly below in the parenchymatous tissue of the rhizome (figs. 35 and 38). Numerous long rhizoids attached the rhizome to the peat. From its resemblance to the protocorm of the young plants of some species of *Lycopodium*, this type of rhizome may be distinguished as protocormous from the stem-like rhizome of *Rhynia*. The largest rhizome met with is represented at a low magnification ($\times 7\frac{1}{2}$) in fig. 31. It is branched, and at first sight appears of a different type, not being evidently lobed. It is, however, characteristic that no vascular system proper to the rhizome is seen. Comparison with the next section of the series showed that a number of stems arose from this rhizome, the plane of section in fig. 31 passing horizontally through the rhizome below the bases of the steles of these stems.

The general structure of the rhizome is shown in the vertical section in fig. 29. The plane of section just misses the stem, and the rhizome appears as a massive, somewhat flattened body, about 8 mm. across by 2 mm. thick. It is composed of thin-walled parenchymatous tissue, between the cells of which are small intercellular spaces.* Towards the periphery the cells are somewhat smaller, and tend to be arranged in rows vertical to the surface, giving the appearance of an ill-defined outer cortex. The superficial layer constitutes a rather ill-defined epidermis, the small cells of which on the lower side of the rhizome bear the long rhizoids.

The rhizoids, which are visible in a number of the illustrations (figs. 29, 30, and 38), are non-septate, and each is a protrusion of the middle portion of the outer wall of an epidermal cell, from the cavity of which the rhizoid is not separated by a wall. Fig. 30 shows the rhizoid-bearing surface in vertical section, while in fig. 32 the surface is cut tangentially. Fig. 33 is a more general view of the latter section, and shows the long rhizoids extending from the small-celled epidermis.

The structure of all the rhizomes shown on Pls. IV, V, VI corresponds to that described above, some showing particular features more clearly. A number of them show the lobed form of the rhizome (figs. 27, 28, 35). In this connection the specimen in fig. 34 is of interest. A rhizome with a stem has apparently been cut obliquely, and two adventitious lateral growths had evidently developed from the superficial tissues as small protocormous rhizomes. The one shown in the figure bears rhizoids at *rh.*

No vascular elements were present in the section of the rhizome in fig. 29, though some of the internal cells have peculiar brown walls, and in their neighbourhood the

* The question whether the fungal hyphæ which occur in the intercellular spaces of the rhizome are to be regarded as saprophytic or mycorhizic will be considered in a later paper when dealing with the fungi occurring in the Rhynie peat. Their frequent presence must, however, be mentioned here.

section was just touching the edge of the base of a stem-stele. The stems attached to the protocormous rhizomes in most of the specimens figured show their steles at some point or other.

The characteristic base of the vascular strand of a stem springing from a rhizome is best seen when the section is truly vertical to the rhizome and follows the median plane of the stem (figs. 35–38). The best specimen is that shown in figs. 35 and 36, the other two specimens serving to confirm it. As fig. 35 shows, one lobe of a rhizome has been cut vertically, and the section follows in an accurately longitudinal direction the stele of the stem arising from the lobe; the cortex has decayed from the further part of the stele as it lies in the peat. The rhizome shows the structure already described, and bore rhizoids below. While there is no vascular tissue in the rhizome itself, the stele of the stem when traced downwards into the upper part of the rhizome (figs. 35, 36) ends in connection with a brown-celled tissue without tracheidal thickenings. The inverted cup-shape of this mass of tissue is characteristic, though not often so favourably shown as in this specimen; it is seen also in figs. 37 and 38. It explains the frequent occurrence of patches of brown tissue in sections of rhizomes (*cf.* figs. 29 and 31).

Stem. (Plates VII and VIII.)

The basal regions of the stems attached to the rhizomes described above were often more or less decayed, but were sometimes well preserved. Portions of both the upper and lower regions of similar stems in various stages of decay make up the peat. A group of the best-preserved specimens is shown in fig. 39, some being cut in transverse and one in longitudinal section. The general similarity in structure to the stem of *Rhynia* will be evident, though the preservation is not so good in the material of *Hornea* yet examined. The well-defined cuticle and thickened epidermal wall, the broad cortex, and the stele with a zone of phloem surrounding the rather stout central strand of xylem, are distinguishable in fig. 39. The transverse section of a small stem from the upper region of the plant in fig. 40 may be compared with this. The corresponding regions are shown in longitudinal section in fig. 41.

The tissues may now be described in greater detail, starting from the outside (figs. 40 and 41). There was a well-marked cuticle. The epidermis had its outer walls somewhat thickened, but otherwise did not differ much from the underlying cortical cells. No stomata have been observed, but owing to the state of preservation of most of the material much weight cannot be attached to this negative result. The cortical tissues cannot be sharply distinguished into outer and inner cortex, though the cells diminish in diameter on passing inwards. The cortical cells are somewhat elongated, and have transverse end walls (fig. 41).

Within the cortex and immediately around the xylem was a zone of thin-walled elements which readily collapsed. This zone represents the phloem (figs. 42 and 43). It often has a peculiar appearance, as if the cells were thickened at the angles or small intercellular spaces were present there (figs. 42, 43, 50, 51). In the more decayed stems the phloem may or may not be recognisable. It seems to have been less characteristically developed at the lower part of the stele near its insertion into the rhizome. All that can be said regarding the phloem in longitudinal section is that it consisted of narrower and more elongated elements than the cortex.

The xylem formed a centrally situated, solid strand of tracheides. It exhibits a considerable range in diameter, probably in relation to the regions of the stem-system of the plant. A xylem strand of moderate size is shown in transverse section in fig. 47, and others of larger size at the same magnification in figs. 45 and 48, with which fig. 46 can be compared. The xylem is shown more highly magnified in figs. 50 and 51. A distinction between narrower central, and wider peripheral tracheides is a constant feature. This holds for the steles of moderate diameter near to the rhizome, for the steles of large diameter, which we presume came from a region between this and the finer branches, and for the finer branches themselves. There are no thin-walled cells mixed with the tracheides, but the central xylem often appears broken down within a ring of peripheral xylem composed of wider and intact elements (figs. 43, 45, 46, 48). When such steles are cut longitudinally this appearance is seen to be due to repeated transverse breaks or interruptions of the core of central xylem, the tracheides of the peripheral xylem remaining continuous (fig. 49).

The thickenings on the tracheide walls have in most cases disappeared owing to the decayed condition of the stems. They are often best shown in the region of the stele near to the rhizome. In favourable specimens there is a distinct thickening of narrow bands forming irregularly connected rings or a spiral (figs. 52 and 53). As the extreme base of the stele in the rhizome is reached, the zone of phloem disappears and the tracheides become shorter and wider (fig. 54) and pass gradually into the brown-celled tissue at the base of the stele.

The stems of *Hornea* branched dichotomously, and sometimes show the stele dividing (figs. 55 and 56), or two equal steles enclosed in the same cortex (figs. 42 and 57). From the frequency with which it is met with in smaller stems, this dichotomous branching was probably most marked in the upper region of the plant.

Sporangium. (Plates IX–X.)

Sporangia of a remarkable type occur associated with the remains of the vegetative organs of *Hornea*, especially with the finer branching stems. The proof that they belong to this plant is afforded by sporangia terminating stems with the structure described above (figs. 58, 60, 61).

The general construction of the sporangium will be evident from the longitudinal sections in figs. 58–60, and the transverse sections in figs. 63 and 64. As these show, the sporangial cavity was enclosed by a fairly thick wall, and had a sterile column of tissue projecting so far from its base that the actual cavity is dome-shaped. The resemblance to the columella of some bryophytic sporogonia is so great as to make it convenient to use the name columella for the sterile projection in *Hornea*. The cavity is filled by the numerous spores with cuticularised walls.

The sporangia evidently arose by the transformation of the tips of certain branches of the plant. When the apex was simple, a single sporangium (such as that shown in fig. 58 to the right, and in fig. 64) resulted. When, however, the apex was in a more or less advanced stage of division, this is reflected in the subdivision of the sporangium and the lobing or branching of the columella, as shown in fig. 58 to the left, and in fig. 63.

The stalk of the sporangium is thus simply an ordinary branch of the plant. It shows the same structure as the stem, with epidermis, cortex, and stele more or less well preserved. Stalks bearing sporangia and showing the position of the stele are represented in figs. 58 and 60. The size of the sporangium differs according to the size of the stem bearing it. Thus the sporangium in fig. 58 is about 2 mm. long by slightly over 1 mm. broad, while that in fig. 64 is about 2 mm. in diameter.

The wall of the sporangium was of considerable thickness (about ·25 mm.), and its tissues, like those of the stems, are usually imperfectly preserved. An epidermal layer, a middle zone consisting of a number of layers of thin-walled cells, and a more resistant tapetal layer can be distinguished (figs. 65 and 67), as in the case of the sporangium of *Rhynia.* The wall shows irregularities in outline or projecting processes which do not seem to be wholly accounted for by accidental contraction. A common appearance is the flattening or broadening of the tip of the sporangium, as shown in figs. 58 and 59.

The epidermal layer of the sporangium is, at least in some cases, more marked than that of the vegetative stems. It is bounded by a cuticle, and has the outer walls of the cells thickened, the thickening extending inwards on the lateral walls. No indication of any place of dehiscence has been seen even in complete transverse sections. The structure of the epidermis is seen in figs. 67 and 68, while that of the wall as a whole is well shown in fig. 65. Below the epidermis comes a zone of some six layers of small thin-walled cells; this is usually badly preserved. The innermost layer of the wall is the persistent "tapetum," which is continuous over the columella and thus forms a complete lining to the sporangial cavity. The tapetal cells are well shown in fig. 70. Their walls are dark, and give the impression of having been rigid, as in the case of the corresponding layer in the sporangium of *Rhynia.* No indication of tracheidal thickening of these cells has been met with.

The columella (fig. 69) is composed of narrow, elongated, thin-walled cells which give the tissue, as usually preserved, a peculiar fibrous appearance. Though corresponding in position to a continuation of the stele of the stalk, it exhibits no agreement in histological structure with the central region of this, but resembles rather the phloem of the stele. The specimen shown in fig. 62 shows that the columella is directly continuous with the phloem of the stalk.

The spores are often met with still associated in tetrads (fig. 71), while in other cases they have become isolated in the sporangial cavity (fig. 72). They measure about 50 μ in greatest diameter. Spores are also found distributed through the peaty matrix in which the plant is embedded.

Diagnosis.

Hornea, Kidston and Lang, n.g.

Plant rootless and leafless. Stems arising from protocorm-like rhizomes, dichotomously branched. Sporangia terminal on ultimate branches, with a sterile columella projecting from the base into the sporangial cavity, and cuticularised spores developed in tetrads.

Hornea Lignieri, Kidston and Lang, n.sp.

Plant small, consisting of a lobed rhizome from which arise stems which branch dichotomously and range from 2 mm. in diameter downwards. Stele of stem with a zone of phloem surrounding the xylem composed of small central and wider peripheral tracheides. Sporangia cylindrical, terminal on branches, indehiscent, with thick wall composed of thickened epidermis, thin-walled tissue, and persistent tapetal layer. Sterile columella composed of thin-walled elongated cells extending from base to near top of sporangium. Homosporous. Spores about 50 μ in diameter.

Locality.—Muir of Rhynie, Aberdeenshire.

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

Classification of Rhynia and Hornea.

Rhynia and *Hornea*, while distinguished generically, agree so closely in the simplicity of their organisation that they must be regarded as genera of the same Family. For this Family we suggest the name Rhyniaceæ.

It is characterised by the plants being rootless and leafless and composed of rhizomes which bear rhizoids, branched aerial stems, and terminal sporangia. The vascular system is correspondingly simple, the central stele having a cylindrical strand of xylem either composed of similar tracheides or with a distinction of central and peripheral xylem.

The Family *Rhyniaceæ* comes into the class of Vascular Cryptogams to which we have given the name of *Psilophytales* (Part I, p. 780), since "the sporangia are borne at the ends of branches of the stem without any relation to leaves or leaf-like organs."

The consideration of more complicated types of the *Psilophytales* can be deferred until *Asteroxylon* is described.

The classification of the plants so far described from the Rhynie peat-bed is therefore as follows:—

PTERIDOPHYTA.

Class. PSILOPHYTALES.

Family. RHYNIACEÆ.

Genera. *Rhynia* (2 species).
Hornea (1 species).

COMPARATIVE DISCUSSION.

The Vascular Cryptogams preserved in the Rhynie peat-bed are the most ancient plants of which the internal structure and external morphology are adequately known. They facilitate our understanding of those plants of early Devonian age which are only known as impressions, while these assist in forming a conception of the form and habit of the plants of this remarkable flora. The consideration of this flora as a whole is beyond the scope of the present paper. In this discussion we are concerned only with the simpler types of the Psilophytales which have been placed above in the Family Rhyniaceæ.

The great interest of these plants (*Rhynia*, *Hornea*) is that they acquaint us with a type of construction fundamentally more primitive, not only than that of existing land plants but of most plants composing the Upper Devonian and Carboniferous floras.

Between the Lower and Middle Old Red Sandstone and the Upper Old Red Sandstone or Devonian, as represented by the flora of the Kiltorkan beds, there is a most remarkable difference in the type of plant life. It is doubtful if a single species which occurs in the Lower and Middle Old Red Sandstone of Scotland is present in the Upper Old Red as represented by the Kiltorkan beds. In fact, the botanical affinity of the plants of the latter is with the Lower Carboniferous flora rather than with the Middle and Lower Old Red Sandstone plants.

The type of plant exhibited by *Hornea* and *Rhynia* is the simplest known in undoubted Pteridophyta. We know nothing of the sexual generation, the existence of which there is no reason to doubt, and of the early stages of the sporophyte. The full-grown sporophyte is differentiated into rhizome, stems, and sporangia. It has no leaves or roots. The *rhizome*, which was probably subterranean, was intimately connected to the substratum by long non-septate rhizoids. In *Hornea* it was a tuberous parenchymatous structure from which the stems arose. In *Rhynia* it had a central vascular strand, and is like a peculiar region of the stem. The cylindrical *stems* branched dichotomously, diminishing in diameter. They had a simple vascular system, the stele consisting of a cylindrical strand of xylem surrounded by a zone of phloem. Stomata occurred in the epidermis of *Rhynia*, and there was a well-developed system of small intercellular spaces. The peculiar hemispherical projections of *Rhynia Gwynne-Vaughani* were the seat of adventitious lateral branches, and, whatever their other functions, may provisionally be regarded as dormant branches. The *sporangia* correspond to transformed and more or less specialised ends of stems of various sizes. Their thick wall was indehiscent, and the epidermis was usually specially thickened. There was a peculiar (and possibly tracheidal) tapetum. The spores were developed in tetrads and had cuticularised walls. No sterile cells were mixed with the spores. In *Hornea* the central tissue formed a sterile columella projecting into the sporangial cavity.

This is a simpler type of plant than is known in any existing Vascular Cryptogam, or in any extinct forms from the Carboniferous period onwards. In the Devonian period, however, there are indications of plants of correspondingly simple morphology. It will be sufficient to mention here *Sporogonites* as possibly related to the Rhyniaceæ.

Sporogonites exuberans, Halle,* from the Lower Devonian rocks of Röragen, Norway, consists of a long unbranched axis terminating in a sporogonial or sporangial structure which is similar to the sporangium of *Hornea* in a number of characters. There are distinct differences, however, but the two agree in the presence of a columella rendering the spore-containing cavity dome-shaped. HALLE regards *Sporogonites* as a sporogonium and as finding its "nearest analogy in the sporogonia of the Bryophyta."† Our fuller knowledge of *Hornea*, however, lends weight to another suggestion of HALLE that "the possibility must be faced that it may represent only the upper part of a more highly developed sporophyte, perhaps on the line of descent of the pteridophytes."‡ So far as the evidence afforded by the remains of *Sporogonites* goes, it does not establish the bryophytic nature of the plant. In showing a general resemblance to sporogonia of Bryophytes the sporangia of *Hornea* and *Rhynia* agree with *Sporogonites*, and in them the relations of the sporangia to the whole simple vascular plant is known.

While the comparisons with *Sporogonites* and with some undescribed impressions which we have seen are of great interest, our fairly complete knowledge of the structure as well as the external morphology of *Rhynia* and *Hornea* makes them more suitable for comparison with other plants. In dealing with such simply organised Pteridophyta comparisons must be widely extended, but at present are best only indicated in outline.

The simple organisation of the sporophytes of *Rhynia* and *Hornea* may therefore be briefly compared with some other Pteridophyta, with Bryophyta, and with Algæ.

* HALLE, T. G., "Lower Devonian Plants from Röragen in Norway," *Kongl. Svensk. Vetenskapsaked. Handlingar*, Bd. 57, 1916, p. 27, pl. iii, figs. 10–32.

† *Loc. cit.*, p. 31.

‡ *Loc. cit.*, p. 40.

Comparisons with Pteridophyta.

In comparing the Rhyniaceæ with other Pteridophyta we are limited by the fact that we are dealing with the simplest types of Vascular Cryptogams known. All the other Vascular Cryptogams, including such archaic forms as *Asteroxylon* and *Psilophyton*, are more highly organised than these rootless and leafless plants, the body of which might as well be termed a cylindrical, branched, vascular thallus as a stem. Thus no detailed comparison with the organisation of the whole plant in the higher Pteridophyta is possible, and what we have to say on this question will find its proper place in dealing with *Asteroxylon*.

We can, however, recognise correspondences with particular structures in some other Pteridophyta, and it is not without interest that some of these affect features which have always appeared aberrant in the plants possessing them. This applies especially to the rootless rhizome, which may be first briefly discussed.

The only rootless Pteridophyta at present known that need be considered are the Psilotaceæ.* Both *Psilotum* and *Tmesipteris* have rhizomes embedded in the substratum and attached to this by non-septate rhizoids. It is not at present known whether a root is absent from the young sporophyte of *Psilotum* in its development from an embryo, but none is present in plants arising from the minute bulbils † formed on the rhizome. No root is present in the young plant of *Tmesipteris* ‡ borne on the prothallus. The resemblance between the rhizomes of *Rhynia* and of the Psilotaceæ is close, and in neither case is there anything suggesting that the rootless condition is other than primitive. Although more complicated in the aerial shoots, the Psilotaceæ appear to have retained the simplicity of the subterranean region characteristic of the most primitive Vascular Cryptogams.

The rhizome of *Hornea*, on the other hand, appears to correspond most closely to that remarkable and much discussed region of the young plants of certain species of *Lycopodium* and of *Phylloglossum* known as the protocorm. As is well known since the investigations of Treub,§ the young plant of *Lycopodium cernuum* does not at once initiate a shoot and root, but enlarges outside the prothallus (to which it is attached by a small foot) to form a tuberous parenchymatous body. This protocorm is attached to the soil by numerous rhizoids, and bears on its upper side a number of leaves in no apparent relation to a stem-apex; these leaves are termed protophylls. Later a stem bearing spirally arranged leaves develops, and the first root forms at the base of this shoot. The corresponding stage in *L. laterale* and *L. ramulosum*, two New

* *Salvinia* and some of the smallest Hymenophyllaceæ may be mentioned, but the rootless condition in them appears to be due to reduction.

† Solms, *Annales du Jardin Bot. Buitenzorg*, vol. iv, 1884, pp. 139–190.

‡ Holloway, *Trans. New Zealand Institute*, vol. 1, 1917, pp. 1–44.

§ Treub, *Annales du Jardin Bot. Buitenzorg*, vols. iv and viii.

Zealand species, the life-history of which has been described by HOLLOWAY,* attains a much larger size before a stem-apex is differentiated. "This protocormous rhizome plays a much larger and more important part than does the simple protocorm of *L. cernuum.* It constitutes the plant body for a whole season and may even branch. It appears also that in both *L. laterale* and *L. ramulosum* it is able to reproduce itself vegetatively." † The vascular bundles of the more or less numerous protophylls borne on the protocorms of these three species of *Lycopodium* end blindly below in the parenchymatous tissue, the protocorm itself having no vascular system.

The protocorm of *Phylloglossum,* which in the embryo plant resembles that of *L. cernuum,* appears to be repeated as the specialised resting tuber by means of which this plant perennates. This region in *Phylloglossum* can be regarded as both primitive and specialised.

The rootless plant of *Hornea* appears to retain in the adult condition an organisation comparable to the protocorm stage in the species of *Lycopodium* mentioned above. The relation of the aerial stems of *Hornea* to the rhizome is similar to that of the protophylls to the protocorm in *Lycopodium.*

The resemblance of the protocormous rhizome of the ancient Vascular Cryptogam *Hornea* to the protocorm present as a transient embryonic phase in some existing species of *Lycopodium* supports the suggestion made by TREUB as to the nature of the protocorm. He was led to assume "que chez les ancêtres des cryptogames vasculaires actuels un organe a pris naissance qui a dû avoir beaucoup de ressemblance avec le tubercule embryonnaire des Lycopodes." His discussion is summed up thus:—

"Le tubercule embryonnaire chez les Lycopodes est un *organe rudimentaire.*"

"L'organe admis théoriquement chez les ancêtres des Cryptogames vasculaires actuels, et désigné ci-dessus comme 'predecesseur de la pousse feuillée telle qu'elle se présente maintenant chez les plantes vasculaires' existe encore aujourd'hui à l'état passager, dans le genre Lycopodium. *Cet organe n'est autre que le tubercule embryonnaire.*"

"Aussi je propose de donner au tubercule embryonnaire des Lycopodes le nom de *protocorme.*" ‡

In view of the morphology of *Hornea* it may be said that the existence of this organ does not require to be theoretically assumed in archaic Vascular Cryptogams, but is demonstrated.

So far as the anatomical construction of the Rhyniaceæ is concerned, we can only recognise its simplicity and its direct relation to the primary vegetative functions of land plants, absorption, conduction, aeration, and protection. It is only necessary

* HOLLOWAY, *Trans. New Zealand Institute*, vol. xlviii, 1915, pp. 253–303.

† *Ibid.*, vol. xlix, 1916, p. 90.

‡ TREUB, *Annales du Jardin Bot. Buitenzorg*, vol. viii, 1890, p. 30.

to recall the rhizoids, the simple vascular strand, the intercellular spaces and stomata, and the thick cuticle to indicate how these needs are met.

The simplicity of the stelar anatomy limits comparison with other vascular plants, but may be compared with the rhizome of the Psilotaceæ. In the xylem of the central cylinder of the Rhyniaceæ we find two grades of construction illustrated: (*a*) the strand of equivalent and similar tracheides in many stems of *Rhynia Gwynne-Vaughani*; (*b*) a differentiation of the strand of xylem into smaller inner tracheides and larger peripheral tracheides, as in some stems of *Rhynia Gwynne-Vaughani* and regularly in *R. major* and in *Hornea*. This differentiation suggests comparison with the xylem of the stem-stele and leaf-traces of a number of Pteridophyta in which the protoxylem is surrounded by metaxylem (centrarch).

The sporangia of *Rhynia* and *Hornea* will be compared below with the sporogonia of Bryophyta and the stichidia of the Red Sea-weeds. What in other Pteridophyta may correspond to their simple terminal position will be better discussed in a later paper when the more complicated types of Psilophytales have been considered. A peculiarity of the sporangia of *Rhynia* and *Hornea* is that they are relatively large and indehiscent. The thickened epidermis seems an advance in specialisation, though apparently useless for dehiscence. It looks as if the thickened epidermis, serving for the protection of the spores, had preceded any arrangement for the opening of the sporangium in these plants. The sterile columella of the sporangium of *Hornea* may correspond to the sterile projection from the base of the sporangium in some species of *Lycopodium*.

Comparisons with Bryophyta.

The difficulty in comparing Rhyniaceæ with Bryophyta lies in our ignorance of the sexual generation and the relations of the young sporophyte to it in the ancient Pteridophyta. The simple morphology of the vegetative region of the plants of *Rhynia* and *Hornea* as well as their sporangial structure appear, however, to bring us a step nearer to a comparative morphology of the sporophyte of Vascular Cryptogams and the bryophytic sporogonium. It is sufficient at present to indicate the general resemblances that can be traced between the fertile regions of these Old Red Sandstone plants and the sporogonia of Hepaticæ, of *Anthoceros*, and of certain Mosses. Whether the sporogonium is a simpler parallel development to the sporophyte or is a reduced equivalent of such a plant as that of the Rhyniaceæ must remain an open question. The possibility that these questions, which have hitherto had to be treated in a purely speculative fashion, may be at least partially answered by the discovery of further plants of early Devonian age, is strengthened by the experience of the last few years.

Comparisons with Algæ.

Without implying direct derivation of the Pteridophytes from any more complex Algæ or actual relationship with any known Algæ, it is impossible to overlook the resemblance in habit between the plant of *Rhynia* and *Hornea* and some Algæ. The comparison is closest with some Red Algæ, which show a distinction of a rhizome-like basal region and cylindrical dichotomously branched axes and have their tetraspores developed within the more or less altered ends of some of the branches. As examples, *Furcellaria fastigiata* and *Cordylecladia* (*Gracilaria*) *erecta* may be mentioned. Such resemblances, though they may be superficial, indicate the need of caution in deciding whether impressions of early Devonian plants of this habit were Pteridophyta or Algæ. Formerly a number of these plants, which we now know to be Vascular Cryptogams, were classed as Algæ or Fucoids. We anticipate that others will prove really to be Algæ, and that the comparison between them and the Pteridophyta of the same early geological age will be of peculiar interest.

A more special question concerns the equivalent of the sporangium of the Rhyniaceæ in the Algæ. The tetrads of spores in certain Algæ and the tetrads in the land plants appear to correspond strictly. In some Red Algæ we find the spore-mother-cells (or tetrasporangia) confined to certain special branches, or to the tips of ordinary branches and there situated below the surface. Such special tetraspore-bearing branches are known as stichidia. It is one possible view of the sporangia of Pteridophyta to regard them as the equivalents of such stichidia. The general resemblance and the correspondence in regional anatomy which can be traced between the sporangium of *Hornea* and the less differentiated sporangia of *Rhynia*, on the one hand, and the tetraspore-containing branches of such Algæ as *Cordylecladia*, *Furcellaria*, *Gigartina*, and some Rhodomelaceæ on the other, supports this way of regarding the sporangia of these early Pteridophyta.

We are here probably dealing with a homoplastic similarity which is an expression of general morphology rather than of relationship. The whole question is too wide to be appropriately treated in this place, but the preceding remarks will suffice to indicate the bearing of the new facts upon it. In our ignorance of the complete life-histories and the forms of the sexual and asexual generations, both of the ancient Algæ and of the simplest Pteridophytes, any suggestion of relationship would be dangerous and is not implied in the above comparisons. The facts are, however, consistent with the Rhyniaceæ finding their place near the beginning of a current of change from an Alga-like type of plant to the type of the simpler Vascular Cryptogams.

Conclusion.

If we review the comparisons we have been led to make, it will be evident that all the features of *Rhynia* and *Hornea* point to the Rhyniaceæ illustrating an early stage in the organisation of the sporophyte of Vascular Cryptogams. On grounds of their general structure it may be presumed that these simple plants were land plants. They are somewhat advanced along the line of progression of the land-growing sporophyte, but not so far as to obliterate clues to the origin of this.

Speculations as to the origin of the sporophyte of the Pteridophyta when broadly considered fall into two groups. On the one hand, it has been suggested that the vegetative organs of the sporophyte have arisen as the result of a process of progressive sterilisation within an interpolated phase of the life-history; this phase in its simplest form was composed wholly of reproductive spores. On the other hand, the origin of the sporophyte of the Pteridophyta has been looked for in the modification of a plant body such as we see in the asexual stage of a number of Algæ; this would have a more or less differentiated vegetative portion bearing asexual reproductive organs.

It appears to us that, while not inconsistent with the first of these two hypotheses, the morphology of the Rhyniaceæ is much more in line with the second. The organisation of *Hornea* and *Rhynia* make the transition assumed by this second hypothesis readily conceivable.

We do not, however, desire to enter at present into a discussion of the general problem or to draw conclusions that would be premature. The interest of *Rhynia* and *Hornea* lies in their providing new and definite historical data on early steps in the evolution of land plants. Since we may hopefully expect further discoveries to make the story more complete, any hypothetical construction of the course of evolution would be superfluous. It is sufficient, without entering into particular theories, to have indicated the bearing of the new facts on some of the chief hypotheses as to the early steps in the origin of land plants that have been entertained by morphologists. That these archaic and simple Pteridophyta should compel us to institute comparisons, not only with some existing Vascular Cryptogams but with bryophytic sporogonia and the organisation of the plant in some Algæ, appears to us pregnant with morphological interest whatever the actual lines of descent may have been.

EXPLANATION OF PLATES.

(All the figures are from untouched photographs.)

PLATE I.

Rhynia Gwynne-Vaughani, Kidston and Lang.

Fig. 1. A small rhizome (*r.*) in transverse section attached by rhizoids (*rh.*) and giving off laterally an ascending stem (*br.*). × 14. (Slide No. 2423.)

Fig. 2. Longitudinal (*a*) and transverse (*b*) sections of apical regions of stems. × 14. (Slide No. 2425.)

Fig. 3. The longitudinal section of the apex of a stem shown in fig. 2 (*a*), more highly magnified. × 105. (Slide No. 2425.)

Fig. 4. The transverse section of a stem apex in fig. 2 (*b*). × 105. (Slide No. 2425.)

Fig. 5. Longitudinal section of stem showing incompletely developed tissue with cell contents. × 33. (Slide No. 2426.)

Fig. 6. Basal region of the sporangium shown in Part I, Pl. IX, figs. 63 and 63 (*a*). *ep.*, epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum. × 60. (Slide No. 2392.)

Fig. 7. Apical region of the same sporangium. *ep.*, epidermis; *tap.*, tapetum. × 60. (Slide No. 2392.)

Fig. 8. Sporangium in transverse section. *ep.*, epidermis; *m.l.*, decayed middle layers of wall; *tap.*, tapetum. × 14. (Slide No. 2427.)

Fig. 9. Sporangium in obliquely transverse section full of spores. × 14. (Slide No. 2424.)

Fig. 10. Obliquely longitudinal section of sporangium without tapetum and without specially thickened epidermal layer, the cavity partially filled with fully developed spores. × 14. (Slide No. 2423.)

Fig. 11. Small sporangium in which the mass of spores is enclosed by a wall like the ordinary tissues of the stem. × 33. (Slide No. 2428.)

Fig. 12. Spores in tetrads from the sporangium in fig. 11. × 105. (Slide No. 2428.)

Fig. 13. Mature spores from the sporangium shown in fig. 9. × 160. (Slide No. 2424.)

Plate II.

Rhynia major, Kidston and Lang.

Fig. 14. Transverse section of a moderately large and well-preserved stem. *ep.*, epidermis; *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem; *a*, interruption in outer cortex in relation to a stoma. × 20. (Slide No. 2429.)

Fig. 15. Transverse section of one of the smallest stems met with, showing the relatively large stele. × 20. (Slide No. 2430.)

Fig. 16. Transverse section of stele, photographed to show the phloem. × 33. (Slide No. 2431.)

Fig. 16A. Central portion of specimen seen in fig. 16, photographed with different screen to show details of the xylem. *x.o.*, outer xylem; *x.i.*, central xylem. × 60. (Slide No. 2431.)

Fig. 17. Longitudinal section of stem with well-preserved stele. *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem. × 20. (Slide No. 2429.)

Fig. 18. Longitudinal section of stem, the inner cortex and phloem decayed. *o.c.*, outer cortex interrupted at *a* beneath a stoma; *x.*, xylem. × 14. (Slide No. 2395.)

Fig. 19. Transverse section of large stem showing the breaking down of the inner cortex as the result of decay. *o.c.*, outer cortex; *i.c.*, inner cortex; *ph.*, phloem; *x.*, xylem. × 20. (Slide No. 2398.)

Plate III.

Rhynia major, Kidston and Lang.

Fig. 20. Longitudinal section of stele with the soft tissues preserved. *i.c.*, inner cortex; *ph.* phloem; *x.*, xylem. × 60. (Slide No. 2429.)

Fig. 21. Group of stems compressed in the peat, the one at *a* showing two steles in preparation for dichotomous branching. × 14. (Slide No. 2432.)

Fig. 22. Stele from a stem photographed to show the xylem. *i.c.*, inner cortex; *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem. × 60. (Slide No. 2432.)

Fig. 23. Transverse section of a large decayed sporangium filled with spores. Only the thickened epidermis is preserved, and this is broken and overlapped at *a*. × 14. (Slide No. 2433.)

Fig. 24. Transverse section of sporangium with well-preserved wall. *ep.*, thickened epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *sp.* spores. × 14. (Slide No. 2434.)

Fig. 25. Portion of the silicified peat composed of decayed stems of *Rhynia major* with two sporangia of this species. × 7. (Slide No. 2435.)

Fig. 26. Spores from sporangium in fig. 23. × 160. (Slide No. 2433.)

Plate IV.

Hornea Lignieri, Kidston and Lang.

Fig. 27. Large protocormous rhizome in vertical section with three lobes, a stem arising from each lobe. × 14. (Slide No. 2436.)

Fig. 28. Portion of the silicified peat, the matrix of which is composed of decayed stems of *Hornea* with spores scattered throughout. Portions of three rhizomes are shown. The largest is cut vertically and shows two tuberous lobes from each of which a stem arises. A stele is present in each stem. × 14. (Slide No. 2437.)

Plate V.

Hornea Lignieri, Kidston and Lang.

Fig. 29. Vertical section through a rhizome missing the attachment of any stem, but showing the general parenchymatous structure and the distribution of the rhizoids. *o.c.*, outer zone; *i.c.*, inner tissue; *b.t.*, brown-walled tissue in the neighbourhood of the base of a stele. × 14. (Slide No. 2438.)

Fig. 30. Portion of the lower surface of a rhizome in vertical section showing the rhizoids springing as protrusions of all the epidermal cells. × 33. (Slide No. 2442.)

Fig. 31. Section of portion of the largest rhizome met with. This is a horizontal section of a rhizome below the bases of the steles of a number of stems which arose from it. The brown parenchymatous tissue in relation to some of these is seen at the points marked *b.t.* Lying beside the rhizome at *st.* is an obliquely transverse section of a stem. × 7½. (Slide No. 2441.)

Fig. 32. Tangential section showing the rhizoid-bearing surface of a rhizome. The bases of the rhizoids are cut across at *a*, where they spring from the central portion of each epidermal cell. × 60. (Slide No. 2443.)

Fig. 33. The tangential section of the rhizoid-bearing surface from which fig. 32 was taken, showing the long rhizoids extending into the peat. × 14. (Slide No. 2443.)

Fig. 34. Small protocormous rhizome (*r.'*) with rhizoids (*rh.*) springing as an adventitious growth of the superficial tissues of the main rhizome (*r.*). × 33. (Slide No. 2441.)

Plate VI.

Hornea Lignieri, Kidston and Lang.

Fig. 35. Accurately vertical section of a lobe of a rhizome showing the attachment of a stem. The stele of this on being followed down into the rhizome shows the characteristic base in longitudinal section. The peat around contains spores and decayed stems of *Hornea*. × 14. (Slide No. 2444.)

Fig. 36. Base of the stele shown in fig. 35. *x.*, xylem composed of elongated tracheides; *x.'*, region with short tracheides passing into an inverted bowl-shaped mass of brown-walled parenchymatous tissue (*b.t.*). × 33. (Slide No. 2444.)

Fig. 37. Base of the stem-stele of another specimen showing the same features as fig. 36. *x.*, xylem composed of elongated tracheides; *x.'*, region with short tracheides passing into an inverted bowl-shaped mass of brown-walled parenchymatous tissue (*b.t.*). × 33. (Slide No. 2445.)

Fig. 38. Vertical section of a rhizome showing good rhizoids and with the characteristic base of a stem-stele displaced downwards through the decay of the inner tissue. × 20. (Slide No. 2446.)

Fig. 39. Portion of silicified peat containing fairly well-preserved stems of *Hornea*. These stems, one of which is in longitudinal section, show the structure of the lower region close to the rhizome. × 14. (Slide No. 2447.)

Plate VII.

Hornea Lignieri, Kidston and Lang.

Fig. 40. Slightly oblique transverse section of a small stem, probably from the upper region of the plant. *cut.*, cuticle; *c.*, cortex with indications of outer and inner zones; *ph.*, phloem; *x.*, xylem. × 33. (Slide No. 2448.)

Fig. 41. Longitudinal section of stem about 5 mm. above its origin from a rhizome. *ep.*, epidermis; *c.*, cortex with indications of outer and inner zones; *ph.*, phloem; *x.*, xylem. × 33. (Slide No. 2440.)

Fig. 42. Transverse section of stem with stele just divided in preparation for dichotomy. *cut.*, cuticle; *c.*, perished cortex; *ph.*, well-preserved phloem; *x.*, xylem. × 33. (Slide No. 2446.)

Fig. 43. One of the steles in fig. 42 more highly magnified. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem. × 105. (Slide No. 2446.)

Fig. 44. Small stem with relatively large stele. × 20. (Slide No. 2449.)

Fig. 45. Stele of stem in fig. 44. *x.o.*, outer xylem; *x.i.*, central xylem partially broken down. × 60. (Slide No. 2449.)

Fig. 46. Another large stele with broken-down central xylem. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, position of central xylem. × 33. (Slide No. 2450.)

Fig. 47. Transverse section of stem-stele close to the rhizome. *x.o.*, outer xylem; *x.i.*, central xylem. × 60. (Slide No. 2447.)

Fig. 48. Transverse section of large stele. *x.o.*, outer xylem; *x.i.*, perished central xylem. × 60. (Slide No. 2447.)

Fig. 49. Longitudinal section of xylem of stem-stele showing the continuous outer xylem (*x.o.*) and the central xylem (*x.i.*) interrupted by breaks. × 60. (Slide No. 2441.)

Plate VIII.

Hornea Lignieri, Kidston and Lang.

Fig. 50. Transverse section of stele near its origin from the rhizome. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem. × 210. (Slide No. 2447.)

Fig. 51. Portion of the stele shown in fig. 47. *ph.*, phloem; *x.o.*, outer xylem; *x.i.*, central xylem. × 210. (Slide No. 2447.)

Figs. 52, 53. Tracheides in longitudinal section showing the fine irregularly spiral or reticulate thickening. × 210. Fig. 52 (Slide No. 2452); Fig. 53 (Slide No. 2451).

Fig. 54. Short tracheides from the basal region of a stele showing the fine irregularly spiral or reticulate thickening. × 210. (Slide No. 2442.)

Fig. 55. Stele showing dichotomy. × 60. (Slide No. 2442.)

Fig. 56. Small stem with stele showing dichotomy. × 20. (Slide No. 2452.)

Fig. 57. Small stem *a* showing dichotomously divided stele. × 20. (Slide No. 2453.)

Plate IX.

Hornea Lignieri, Kidston and Lang.

Fig. 58. Portion of peat containing, besides more or less decayed stems of *Hornea*, two slender stems terminating in well-preserved sporangia cut in accurate longitudinal section. The sporangium to the left is bifurcate, that to the right is simple. A portion of the stele (*st.*) is seen in the stalk of each. × 14. (Slide No. 2454.)

Fig. 59. Imperfect sporangium in longitudinal section showing flattened top. *w.*, wall; *sp.*, spores; *col.*, columella. × 20. (Slide No. 2424.)

Fig. 60. Broad divided sporangium terminating a stalk with two steles (*st.*). *w.*, wall; *sp.*, spores; *col.*, columella. × 20. (Slide No. 2456.)

Fig. 61. Portion of peat with spores of *Hornea* distributed through it, and containing on the left a small stem (*a*) and on the right an obliquely cut sporangium (*b*) showing the characteristic stele of *Hornea*. × 14. (Slide No. 2455.)

Fig. 62. Oblique section of the base of a sporangium showing the continuity of the tissue of the columella with the phloem of the stele. *w.*, wall; *sp.*, spores; *col.*, columella; *ph.*, phloem; *x.*, xylem. × 60. (Slide No. 2456.)

Fig. 63. Transverse section of a large partially divided sporangium with a single cavity, but the columella

showing two lobes, one of which is again subdividing. *w.*, wall; *tap*, tapetum; *col. a*; *col. b*; *col. b'*, the three divisions of the columella. × 20. (Slide No. 2457.)

Fig. 64. Sporangium in transverse section lying beside a longitudinal section of a stem. *w.*, wall; *sp.*, spores; *col.*, columella. × 20. (Slide No. 2457.)

Plate X.

Hornea Lignieri, Kidston and Lang.

Fig. 65. Portion of transverse section of a sporangium of *Hornea*. *ep.*, epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *sp.*, spores; *col.*, columella. × 60. (Slide No. 2458.)

Fig. 66. Transverse section of a sporangium showing the thickened epidermis. *ep.*, epidermis; *m.l.*, middle layers of wall; *tap.*, tapetum; *col.*, columella. × 20. (Slide No. 2456.)

Fig. 67. Portion of wall of sporangium in fig. 66 more highly magnified. *ep.*, epidermis with thickened outer walls; *m.l.*, perished middle layers of wall; *tap.*, tapetum. × 60. (Slide No. 2456.)

Fig. 68. Fragment of the epidermis of a broken sporangium showing the thickening of the outer walls extending on to the lateral walls. × 60. (Slide No. 2439.)

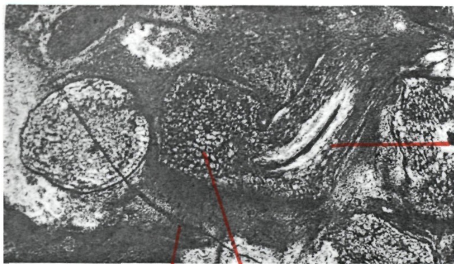
Fig. 69. Portion of one of the sporangia in fig. 58 showing the columella in longitudinal section. *w.*, wall; *sp.*, spores in the dome-shaped cavity lined by the tapetum (*tap.*). × 60. (Slide No. 2454.)

Fig. 70. Portion of a tangential section of a sporangium to show the persistent tapetum. *w.*, wall; *tap.*, tapetum. × 60. (Slide 2451.)

Fig. 71. Spores in tetrads around the columella (*col.*). × 105. (Slide No. 2459.)

Fig. 72. Mature spores in sporangium. *col.*, columella. × 160. (Slide No. 2456.)

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



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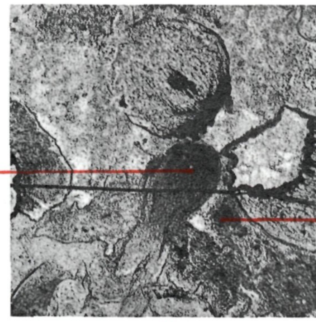

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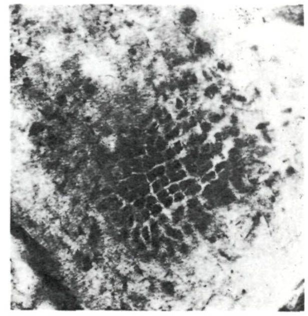
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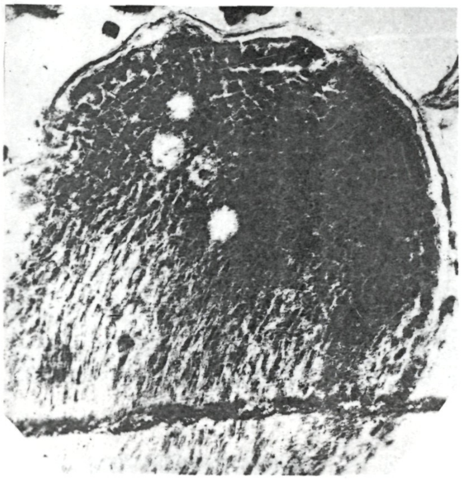
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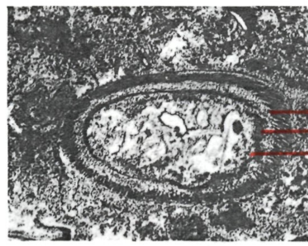

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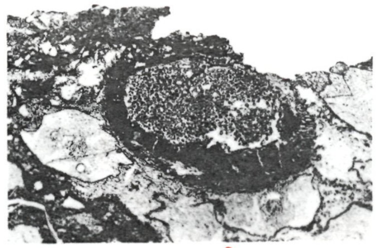
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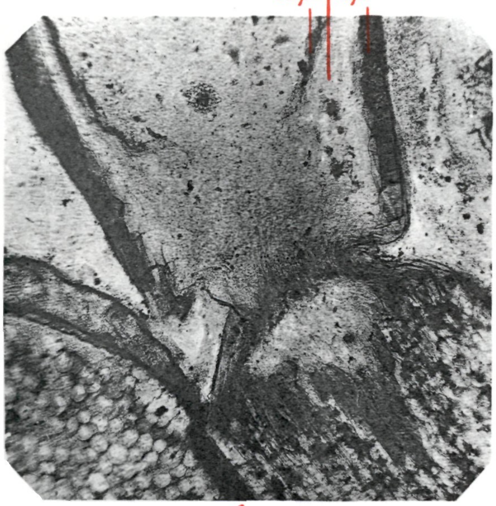

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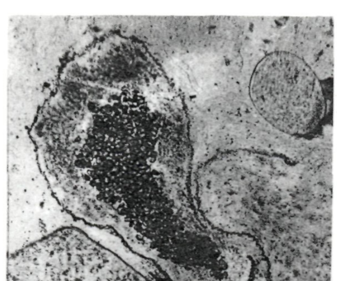
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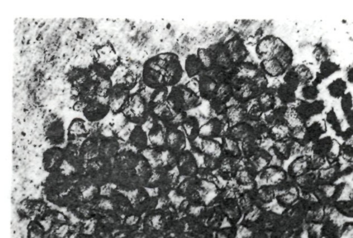
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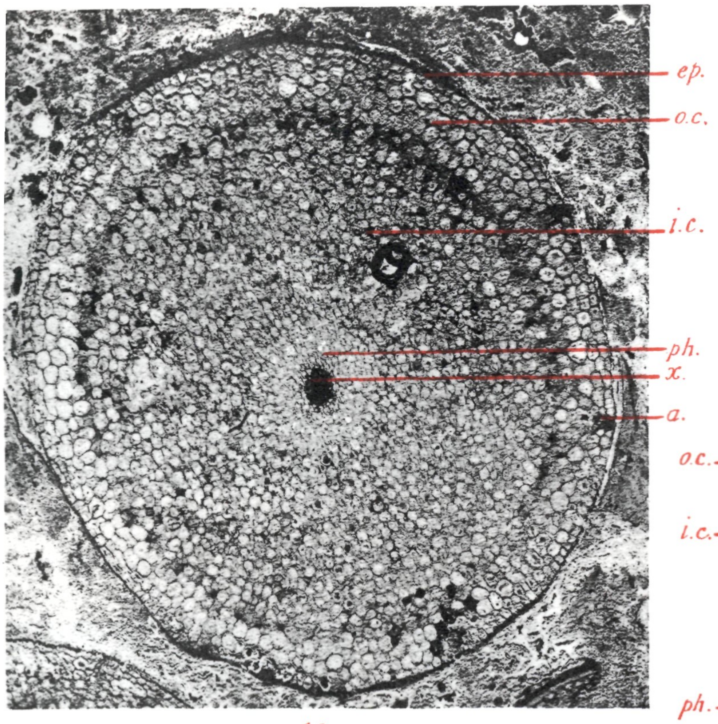

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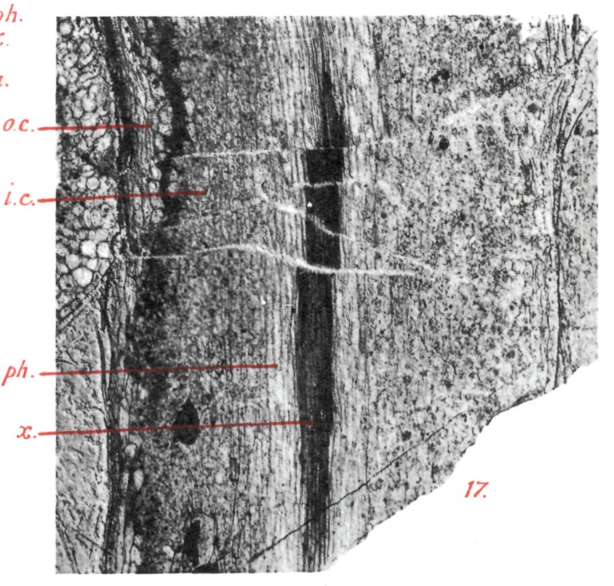

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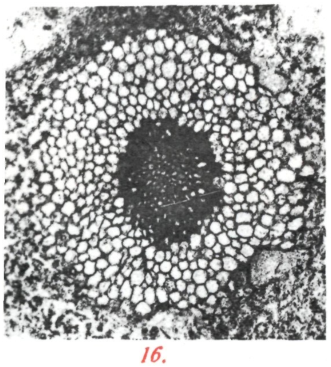

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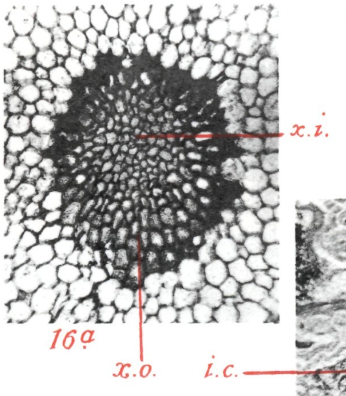

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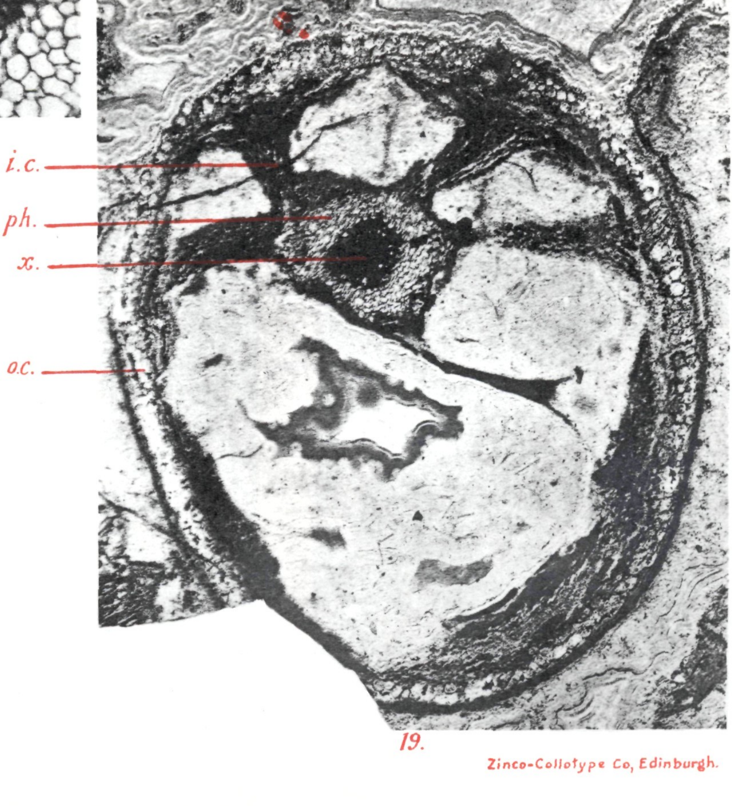

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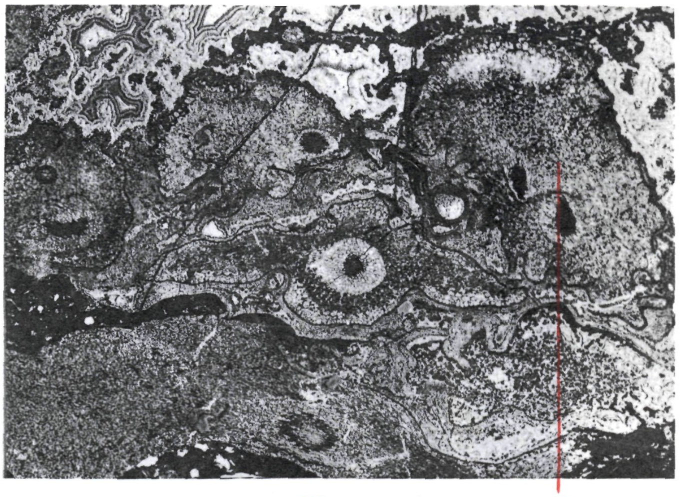

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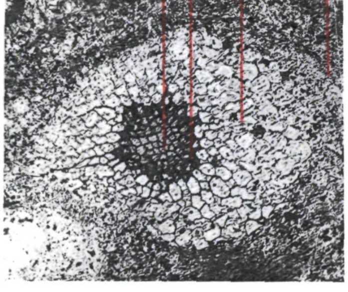

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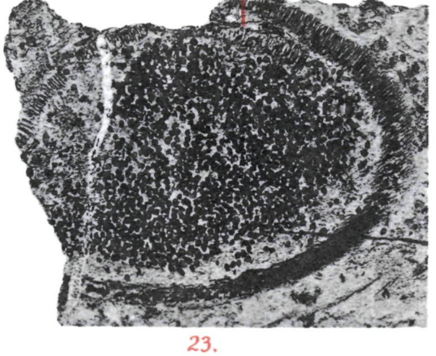

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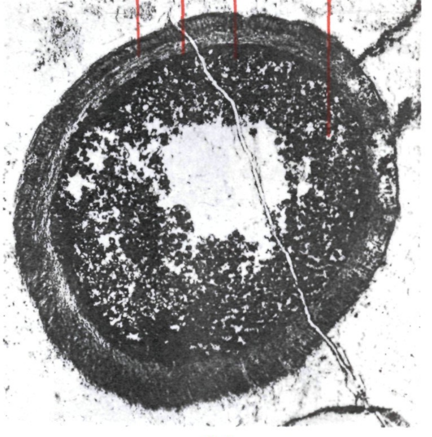

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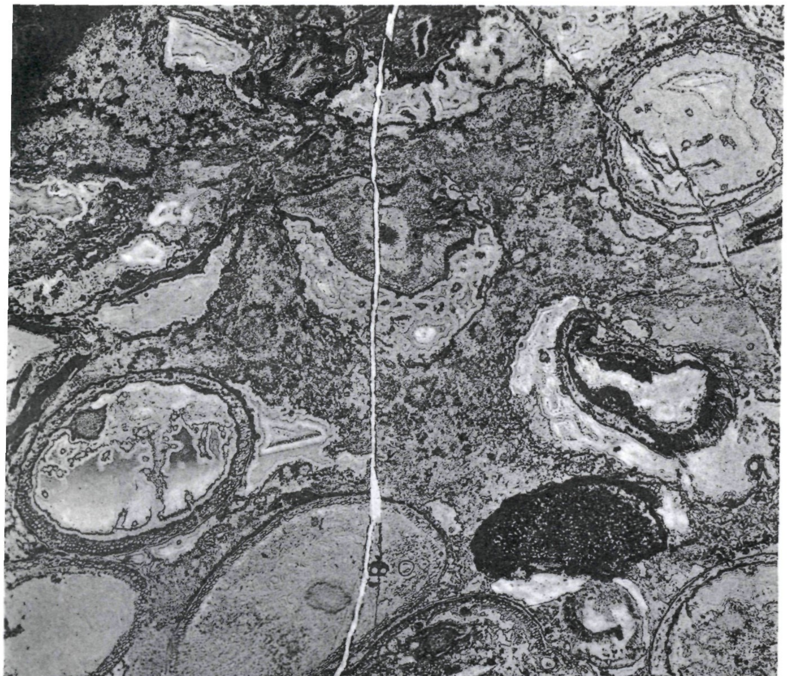

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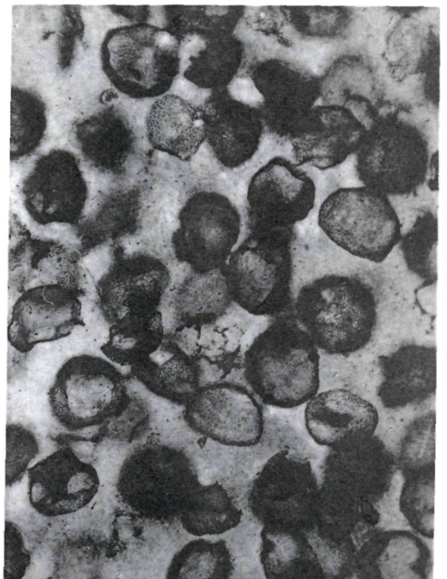

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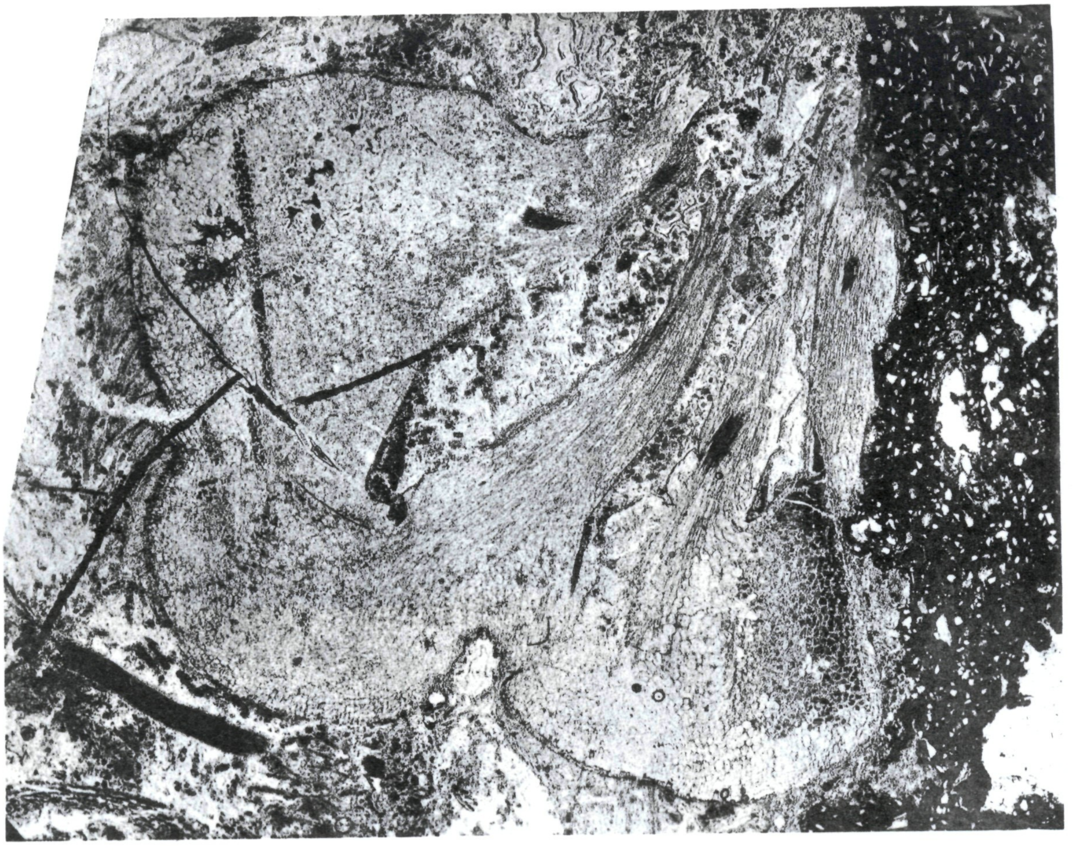

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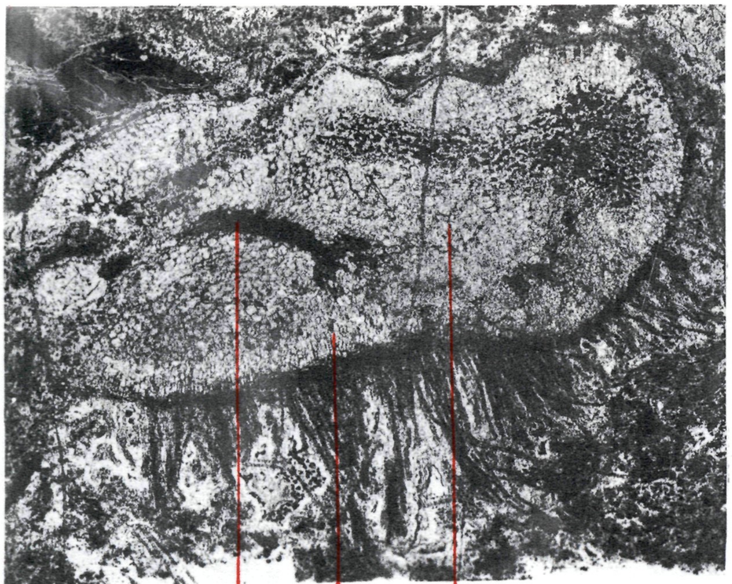

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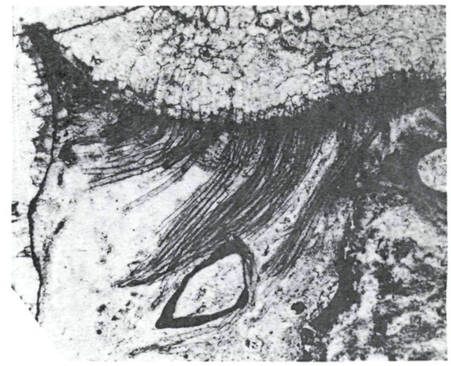
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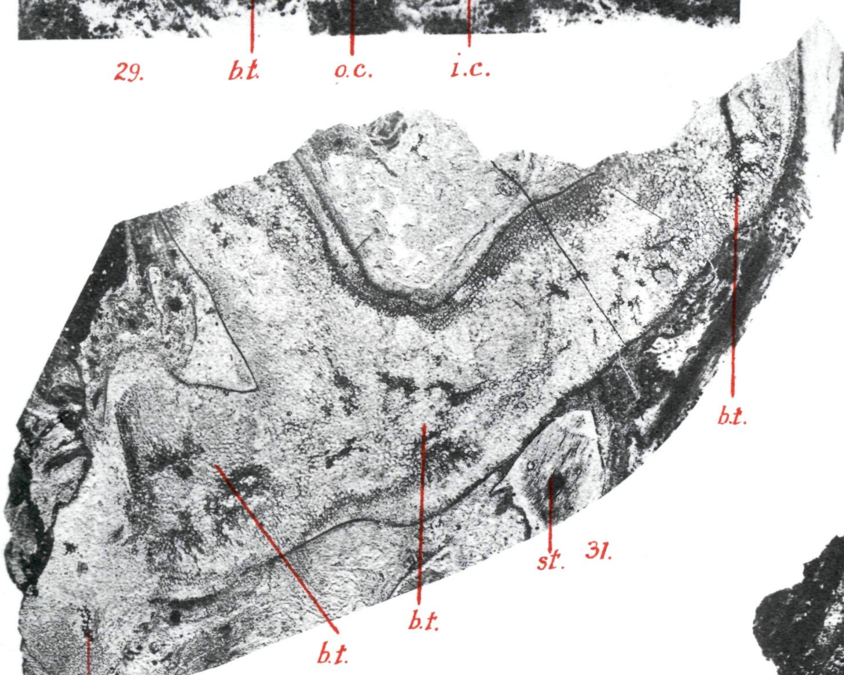

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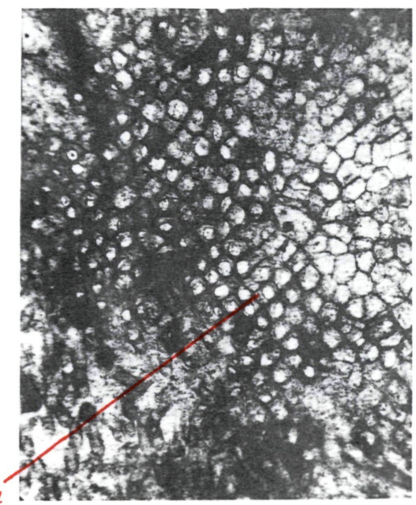

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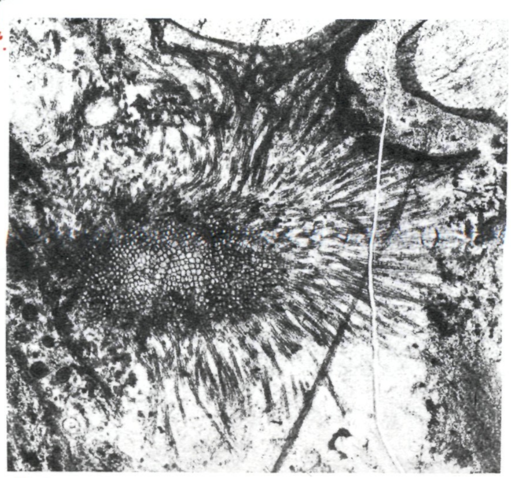
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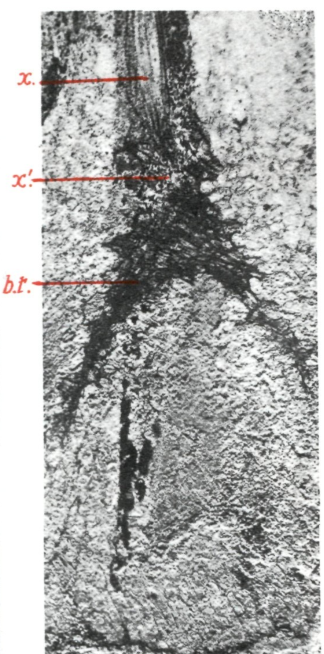

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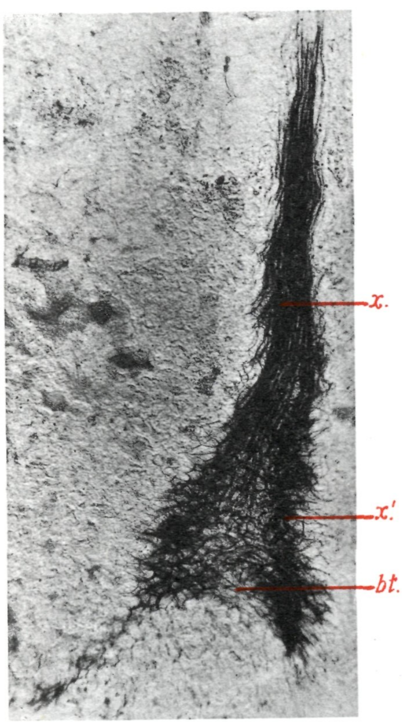

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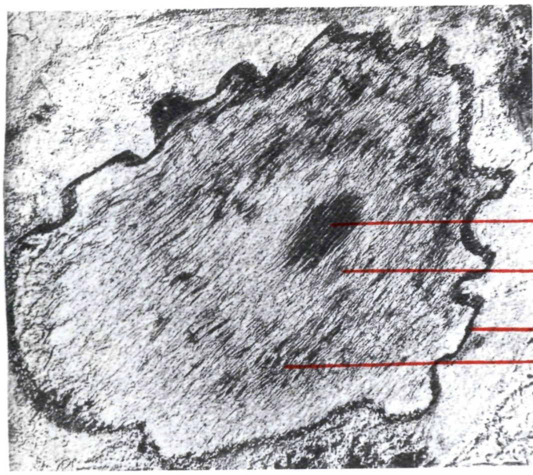

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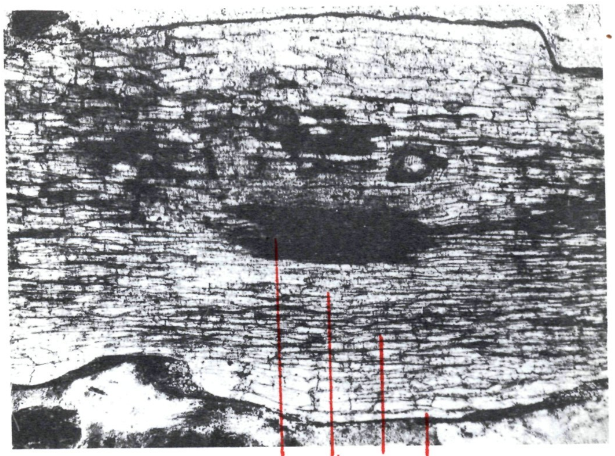

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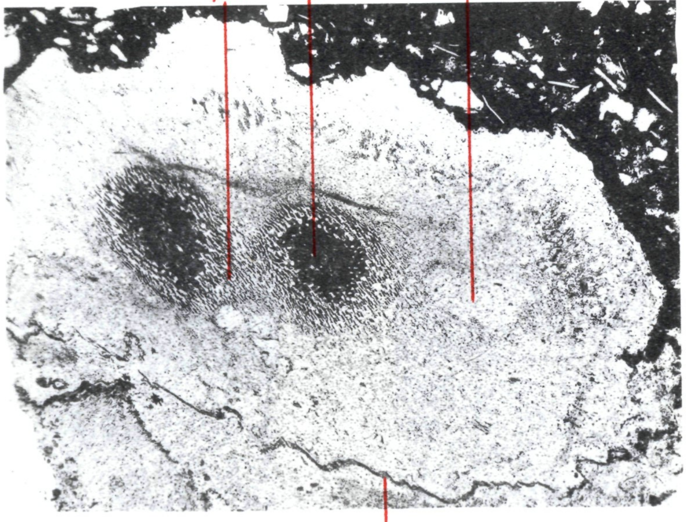

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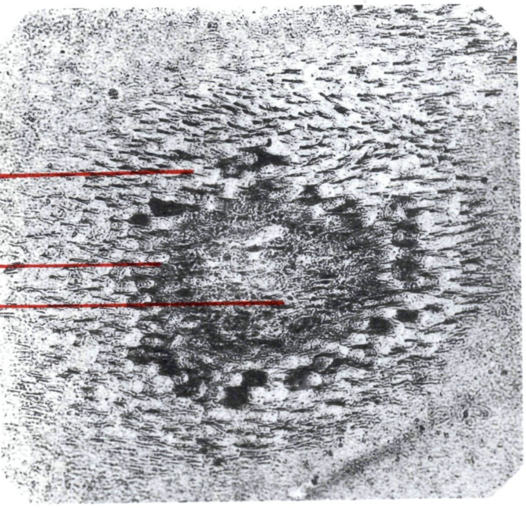

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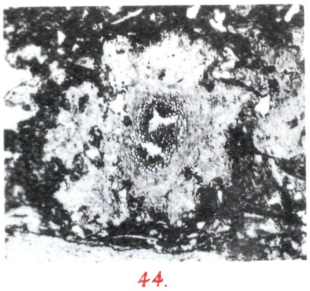

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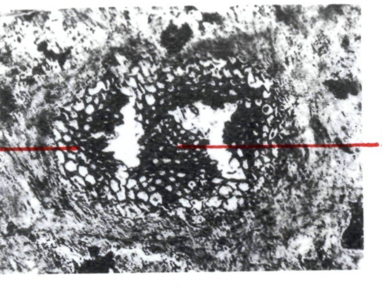

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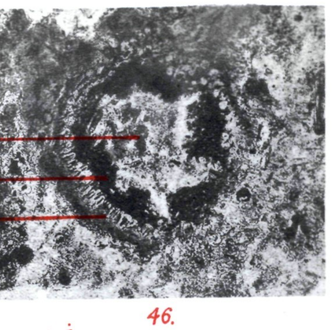

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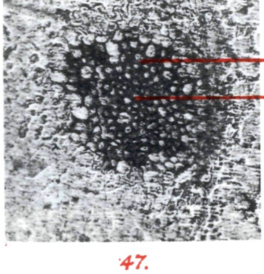

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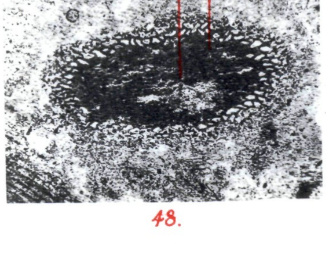

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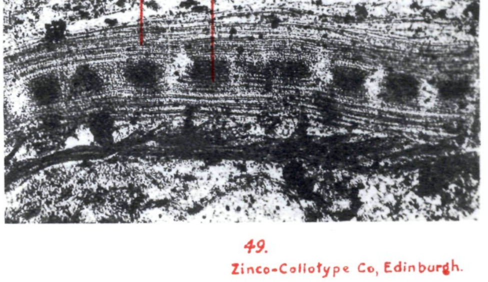

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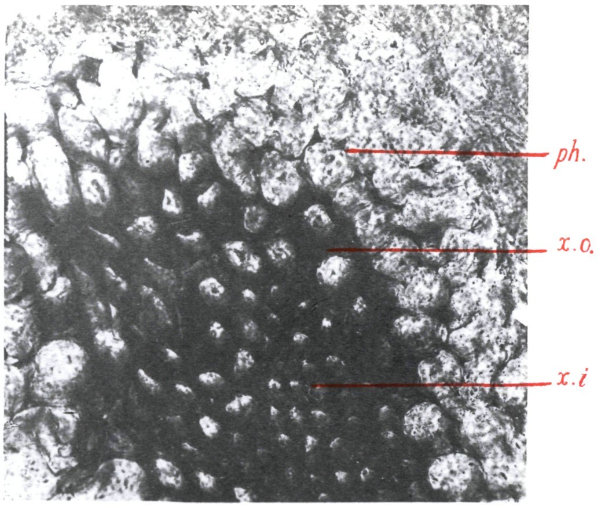

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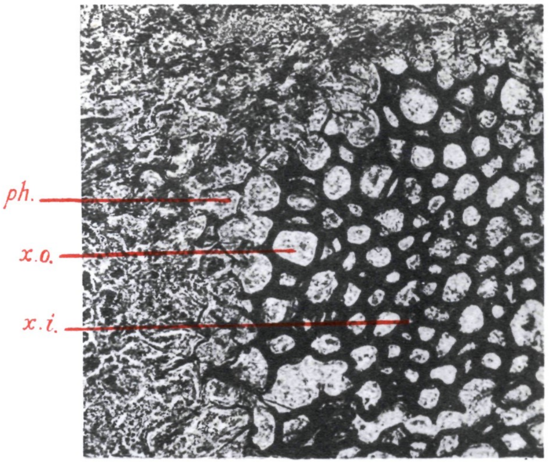

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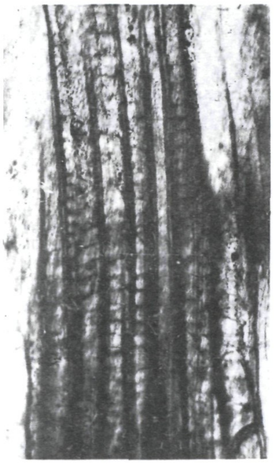

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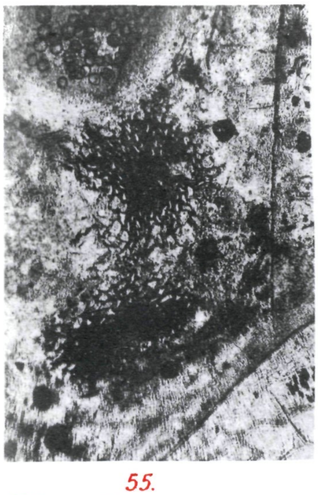

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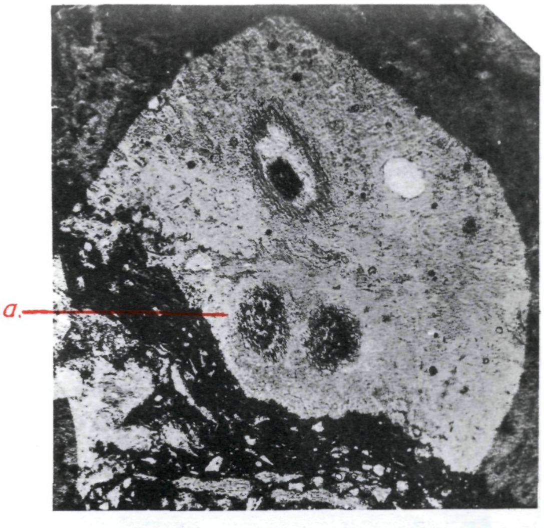

57.

R. Kidston, Photo.
Zinco-Collotype Co, Edinburgh.

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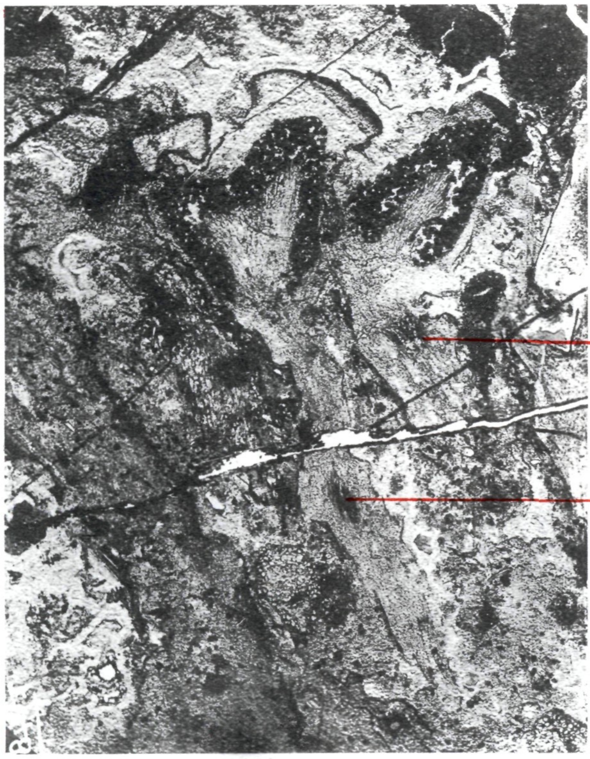

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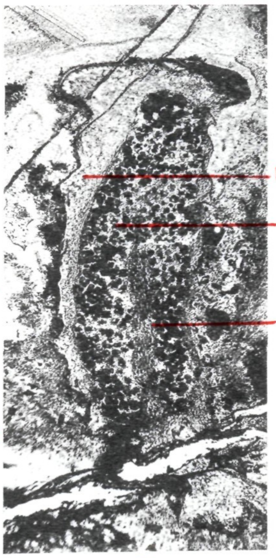

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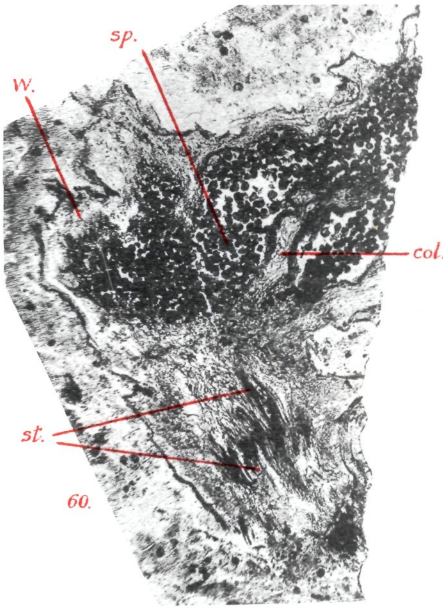

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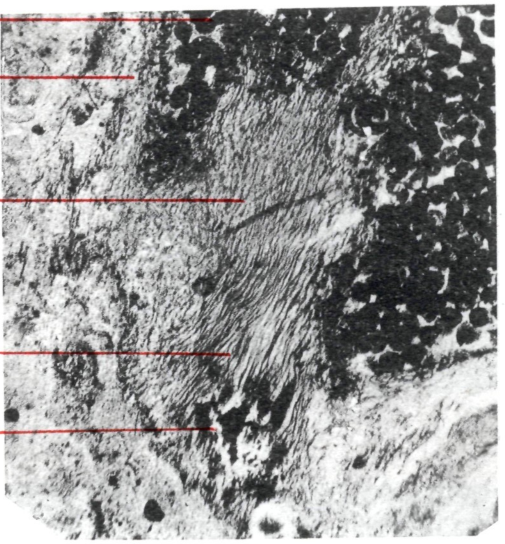

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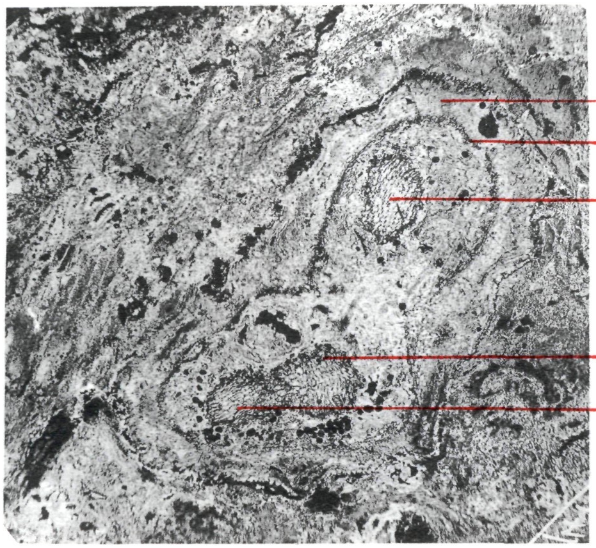

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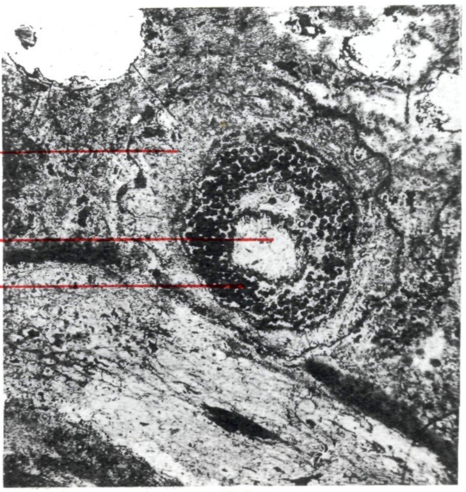

64.

R. Kidston, Photo.

Zinco-Collotype Co, Edinburgh.

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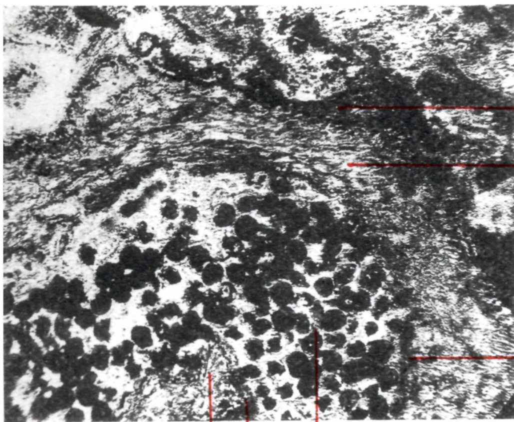

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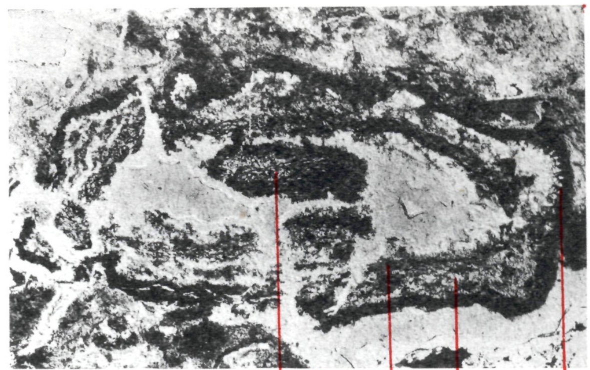

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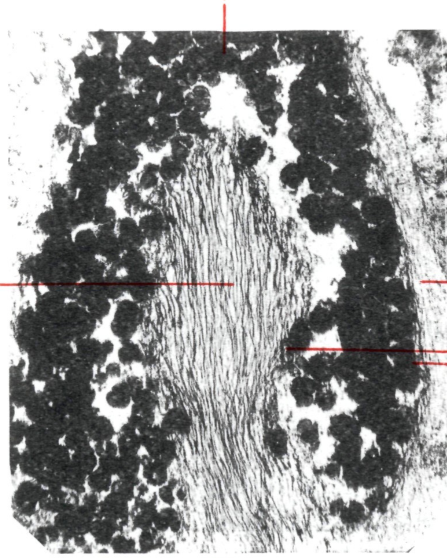

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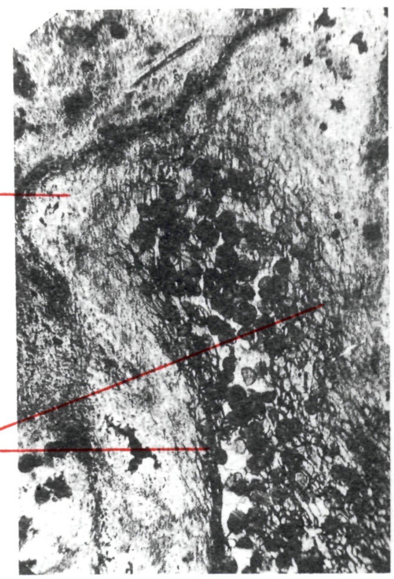

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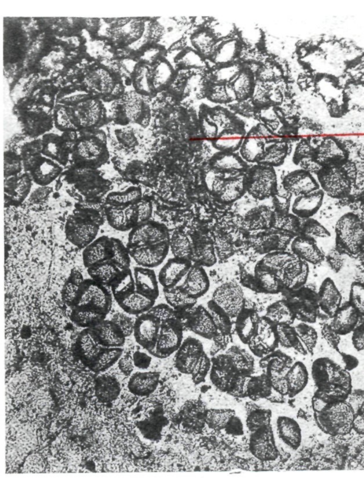

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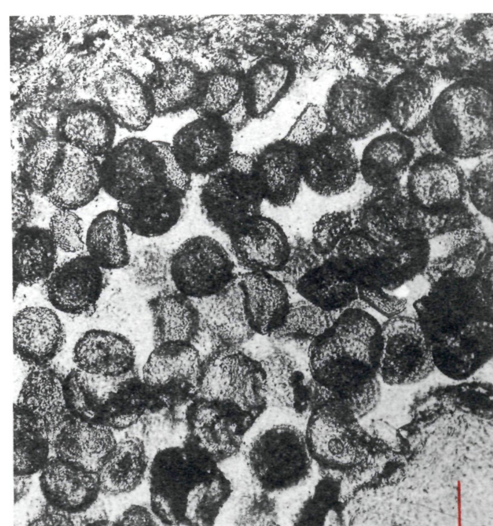

72.

R. Kidston, Photo.

Zinco-Collotype Co, Edinburgh.

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