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*Some new facts about the structure of the cuticles in the Russian paper-coal and their bearing on the systematic position of some fossil lycopodiales.*

*On protocalamites.*

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# SOME NEW FACTS ABOUT THE STRUCTURE OF THE CUTICLES IN THE RUSSIAN PAPER-COAL AND THEIR BEARING ON THE SYSTEMATIC POSITION OF SOME FOSSIL LYCOPODIALES.

by Jessie A. R. Wilson. B.Sc.

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## Historical Introduction.

The fossil cuticles of the paper-coal from the Moscow Basin in Central Russia were first described by Auerbach and Trautschold[1] in 1860. Since then these cuticles have been the subject of much discussion, especially with regard to the interpretation of their numerous regularly disposed perforations. According to the various views of previous investigators, several generic and specific names have been assigned to these cuticles. Auerbach and Trautschold, regarding the perforations as the result of the fall of the leaf-cushions as well as the leaves, considered the cuticles to belong to the genus Lepidodendron, and named the plant Lepidodendron tenerrimum. Previously Eichwald[2], in "Letheae Rossica", had described impression material, also from

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[1].- Auerbach & Trautschold(1860), p.40, Pl.III, figs.1-5.

[2].- Eichwald(1854), p.108, Pl.V, figs.10-13.

the Moscow Basin, under the name *Lepidodendron Olivieri*, which Zalessky[1] believed to be specifically identical with the cuticles described by Auerbach and Trautschold.

Göppert (fide Zalessky[2]) also regarded the cuticles as parts of a *Lepidodendron*, but referred them to *Lepidodendron obovatum* Sternberg. He considered the perforations as marking the exit of the vascular tissue to the leaves. Until the investigations of Zeiller, the membranes found in the paper-coal were regarded as the epidermis of the stem, but he demonstrated clearly that they must be regarded as as the cuticle alone[3]. Interpreting the gaps in the cuticles as due to the fall of the leaves, Zeiller refers these fossils to the genus *Bothrodendron*, and from a comparison with Lindley and Hutton's specimens to the species *Bothrodendron punctatum* L. and H.[4] Zeiller figures the cuticles upside down, showing the openings constricted towards the upper end. He attributes the shape of each opening to the fusion of two gaps in the cuticle, the lower and larger representing the leaf-scar, and the smaller upper one the opening to the ligular pit.

The classification of these remains with *Bothrodendron* was also adhered to at first by Nathorst[5], but

1.- Zalessky(1915), p.42.
2.- Zalessky, ibid., p.28.
3.- Zeiller(1882), p.221, Pl.X, figs.13-14.
4.- Zeiller, ibid., p.224, figs.1-12.
5.- Nathorst(1894), p.45.

he later[1] changed his mind, preferring the generic name Porodendron previously proposed by him for some Spitzbergen fossils which he considered were specifically identical with the Russian cuticles. Zalessky[2] at first adopted this nomenclature and referred some fossils from the Lower Carboniferous of the Mugodschari Mts. to Porodendron tenerrimum. In 1915, however, Zalessky, as a result of an investigation of Auerbach and Trautschold's specimens, readopted the name Lepidodendron for the cuticles[3]. With regard to the peculiar strap of cuticle which extends over the perforations, Zeiller and Zalessky both considered that it represented a strip of cuticle from the surface of the leaf - according to Zeiller from the abaxial surface, which view was necessitated by the manner in which he orientated his specimens, but according to Zalessky from the adaxial surface.

Fresh light was thrown on the nature of the cuticles by Professor Walton's interpretation of the strap of cuticle as the cuticular lining of the ligular pit.[4] Viewed in this light, the perforations must needs be regarded as due to the loss of the leaves and not so much as due to the disappearance of the leaf-cushions, and on the strength of this interpretation the cuticles are referred to the genus Bothrodendron. Bode recently put forward

1.- Nathorst(1914), p.68.

2.- Zalessky(1909), p.5, Pl.I, figs.1-4.

3.- Idem. (1915), p.43.

4.- Walton(1926), p.121.

another interpretation for these straps of cuticle. He regards them as due to the rolling up of a cuticle which he supposes forms over the abscission surface after the leaf fell off.[1] This implies that the perforations correspond to the leaf-scars, and as Bode could find no indication of the presence of a ligule, he classes these plant-remains amongst the Eligulate Lycopods, and with Nathorst's genus Porodendron[2]. This genus is characterised by the absence of a ligule, by the possession of small, compact leaves, not situated on leaf-cushions, and by the presence of only one small print upon the leaf-scar. Among the cuticles Bode distinguishes two types, to which he gives separate specific names, viz. Porodendron lepidodendroides and Porodendron pinakodendroides, the characters of which are based upon the form and arrangement of the leaf-scars.[3]

Thus from the foregoing it is apparent that the systematic position of the plants which produced these cuticles may be closely correlated with the interpretation of this strap of cuticle, which extends into the openings from their upper edge, and on Professor Walton's suggestion a reinvestigation of the cuticles was undertaken, in view of the facts recently stated by Bode.

1.- Bode(1929), p.131.

2.- Idem., p.133.

3.- Idem., p.135.

## Description of Some New Specimens.

This present investigation was carried out upon a sample of paper-coal from Tovarkovo in Central Russia. This coal is composed of masses of cuticular membranes bound together by disintegrated plant-remains. Fragments of cuticle for examination were prepared by Schultze's Maceration Method. This consists in treating pieces of the paper-coal for one or two days with concentrated Nitric Acid, to which has been added a few crystals of Potassium Chlorate. The released cuticles are then washed in a weak solution of Ammonia, until no more brown colouration is extracted; being finally washed in water. In addition, microtome sections were cut of samples of the cuticle with perforations which showed a well-defined strap. This material was dehydrated, embedded in paraffin wax(M.P. 52°C.), and sections cut at 10μ thickness. As the sections were liable to be washed off the slide, during subsequent immersion in Xylol, collodion dissolved in clove oil was employed to fix the paraffin ribbons to the slide instead of egg albumen.

Sections cut transversely through the strap show in most cases that it consists of two membranes closely pressed together (Pl.I, fig.1). In some sections these membranes have become more widely separated, and it is then evident that they are usually continuous with each other at the two ends (Pl.I, fig.2, and Pl.III, fig.13). This implies that the strap is really a tube which has become flattened. The main cuticle in transverse section appears smooth on one side and irregular on the other, the irregularities being due to the moulding of the cuticle to the contour of the epidermal cells[1]. Although its cuticle is much thinner, a similar appearance is evident in the section of the strap, where the smooth sides of the membrane face each other, and the small projections are seen at regular intervals on their outer side (Pl.I, fig.1). This would seem to indicate that the tube was surrounded on all sides by tissue.

Other fragments of cuticle were examined entire. This leads to the same conclusion, that the strap of cuticle is a tube, open at both ends, the lower opening of which is plainly shown in Professor Walton's figure (loc. cit., fig.6), while the upper opening is indicated here in Fig.3(Pl.I). In this figure the portion of cuticle which intervenes between this opening and the perforation still persists as a flap, stretching across the upper end of the tube and continuous with the rest of the cuticle on either side. A striking feature of the cuticle at this region is the radiation of linear series of epidermal cells from this opening, as indicated by the cell outlines; this is seen on the flap as well as on the surrounding cuticle (Pl.I, fig.3). The outlines on the tube show that the cells here were elongated in the longitudinal direction (Pl.III, fig.12).

In some perforations where the outline is rather

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1.- Zeiller(1882), p.221.

irregular, the margin consists of a much thinner cuticle as compared with the rest of the membrane (Pl.III, figs.9&10). Some of the cells in these thin regions produced a still more delicate cuticle with cuticular papillae regularly arranged on their surface (Pl.II, fig.5; Pl.III, fig.10,$P_1$). Less frequently another type of papillate cell is met with in this region, where a single large papilla occupies a central position on the cell (Pl.I, fig.4). Another remarkable feature of this thin area of cuticle is the presence of stomata (Pl.III, figs.10&11; Pl.II, fig.8). These have only been found toward the lower edge of the perforation. The stomata are orientated in the direction of the long axis of the leaf-scar perforation, and as indicated by the cell outlines on the cuticle, have possessed two semi-circular guard-cells with a rim of cuticular thickening bordering the pore on either side. It can further be deduced that the stomata were unaccompanied by special subsidiary cells, the surrounding cells being similar in shape and direction to the other epidermal cells, which were bounded by straight walls and were more or less rectangular, with the long axis of the cells running longitudinally.

## Conclusions.

A consideration of these facts leads one to favour the interpretation of the strap as the cuticle which covered the surface of the ligular pit, in which case the perforations in the paper-coal cuticles are due mainly to the loss of the leaves. The small projections, seen in transverse section of the strap, present on the outer sides of the membrane are then the projections of the cuticle external to the anticlinal walls of the cells which line the pit (Pl.I, fig.1). The openings of the tube now become intelligible; the lower indicates the point of attachment of the ligule, which would therefore seem to have been similarly placed to the ligule in *Lepidodendron* (see below, remarks on *Lepidodendron selaginoides*), while the upper opening is the actual mouth of the pit. In *Bothrodendron* stems linear series of epidermal cells radiate from the mouth of the ligular pit similarly to what has already been noted on the cuticles. (My attention was directed to this feature by Professor Walton in the case of *Bothrodendron minutifolium*.) The flap of thin cuticle which hangs down in front of the tube and is continuous with the edge of the tube facing the perforation evidently represents that part of the leaf-surface intervening between the mouth of the pit and the upper edge of the abscission scar. This flap is represented diagrammatically in Pl.II, fig.7 at (b).

Since the perforations correspond to the leaf-scars, the irregular thin areas present round their margins must be cuticle from the leaf-base or cushion, and showing characters of the leaf-cuticle, which was probably in this instance thinner than that of the stem-cuticle. The remarkable structures found in these regions bear this out; papillate cells and stomata being foliar characters.

These papillate cells of the first and most frequent type are reminiscent of cells in the leaf-epidermis of various species of *Selaginella*, such as have been described by Harvey Gibson[1], and the stomata are also similar to those found in *Selaginella*, in which genus thay are oval to circular in shape, as seen in surface view, have no subsidiary cells, and are disposed in rows parallel to the mid-rib of the leaf. Bode explained this delicate cuticle round the edge of the gaps as remnants of an abscism cuticle - the main area of which having rolled up to form the strap; but the occurrence of leaf-characters on these areas refutes this idea, and perhaps the round cell seen towards the lower edge of a perforation in one of his figures (loc. cit., Pl.XXI, fig.18), and for which he could give no interpretation, may be something in the nature of our second type of papillate cell.

The interpretation of Bode concerning the strap of cuticle cannot be maintained in view of the above facts. If the strap were indeed the result of rolling up, this would be seen in the transverse section, but no evidences of such can be established. On the contrary many of the sections appear as complete rings, flattened indeed but with no obvious slit at any point. Examination of numerous perforations reveals no correlation between the shape of the opening and of the tongue, as would be

[1] Harvey Gibson(1897), p.134, Pl.IX, fig.16.

expected if Bode's hypothesis were correct, since the gap represents the abscission surface, but the tongue at times is even longer than the opening, depending on the amount of leaf-base left attached at the fall of the leaves. The shape of the cell outlines on the tongue also belies the possibilty of it being an absciss cuticle, the cells of which would most probably appear iso-diametric. Although isolated cutinised patches may be formed upon the cells of an absciss layer, it is questionable if complete cuticularisation of an abscission surface is known to occur in any plant. The presence of the flap of cuticle occurring in front of the tongue (Pl.III, fig.12; Pl.I, fig.3) is also inconsistent with Bode's view, for if the tongue represented the absciss cuticle, then the upper end of the tongue would coincide and be continuous with the upper edge of the leaf-scar perforation, but this is not so in the most completely preserved samples..

This collective evidence favours the interpretation of the tongue as the cuticular lining of the ligular pit and not as a rolled-up absciss cuticle.

Pl.II, fig.8, I,II,and III, are diagrammatic representations of various sections of leaf-cushions of *Lepidodendron selaginoides* from specimens in the Kidston Slide Collection. From these a diagram of the leaf-cushion in surface view has been proportionally constructed (Pl.II, fig.5,IV). *Bothrodendron* and *Lepidodendron* are intimately related genera, the former only differing in the flattening out and disappearance of the leaf-cushions in older stems[1], and we see that if only the cuticular parts of this Lepidodendron leaf-cushion remain, then we get exactly what we have here before us in these paper-coal cuticles; the cuticle of the ligular pit would hang down as a tube behind the leaf-scar.

The plants from which these cuticles have been derived have obviously been in possession of a ligule, and must be classed amongst the Ligulate Lycopods. Since the perforations represent the leaf-scars and there is no evidence of any flattening of raised portions of the cuticle surrounding them, the membranes belong to a Bothrodendroid stem. In the published form of this paper[2] these cuticles from the Russian paper-coal were designated as Bothrodendron Olivieri Eichw. sp., the writer basing her authority for the specific nomenclature upon Zalessky's account of the specimens of Eichwald and Auerbach and Trautschold, which he believed to be specifically identical; the earlier work of Eichwald then determining the specific name employed. But since then Dr. Jongmans[3] has drawn attention to the fact that Zalessky is not justified in the above conclusion, and that proof of connection between Lepidodendron Olivieri with the membranes of the paper-coal is lacking. Eichwald's original specimen is unavailable

[1] .- Seward(1910), p.253.

[2] .-Wilson(1931), p.112.

[3] .-Jongmans(1931), p.85.

for examination and his illustrations, in Dr. Jongmans' opinion, are entirely indefinite. In view of all this these fossil-cuticles should then be known as *BOTHRODENDRON TENERRIMUM* Auerbach and Trautschold sp.

It is worthy of note that Zalessky[1] in 1918 figured some fossil cuticles bearing striking resemblance to those of the Moscow paper-coal. The perforations are smaller and more circular than those of the Russian specimens, but a similar strap of cuticle is present attached to the upper edge of the perforation. Zalessky interprets these openings as due to the loss of the leaf-cushions, and the small strap as a portion of cuticle derived from the adaxial surface of the leaf. The cuticle at the lower edge of the perforation is remarkably thinner than the rest of the membrane (loc. cit., Pl.LXIII, fig.2). Zalessky regards these cuticles as belonging to a Bothrodendroid stem, but institutes for them a new genus *Angarodendron*. Figured along with these cuticles are impressions of stems under the generic name *Caenodendron*. These show oval-shaped leaf-cushions, possessing circular leaf-scars, the upper edge of which is almost coincident with the upper edge of the cushion (loc. cit., Pl.LXIII, fig.2,a). This relation of the leaf-scar to the leaf-cushion is suggestive in connection with the cuticles of *Angarodendron*. From a comparison with the impressions

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[1] 1.- Zalessky(1918),p.9, Atlas, Pls.LX-LXIII.

the perforations of the cuticle may be regarded as corresponding to the leaf-scars and the small area of thinner cuticle found at their lower edge to the leaf-cushions. This comparison may be carried further and applied to the Moscow paper-coal cuticles. In these it is significant that the thinner cuticle occurs only on the lower edge of the perforations (Pl.III, fig.10). If this cuticle represents that which covered the leaf-cushion, and the actual opening corresponds to the leaf-scar, then these plants which produced the cuticles may have possessed a very small triangular leaf-cushion on the lower side of the leaf-base. Even although the loss of this leaf-cushion were involved in the fall of the leaves, it would not prevent the preservation of the cuticle of the ligular pit, the position of which is above the leaf-scar.

In fossil-cuticles, such as have been described in the foregoing account, it is impossible to say, unless a ligular strap is present, whether they belong to Ligulate or Eligulate plants. If the cuticles have been produced from fertile stems, then no trace of a ligule can be expected, as the ligular pit is situated in the sporophyll between the extremity of the leaf and the sporangium; the fall of the leaf would thus necessitate the disappearance of the ligular pit and ligule. Professor Walton[1] in a

[1] - Walton(1931), p.114.

recent note pointed this out and indicated that, at present, there is no satisfactory evidence of the existence of eligulate heterosporous Lycopodiales. Bode[1] seemed to have established such from his suggestion that the cone, *Porostrobus*, was related to the plants bearing the fossil-cuticles found in the same locality. But as it has now been proved that these cuticles are produced by plants, possessing a ligule, then the existence of such a group, based on Bode's suggestion is unjustified.

[1] Bode(1929), p.135.

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# EXPLANATION OF PLATES.

## Plate I.

Fig.1. Transverse section of a strap of cuticle, which extends into a leaf-scar perforation. The small projections occurring at regular intervals on the outer side of the membranes are the portions of cuticle above the lateral walls of the cells which surrounded the ligular pit. x 570.

Fig.2. Transverse section of cuticle through a perforation, bearing a cuticular strap such as is shown in Pl.III,fig.12. The outlines of the cells which surround the ligular pit are evident at the left side of the section of the strap. x 90.

A and B,- stem cuticle at sides of leaf-scar.
C,-cuticular strap.

Fig.3. Drawing of specimen shown in Pl.III, fig.12. Portion of cuticle showing upper part of a leaf-scar perforation with the strap of cuticle attached. x 270.

m = mouth of ligular pit.
f = flap of thinner cuticle representing the epidermis which extends between the mouth of the ligular pit and the upper edge of leaf-scar. The upper part of the cuticular strap is torn at the right-hand side.

Fig.4. Portion of cuticle at the margin of a perforation. x 570.

$P_2$ = papillate cells of the second type, with thin cuticle and a single large papilla.

## Plate II.

Fig.5. Portion of thinner cuticle at the margin of a perforation. x 570.

$P_1$ = papillate cells of the first type, with very thin cuticle and numerous small cuticular papillae.

Fig.6. Portion of the thinner cuticle at the lower edge of the perforation shown in Pl.III, fig.9. x 570.

$P_1$ = papillate cells.

$s_1, s_2, s_3$ = stomata.

Broken lines represent fine wrinkles on the surface of the cuticular membrane.

Fig.7. Diagrammatic longitudinal radial section of stem at base of leaf of plant which proddced the paper-coal cuticles. x 70.

a = ligular pit.

e = leaf-scar.

b = that part of leaf-surface which extends from the mouth of the ligular pit to the upper edge of the leaf-scar.

Fig.8. I - Diagram of longitudinal section of leaf-cushion of Lepidodendron selaginoides. (Drawn from Slide No. 988 of the Kidston Slide Collection, Dept. of Botany, University of Glasgow.)

II - Diagram of tangential section of a leaf-cushion of Lepidodendron selaginoides. (Drawn from Slide

No.926 of the Kidston Collection.)

III - Diagram of section transverse to the stem axis of a leaf-cushion of *Lepidodendron selaginoides*. (Drawn from ~~a~~ slide No.1355 of the Kidston Collection.)

IV. -Diagrammatic representation of leaf-cushion of *Lepidodendron selaginoides*, constructed from I, II, and III, to show the relation between ligular pit and leaf-scar.

m = mouth of ligular pit.
a = ligular pit.
d = soft tissue at base of pit.
e = leaf-scar.
c = leaf-cushion.
v = vascular strand.
l = ligule.

All approx. X 10.

### Plate III.

(All figures from untouched photographs.)

Fig.9. Photograph of a portion of cuticle, showing a complete leaf-scar perforation, at the lower edge of which is an area of thinner cuticle(t). x 50.

Fig.10. Photograph of lower edge of the perforation of Fig.9. Note the occurrence of papillate cells ($p_1$) of the first type and three stomata ($s_1, s_2, s_3$) on the thinner cuticle. x 150.

Fig.11. Photograph of one of the stomata ($s_2$) seen in Fig.10. x 570.

Fig.12. Photograph of a portion of the cuticle, showing attachment of the tongue to upper edge of leaf-scar perforation. Explanation of various parts as for Pl.I, fig.3. x 110.

Fig.13. Photograph of a transverse section cut by microtome through a tongue of cuticle seen also in Pl.I, fig.2. x 380.

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# ON PROTOCALAMITES.

by Jessie A. R. Wilson. B.Sc.

## Historical Introduction.

The type specimen upon which the genus Protocalamites is founded was discovered by Dr. D. H. Scott in material from the Calciferous Sandstone Series at Burntisland. In a Report to the British Association in 1901, he gave a short account of this stem, remarking upon the occurrence of centripetal xylem in the Vascular bundles as a unique feature in the anatomy of Calamite stems. He provisionally named it Calamites pettycurensis,[1] from the locality where it occured.

The genus Asterocalamites, also of Lower Carboniferous age, had long been recognised as a primitive type of Calamite. It shows points of similarity with the group, Sphenophyllales, in the superposition of the leaves in successive whorls. In Calamites the leaves of consecutive nodes alternate. It thus occupies an intermediate position between the Sphenophyllales and the Calamarieae. On this account Potonié[2] made a special family, Protocalamariaceae, to include this single genus, Asterocalamites.

[1] Scott(1901), p.2.

[2] Potonié(1899), p.183.

After the discovery of this new Calamite stem by Dr. Scott, Lotsey[I] suggested the generic name Protocalamites, as signifying its link to the Sphenophyllales anatomically. In the Pettycur stem the primary xylem has developed in both an inward and an outward direction and it is this mesarch condition of the Vascular bundle, which forms the basis of this genus, Protocalamites Lotsey.

Material.

The material upon which this present investigation has been carried out is from the famous Arran stems, discovered on the shore at Corrie, by Mr. Edward Wunsch in I865.[2] These stems are of Lepidodendroid trees, which became overwhelmed by volcanic ash in the early part of the Carboniferous period. The only remaining parts of the original stems are the steles and the bark, the more delicate tissues having been destroyed, their place being taken by ash, containing a various assortment of vegetable debris. Amongst this debris occur the Protocalamite stems. The preservation of these stems is poor, the wood and other thick-walled tissues being usually the only parts preserved, and even in these resistant parts, such finer details as the pitting on the tracheid walls is partially destroyed.

The method of investigation of these stems has been by sectioning, according to Professor Walton's Cellulose

I- Lotsey(I909), p.525.

2- Williamson(I879), p.493.

Peel Method. This consists in, first of all, painting the the surface to be sectioned with shellac, so that all cracks are filled up and cannot be eaten into by the acid. The shellaced surface is ground down with various increasingly fine grades of Carborundum Powder. This smooth surface is etched with a I:30 Hydrochloric Acid solution for 20-- 30 seconds, after which it is washed and dried. The etched area is then covered with a cellulose solution, after being previously moistened with the solvent used in dissolving the cellulose, which obviates the appearance of air-bubbles in the film. The particular solution employed here was made by dissolving Cinema Film in amyl acetate until the necessary consistency was reached. The solution dries to a thin film in two to three hours and can then be removed from the block. The desired section is cut out from the peel, but before mounting in Canada Balsam, it is immersed for a short time in the same strength of Hydrochloric Acid solution as was used for etching , so as to remove any loose material, which may be adhering to the side of the peel next to the stone. After washing and drying, it is cleared in Xylol for a short time and mounted in the usual way.

Approximately serial sections have been obtained by this method, since successive peels can be removed from the same block with only a certain amount of grinding between each etching in order to regain the smooth surface of the stone, The distance between each section has been estimated at approximately 60 - 90 µ. This distance could of course be much less, but it is more expedient to grind away part of the surface each time, as otherwise the number of sections involved in the taking of a series would be very considerable.

## Structure of the Stem.

Stems in which the primary structure is as yet unaltered are of very rare occurrence. Only one has been found, in which it could safely be said that there has been no secondary activity. This stem, like practically all the stems in these blocks, is decorticated, and in this condition measures 1.7 m.m. by .25 m.m., the axis having been flattened during fossilisation. Thirteen vascular bundles are present, their position being clearly shown by the carinal canals (Pl.1, fig.1). These canals are very large, and, as in the Calamites mark the position of the first formed elements of the xylem. Some contain a few loose rings of thickening adhering to the sides of the canal. The primary xylem is very small in amount, indicated by the thicker-walled cells on the inner and outer sides of the canals. This inner,centripetal xylem is the distinguishing characteristic between the Calamite and Protocalamite stems. A pith is present in this stem, of rather large, hexagonal cells, whose walls have no doubt been thickened in life, thus their occurrence here. The pith is interrupted in the centre, but whether this break is due to decay or not cannot be determined. It is probable that the pith in the younger stems was solid, later becoming hollow, as will be noticed in the older stems.

Two other stems may be mentioned here. These might be called primary, but if not, the development of secondary wood has certainly not proceeded far. One is very small, measuring 1 m.m. in diameter. Seven carinal canals are present with their accompanying xylem elements. The pith is well preserved, unless in the very centre, where it is absent, which is perhaps due to the fact that the cells there were thin-walled and so decayed before petrifaction. The other stem is more interesting as presenting a striking contrast to that illustrated in Fig.1. This is due to the very large vascular bundles, which are almost contiguous, the primary medullary-rays being very narrow (Pl.1,fig.2). The centripetal primary xylem is of considerable extent, even more so than the centrifugal portion. At parts the xylem is cut obliquely, and when this so, the scalariform thickening on the walls can be seen. The pitting occurs on tangential as well as radial walls. The carinal canals are small and in most cases are completely filled with fragments of thin bars of thickening. Secondary activity has perhaps just commenced in this stem, as the few outer rows of xylem elements present a very regular appearance.

A primary stem in longitudinal section is not known on this material, but characteristics of the primary xylem as seen in this view will be dealt with in the description of the older stems.

In all the other stems examined secondary activity has commenced and as a result a considerable zone of secondary wood has been formed. Such is shown in Pl.1,fig.3. This decorticated specimen has an average diameter of 2.7 m.m. The secondary wood forms a complete ring with the mesarch primary bundles marking its inner limit and projecting into the pith. The pith is hollow, which has most likely been its condition in life, and is not merly a false appearance due to imperfect preservation, as the pith is sharply delimited on the inner side. The cells of this tissue are large and iso-diametric in form. The secondary wood presents a very regular appearance due to the arrangement of its elements in radial series (Pl.1,fig.4), with rows of thinner-walled cells occurring amongst rows of thicker-walled elements. The former are the secondary medullary-rays, the latter the tracheides. No marked primary medullary-rays occur in the interfascicular region. In such stems as the foregoing it is difficult to differentiate between the secondary and the primary xylem, especially the centrifugal part of the latter, as the radial rows of tracheides seem to run right from the edge of the carinal canals. In longitudinal sections these tissues are readily distinguished, because of the different type of wall- thickening. Fig.5 (Pl.1) is a radial longitudinal section of a portion of a stem through the carinal canal. The latter contains the rings of the disorganised protoxylem, and on either side of the canal is the primary xylem, which shows scalariform pitting on its radial walls. From oblique transverse sections it is seen that the tangential walls are also pitted. On the inner side of the centri-

-petal xylem a few pith cells are present; these are large, rectangular and elongated vertically. A reticulate type of pitting also occurs in the primary xylem and in one stem a very curious and unique form of wall-thickening was noticed. This is illustrated in Pl.2,fig.10. The section has passed radially through a carinal canal, which is occupied by the disorganised protoxylem. This protoxylem appears to have been reticulate and as such would not permit of the same stretching as in the annular type, transverse rupture would necessarily occur during elongation. This would explain the discoidal appearance of this earlier xylem tissue. In the metaxylem we find this extraordinary pitting, in which narrow bars of thickening material alternate with broader bars. It is possible that the thin bars might be those of the adjoining tracheid, appearing from behind, but this seems unlikely as the thickening appears to be all in the same plane.

The tracheides of the secondary wood are long and narrow and exhibit a type of pitting quite distinct from that of the primary xylem, in that the pits are circular, disposed in single rows and occur only on the radial walls (Pl.1,fig.8). Occasionally there may be more than one row of pits on the same radial wall. Whether these pits are bordered or otherwise is difficult to ascertain. Fig.7 (Pl.1) represents a few tracheides of the secondary wood in tangential view. The pits are seen in section, but no satisfactory evidence of a border can be established.

The tracheid wall shows a "Vertebrate" appearance, due to the opposed pits being inclined at different angles. The xylem elements have been spoken of as tracheides, their oblique end walls being clearly seen, but occasionally transverse walls also occur. Regarding a similar phenomenon in the tracheides of the Calamites, Dr. Scott[1] remarks that "the elements of the wood were occasionally septate, unlike true tracheides, but there is no proof that they ever arose by cell-fusion, and we cannot therefore regard them as vessels in De Bary's sense." No xylem parenchyma can be detected amongst the tracheides apart from the medullary-rays. These rays run throughout the secondary wood and are seen as plates of cells in radial view. In tangential section they appear to range from one to many cells in depth, but never more than one cell broad. Some of these rays are of exceptional length, because the individual cells are themselves elongated longitudinally. These long cells are also a feature of the secondary medullary-rays in Calamite stems. One of these rays, seen in Pl.2, fig.9, attains a length of 1.6 m.m.

No phloem is preserved in any of these stems; usually there is a sharp break on the outer side of the secondary wood. In one or two cases a crushed, indeterminate mass immediately adjoins the secondary xylem, but no cells can be detected.

Stems showing extra-xylar tissue are very rare. One such is illustrated in Pl.1, fig.8. The carinal canals

[1] Scott(1920), p.28.

of the stem are clearly seen, with their external badly-preserved region of secondary xylem. Beyond this is a clear gap, except at one point, where the xylem is connected to a band ot tissue, which from the large gaps appears to be of a lacunar nature. These lacunae are separated by trabeculae composed of small cells. This tissue is reminiscent of the middle cortex of the Astromyelon type of root. It is similar to the latter in structure,but not in position, as here it seems to occupy the outer cortex, unless there has been further external tissue, which is not preserved. Whether this cortical structure throws any light on the habitat of these Protocalamite stems, it is not safe to conjecture, as this is the only stem in which a cortex is present. No lacunar tissue occurs in the stems of Calamites, but our modern Equisetums possess large cortical air-cavities.

## Structure at the Node.

The pith cavity in the stem appears to be continuous throughout successive internodes, - no diaphragm of tissue being present at the node, as in the stem of Calamites; but this may be a wrong conclusion, as the plate of tissue, if present in life, would be composed of parenchymatous cells, the nature of which would not permit of their preservation in this type of petrifaction.

At the node there is an increase in the amount of xylem, and strands of metaxylem anastomose between the bundles. The tracheides of the nodal xylem are short and broad with scalariform and often reticulate pitting.

In a transverse section through a node, a whorl of outgoing bundles are seen passing through the secondary wood. These are the leaf-traces and are directly continuous with the protoxylem of the stem (Pl.2,fig.11). In a section cut tangentially through the wood, these foliar bundles are intersected transversely, so that they must depart almost at right angles to the stem. In passing outwards the tracheides of the secondary wood curve round them.

Course of the Vascular Bundles.

In order to investigate the course of the vascular bundles, serial sections were taken through nodes both transversely and longitudinally. The stem which is cut transversely shows a considerable amount of secondary wood. No pith is present and the position of the primary bundles is indicated by projections on the inner side of the wood. The leaf-traces are given off in a whorl from the protoxylem of the stem; their course through the secondary wood shows that the sections are taken from the node upwards, as in successive sections the traces move outwards. No forking or fusing of the protoxylem groups takes place either before or after the leaf-traces are given off. This would seem to indicate that the bundles of the stem pass straight through from one internode to the next without any alternation. In a stem where alternation of the vascular bundles does occur, as in the Calamites, the bundles fork after the departure of the leaf-traces, the resultant branches then joining to form those of the ~~of the~~ internode above.

In the Protocalamite stem in question there is no forking of the protoxylem after the exit of the leaf-trace, which indicates non-alternation at the node. This conclusion is also borne out by a series of longitudinal sections taken through a node. This stem possesses a large development of secondary wood and where a carinal canal has been passed through radially the centripetal xylem is well seen, thus establishing the Protocalamite nature of this stem (Pl.1, fig. 5 ). As far as can be gathered from the sections, the stem has been compressed and the plane of sectioning is oblique to the flattened axis. This explains the section illustrated in Pl.2, fig. 12. At the right-hand side of the pith the wood has been cut radially and a leaf-trace is thus seen passing out horizontally, while on the other side of the pith the direction is almost tangential, three leaf-traces being sectioned transversely. In one leaf-trace, the protoxylem canal runs directly into the foliar bundle and reappears on its other side. This indicates that the stem-bundles maintain a straight course through the node, as otherwise it would be impossible for the canals to be evident on either side of the trace at the same time. Another example, proving the non-alternating course of the vascular bundles will be dealt with later in the description of a series, which, because of some notable features, merits a separate account.

Branching of the Stem.

Only one example of a branch in connection with a stem has been found, but as the description of this node is being deferred until later, nothing shall be said regarding it at present.

Structure of the Root.

Distributed throughout the peels from the Arran stems are sections of organs, whose structure is definitely that of a root. These are very numerous amongst the debris, especially so in the proximity of the Protocalamite stems. Accordingly they were thought to be the roots of *Protocalamites*. This supposition has now been proved correct, as evidence of organic connection between these structures and the stem has been established. Fig. 13(Pl.2) represents two roots passing through the secondary wood of a parent axis. The presence of leaf-traces indicates that we are dealing with a stem and not a large root, from which it would otherwise be indistinguishable. As it is impossible to tell the orientation of this stem, nothing definite can be said regarding the relation of the roots to the node. It seems as if they arose practically on a level with the node, since the leaf-traces are very close to the outgoing roots. The central tissue of these roots is practically disintegrated. In this condition they might easily be mistaken for lateral branches, but a more external tangential section establishes their root-nature(Pl.2, fig.14). If this were a stem branch there would have been evidence of the primary bundles, even although the carinal canals were not yet formed; but the centre is occupied by the primary tracheides and secondary thickening has been in progress for some time. As the connection of root and stem has now been proved, the description of these isolated roots will be given.

No root in the primary state has been found. Fig.15 (Pl.3) illustrates the nearest approach to such. This small root is triarch, as indicated by the three protoxylem groups and measures .4 m.m. in diameter. The primary xylem is centripetally placed from these three points and in this root secondary activity has just commenced. The majority of roots examined have four primary groups, the primary xylem being confluent; the number of groups is indicated by the number of protoxylem angles. These are often very distinct, as in Fig. 17 (Pl.3). One diarch root has been noticed, a few triarch, but the most frequent condition is tetrarch and none of a higher order than this have been seen. In all the other roots examined there is a considerable development of secondary xylem, radiating outwards from the central primary portion in very regular rows. (Pl.3, fig.16). This xylem is composed of tracheides and secondary medullary-rays, the latter being distinguished by their thinner walls, which have frequently broken down, leaving instead an empty space between the tracheal rows. In these small roots the centre is occupied by primary xylem, but in some cases it is hollow, due to the occurrence of a small pith, which has decayed as in the stems (Pl.3, fig.17). In longitudinal section the secondary tracheides show scalariform pitting, occasionally a reticulate type is found, but very seldom does the round form of pit occur. This latter type of pitting seems to belong almost exclusively to the secondary xylem of the stem, thus stems and roots may be distinguished in longitudinal view. Imbedded amongst the xylem tracheides are occasionally very narrow annular elements, which belong to the protoxylem - no carinal canals are associated with these in the root.

As in the stem, the roots are usually decorticated. Only one example of a corticated specimen has been seen and this occurs in a peel from one of the Manchester blocks. The root in question is larger than the majority and a small one is also seen close to it (Pl.3, fig. 18). The larger root is hollow in the centre, being due perhaps to its advanced age or to decay. External to the secondary xylem is a narrow band of crushed, indefinable tissue and beyond this is the preserved cortex. This outer region appears to be composed of a loose parenchyma, the state of preservation not allowing of any further detailed description. At least the cortex is not lacunar as in the corresponding rootlets of Calamites. It seems surprising when one reflects on the nature of the cortex of the stem, that the root should possess an outer tissue completely devoid of large air-spaces. In the Calamite roots the cells of the trabeculae often protrude into the lacunae(see Fig. 17, Scott's Studies, Pt.I), and Professor Weiss[1] in speaking of this phenomenon,

[1] .- Weiss(1925), p.302.

records, having observed in a few roots "that the spaces may become almost entirely obliterated by such cells." Perhaps this is the explanation of the solid appearance of the cortex in the specimen described.

These Protocalamite roots correspond in structure to those of *Calamites*, which were called *Myriophylloides* by Hick and Cash[1]. These are spoken of by Williamson and Scott[2] as "rootlets", as they appear to be the finer branches of those which are borne directly on the stem. These latter bear the generic name, *Astromyelon*, and are of larger dimensions than the former, possessing a pith, which is usually hollow. One specimen, comparable to these Astromyelon roots has been found in one of the Arran peels. No pith or cortex is preserved, but there is a very large amount of secondary wood. On its inner edge very tiny carinal canals are sometimes present, with an adjoining arc of centripetal xylem. In the case of *Calamites* the presence of centripetal xylem would be sufficient to designate the structure as a root, but this distinction does not hold in *Protocalamites*. In the specimen in question the small size of the canals, when present, favours the view that we have here a large root. Williamson and Scott[3] record the greatest dimensions of an Astromyelon as 25 m.m. by 11 m.m.; this Protocalamites specimen measures 8 m.m. by 6 m.m., so that it is not too

1.- Hick and Cash(1881), p.404.

2.- Williamson and Scott(1895), p.690.

3.- loc.cit., p.688.

large to be a root of this type.

This large root is cut at a region of branching, where a lateral root of considerable size is being given off. When this lateral is cut medianly its pith is directly continuous with a protoxylem group of the main axis. Subsequent sections show the exit of four smaller roots, two branching from the lateral root, the other two being given off from the main axis directly. These roots arise from the protoxylem of the parent root, and their mode of origin is endogenous. Fig. 19 (Pl.3) represents one of these smaller roots as it leaves the main axis. This rootlet, in a later section shows a primitive type of branching. After it leaves the main root it seems to fork (Pl.3, fig.20). The primary xylem simply divides and as a result two separate rootlets are formed, similar to all appearances in size. There is no evidence of one being the branch of the other. This type of branching is corroborated by another section (Pl.3, fig.21). Here the forking rootlet is cut sufficiently transversely to permit of no mistake as to its identity. It appears to bend, so that it is also seen in longitudinal view. At this part it clearly divides into two, each division being a small rootlet, the one quite distinct from the other. Preceding and subsequent sections to this one have been examined and no other interpretation seems feasible than that we are here dealing with a bifurcating root.

<u>Description of a Node, possessing Leaves</u>.

As casts and impressions of <u>Protocalamites</u>

are as yet unknown, direct information as to the external appearance of the leaves is not available. The leaves of Calamites had long been known as impressions before their internal anatomy was described. But from this present investigation such information has been collected as enables one to get indirectly some idea of the foliar appendages of our Arran species. Sections of leaf-like structures are fairly common amongst the internal debris of these Lepidodendroid stems - some will belong to these trees themselves, but perhaps others have been overlooked because of their detached condition and probably Protocalamites may lay claim to not a few. But only in one case have the foliar appendages of Protocalamites been found in organic connection with a stem. The node of this stem presents such notable features as warrants it the following separate account. Unfortunately the preservation of this stem is extremely poor, the cell-walls being replaced by a very black carbonaceous material, which is often so broken up as to entirely obliterate the form of the cells.

The first section taken showed a small stem, with a band of tissue attached at one side in which small vascular strands could be detected, and close to this a small round structure, also possessing a vascular bundle. These accompanying structures would have been difficult to explain, if further sections had not been obtainable. About fifty sections have been taken from this region on the block and in their preparation almost 3 m.m. of stone have been ground away, so that the distance between each successive section does not exceed 60 µ. A few sections of the series are represented diagrammatically in Pl.4, fig.22 (a-f). In Fig.23 (Pl.5) , which is the same as that of Fig. 22,(a) the small stem is cut obliquely, the angle of obliquity being approx. 45°. It possesses a solid pith surrounded by a ring of ten bundles, in which no definite carinal canals are apparent, but the disorganised protoxylem can be distinguished near the inner angles of the xylem wedges. The absence of the protoxylem lacunae is no doubt due to the approaching insertion of the stem upon the parent axis. At one side is attached a wing of parenchymatous tissue, showing at intervals three vascular strands; this , as will be proved later, is part of the leaf-sheath of the main stem, in the axil of which this smaller stem is situated. At one side of this leaf-sheath is an isolated structure, possessing a central vascular bundle. This is one of the linear segments of the sheath. In subsequent sections this structure joins on to the sheath and on its outer side appears another similar section. Simultaneously on the other side of the stem another leaf-segment has become joined up. This is shown in Fig.22(b), where the stem has now become connected by a narrow strand of tissue to a larger structure, in which carinal canals are clearly seen. This latter is the main stem. As one follows through the series, the isolated leaves,as they appear join on in rotation to the extremities of the leaf-sheath.

In the small stem the pith decreases in size as it approaches the larger stem - the intervening part between the two being bridged by strands of parenchymatous tissue (Fig.22,c). This main stem possesses very large and widely separated carinal canals. An approximately longitudinal section passing radially through one of these canals is illustrated in Fig.10 (Pl.2), and has already been discussed. Centripetal xylem is present on the side next the pith, which proves the Protocalamite nature of this stem. No extra-xylar tissue can be distinguished, only a very irregular black band occuring external to the xylem. The stem is hollow, but a considerable amount of large-celled pith still persists. The carinal canals are cut very obliquely, so that the stem must be lying at a considerable angle in the block. The actual obliquity was calculated by measuring, at various intervals, the distance of the stem from another object, which was known to run vertically through the block. This method showed that the stem was lying at an angle of 5° to the horizontal. This explains the almost longitudinal view of the xylem obtained in the later sections of the series. In Fig.22(d) the branch has entered the larger stem and as far as the state of preservation permits of a definite statement regarding the origin of the branch, it is inserted above the node, directly in line with a primary strand of the parent stem. In the diagram the crushed remains of the lateral branch are situated between an in-coming leaf-trace and the carinal canal of the main axis.

As the sections pass through the node, the leaf-traces pass inwards and join directly with the protoxylem of the stem; thus the leaf-sheath is that surrounding the larger stem. From this set of serial sections a hypothetical reconstruction of the node of a Protocalamite stem has been made (Pl.5, fig.25). The dotted lines represent the level of the various sections in Fig. 22. At the node there is a whorl of small, cylindrical leaves, fused basally to form a sheath, in the axil of which stands the lateral branch. The leaves are each traversed by a single vein, but as their ultimate portions are unknown no information is available as regards the branching, if any. Fig.26(Pl.5) is a possible diagrammatic view of a node cut longitudinally. The xylem of the various parts is indicated in black. From this it is seen that the pith of the branch gradually becomes smaller as it nears its junction with the stem. Therefore a pith cast of a Protocalamite branch would be similar in appearance to that of a Calamite, which is characterised by the tapering end.

The leaves of *Protocalamites*, as seen from these transverse sections are composed of uniform parenchymatous tissue, with a central vascular bundle (Pl.5, fig.23); only the xylem of which is preserved. No recognisable palisade layer is present in these leaves, but this may be correlated with the basal position of these sections. Perhaps the main photosynthetic activity is carried out in their more distal parts. A few isolated sections of leaves have been noticed throughout the peels, which show a similar appearance to those just described, except that they possess a sub-epidermal layer of cells, which has possibly been photosynthetic in life. One such section has been found in the vicinity of this node and is illustrated in Fig.24 (Pl.5). The epidermis appears to be composed of very small cells, and the layer inner to this consists of large cells, elongated radially; or, possibly the spaces seen are intercellular and the cells are represented by the irregular black lines. (The leaves of <u>Calamites</u> possessed very large air-spaces.[1]) But whichever view is correct, this layer is different in structure from the inner parenchyma cells and has been in all probability the palisade layer. It is thought that these isolated structures are related to the segments of the leaf-sheath, as they compare in size and form and are perhaps the leaves cut at a higher level. Those leaves attached to the leaf-sheath measure approx. .8 m.m., while the isolated ones are about .5 m.m. This difference would be explained by the leaf narrowing towards its extremity.

Before leaving the description of this node, an account of the course of the vascular bundles will be given, which is in the nature of corroborative evidence for their non-alternation in successive internodes. In the sections of the larger stem above the entrance of the leaf-traces, the

[1] .- Thomas(1911), p.82.

primary xylem bundles are distinct and show no forking of the protoxylem before they are joined by the foliar bundles. When this occurs (Pl.4, fig.22,d) the tracheids of the stem-bundle divide, the dividing parts curving round the leaf-trace to join on its other side - the xylem of the trace merges into the protoxylem canal. After the node the stem-bundles continue on in their same course. In Fig. 22(d) leaf-trace l' is in the act of joining on to the stem-bundle and in the following diagram this bundle, after receiving the foliar trace continues its straight course. If alternation was occuring at this node, then forking and fusing of the protoxylem groups would be evident before the entrance of the foliar bundles. But such is not the case. Thus the conditions in this node give added support to the conclusion arrived at previously, viz., that the vascular bundles of the stem maintain a straight course through the node. In this case, does the Vascular tissue of the stem then exist in separate units, which have never any means of inter-communication throughout their entire length? This would be a disadvantage to the plant, and to obviate this we find that at the node there is anastomoses of the metaxylem between the bundles (Fig.22,e). Strands of scalariform tracheides branch off from one bundle, either joining on to the neighbouring one or fusing with similar strands.

Fig.27 (Pl.5) is a diagrammatic representation of the course of the bundles in *Protocalamites*. The black primary xylem bundles are distinct and show no forking of the protoxylem before they are joined by the foliar bundles. When this occurs (Pl.4, fig.22,d) the tracheids of the stem-bundle divide, the dividing parts curving round the leaf-trace to join on its other side - the xylem of the trace merges into the protoxylem canal. After the node the stem-bundles continue on in their same course. In Fig. 22(d) leaf-trace 1' is in the act of joining on to the stem-bundle and in the following diagram this bundle, after receiving the foliar trace continues its straight course. If alternation was occuring at this node, then forking and fusing of the protoxylem groups would be evident before the entrance of the foliar bundles. But such is not the case. Thus the conditions in this node give added support to the conclusion arrived at previously, viz., that the vascular bundles of the stem maintain a straight course through the node. In this case, does the Vascular tissue of the stem then exist in separate units, which have never any means of inter-communication throughout their entire length? This would be a disadvantage to the plant, and to obviate this we find that at the node there is anastomoses of the metaxylem between the bundles (Fig.22,e). Strands of scalariform tracheides branch off from one bundle, either joining on to the neighbouring one or fusing with similar strands.

Fig.27 (Pl.5) is a diagrammatic representation of the course of the bundles in *Protocalamites*. The black circle indicates the relation of the lateral branch to the node.

## Comparison with *Protocalamites pettycurensis*, Scott.

A few slides of *Protocalamites pettycurensis*, Scott, from the Calciferous Sandstone Series at Burntisland were examined by way of comparison with the Arran stems. (I am indebted to Professor J. Walton for permission to consult those slides of this species, contained in the Kidston Collection).

One slide includes a very beautiful section of a small primary stem, comparable in structure to that illustrated from the Arran material. It is decorticated and in this condition measures .55 m.m. It possesses six primary bundles, which are conspicuous by their large carinal canals, the primary xylem being recognisable as thicker-walled cells on either side of the canal. The pith is almost solid, only one or two cells in the centre having disappeared.

All the other stems show a considerable amount of secondary wood and are similar in appearance to those illustrated in the preceding account. In all cases there is a well-defined arc of centripetal xylem. In longitudinal section the secondary wood is interesting as regards the pitting of the tracheides. The radial walls show in some cases rows of scalariform pits, which are broadly elliptical; in others, round pits occur in multiseriate arrangement, seldom uniseriate. This is distinct from that occurring in the Arran stems, where the scalariform type of pitting circle indicates the relation of the lateral branch to the node.

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Sections through a node are few, but in one such transverse section a leaf-trace was evident and its position, a little way out in the secondary wood, was mid-way between the protoxylem groups, as if these had forked after its departure. This would seem to indicate alternation of the Vascular strands at the node. One tangential longitudinal section passes through a node, but from it, it would be difficult to give any opinion as to the course of the strands. They appear to fork, but this may be only the branching of the metaxylem, as in one or two cases they seem to rejoin, while in another the strand continues on the other side of the node in the alternate position. Any statement made upon such slender evidence would be unreliable, but in conjunction with the transverse section it seems to point to the condition of alternation of the Vascular strands at the node.

One section of a root was noticed in proximity to a stem, but its structure is similar to these described from the Arran locality. It possesses solid primary xylem, showing two protoxylem groups, and a fair amount of secondary wood.

Thus the Burntisland specimens agree generally in their stem anatomy with those from Arran, differing in the pitting of the secondary tracheides and, if the above suggestion is correct, also in the course of the Vascular bundles.

### Discussion.

From the foregoing account of *Protocalamites* its general features, as far as they are known, may be summed up as follows: - Cylindrical stems, possessing at the nodes whorls of narrow leaves, fused at the base to form a sheath, from the axil of which proceeds the lateral branch. The stem contains a ring of primary bundles, with external secondary wood. The xylem of the primary bundles is developed in both centripetal and centrifugal directions. It is composed of scalariform tracheides and the position of the protoxylem is indicated by carinal canals. The tracheides of the secondary wood show round pits on the radial walls in uni- or multiseriate arrangement; scalariform pitting may also occur. The secondary medullary rays are one cell broad and very deep. Vascular bundles of successive internodes may or may not alternate. Root structure similar to that of *Calamites* - branching of the roots is endogenous, but occasionally bifurcating roots occur.

The generic distinction of *Protocalamites* lies in its possession of centripetal primary xylem, which distinguishes it from the contemporary genus, *Asterocalamites*. The stem anatomy of this latter plant is similar to that of *Calamites*, in that the primary xylem is solely centrifugal. Centripetally developed xylem in stems is a primitive feature and Dr. Scott[1] terms it the "old" wood as contrasted with the centrifugally formed primary xylem - the "new" wood. The old wood gradually disappears in the course of evolution, giving place to the new, and is only now existant in such organs considered as retentative of ancestral characters, such as the reproductive parts. Eames[2] describes the presence of mesarch bundles in the cone-axis and sporophyll-traces of various living species of the genus Equisetum, but in the internodal regions of the stem, as also in Calamites and Asterocalamites, all vestige of centripetal xylem has vanished. In the group Sphenophyllales we see the other extreme - where the stem axis possesses a solid protostele which is wholly centripetal. Thus Protocalamites, as has already been pointed out by various authors[3], supplies a link between the "old" wood of the Sphenophyllales and the "new" wood of the Calamarieae. Potonié[4], in comparing the secondary tissues of these two groups, suggests that if you take away the primary xylem of the former you get the condition seen in the Calamite stem. Professor Bower[5] in the "Origin of a Land Flora" puts forward Gwynne-Vaughan's modification of this, that the protostele of the Calamite ancestors has gradually

1.- Scott(1906), p.25.

2.- Eames(1909), p.595.

3.- Scott(1906), p.157; Lotsy(1909), p.523.

4.- Potonié(1912), p.194.

5.- Bower(1908), p.390.

disappeared by the progressive development of parenchymatous pith - the condition in Protocalamites being an intermediate stage in this transition. Gwynne-Vaughan[1] mentions a comparable series within the Lepidodendreae.

As regards the more detailed structure of the xylem the stem of Protocalamites agrees generally with that of both Calamites and Asterocalamites. The long medullary-rays are characteristic of all three genera. The pitting compares with that of Asterocalamites where the primary xylem shows scalariform pitting and the tracheides of the secondary wood, round pits either in one or many rows.

The branching of the stem is another link with Asterocalamites. In this genus the lateral branches, as shown by casts and impressions are usually inserted on the stem in line with the Vascular bundles. Examination of Renier's[2] photograph of an impression shows branch scars situated on the grooves, but in a few cases between them; so that the branching in this genus is not constant. In Calamites and in living species of Equisetum the branches arise between the Vascular bundles, as they are seen passing through the stem between the outgoing foliar traces. In Equisetum, where it is possible to follow the development of the lateral shoots, they are found to arise from cells situated above the leaf-sheaths, but in a position between the teeth, therefore the lateral branches are not axillary.

1.- Gwynne-Vaughan(1901), p.776.

2.- Renier(1901), Plate 38.

As they develop they burst through the leaf-sheath. In *Protocalamites* they are axillary in relation to the leaves, but do not break through the sheath, the latter being not so deep as in *Equisetum*.

Yet another point of agreement with *Asterocalamites* and one which is of considerable importance, is the non-alternating course of the Vascular bundles in consecutive internodes. In *Calamites* the general rule is alternation, but there are departures from this, especially in those stems found in the Lower Carboniferous strata, which have been grouped together by Hirmer[1] as the *Mesocalamites*. These are described by Kidston and Jongmans[2] in their "Monograph of the Calamites of Western Europe" under Section II. They occupy an intermediate position between *Calamites* and *Asterocalamites* in that the course of the Vascular bundles is variable, and they are confined to the Upper strata of the Lower Carboniferous. In the Sphenophyllales we find the course of the Vascular bundles as in *Asterocalamites* - the leaves of successive whorls being superposed. This is the condition which has been found in the Arran specimens of *Protocalamites*, but whether the contrary arrangement exists in these stems from the Burntisland beds has not yet been conclusively proved.

The roots of *Protocalamites* agree in structure with those of *Calamites*, especially the Myriophylloides

1.- Hirmer(1927), p.382.

2.- Kidston and Jongmans(1917), p.188.

type. The only example of the Astromyelon type is questionable.. The branching is endogenous and the occurrence of dichotomy in the smaller roots bespeaks a primitive feature. Such branching is figured by Stur[1] in a rhizome of *Archaeocalamites radiatus*. Bgt. Referring to this illustration the author remarks that "das Rhizom zeigt an drei Knoten einfache oder unregelmässig dichotome Wurzeln." Hirmer[2] also mentions this type of branching in the roots of *Asterocalamites scrobiculatus*. Renault[3] in his account of "Les Calamariées" figures a dichotomising root of *Bornia*, which is a synonym of *Asterocalamites*. So it is not surprising to find this type of branching in the roots of *Protocalamites*.

The leaves of the Arran stems are as yet imperfectly known, but information so far shows that they agree generally with those of the Calamarieae. Two types of Calamite leaves are known from impressions, as *Annularia* and *Asterophyllites*. The leaves occur in whorls at the nodes, but in the former the segments are slightly united into a sheath, while in the latter the leaves, while narrower than those of *Annularia* are free to the base. In the foliage of *Asterocalamites* the leaves are long, narrow structures, dichotomously branched and situated free in whorls at the nodes. The breadth of the Asterocalamites leaves, as figured by Stur[4]

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[1] 1.- Stur(1875), Plate I, fig.4.

[2] 2.- Hirmer(1927), p.377.

[3] 3.- Renault(1895), Part I, Plate II, fig.7.

[4] 4.- Stur(1875), Plate III.

compares favourably with that of the Protocalamites leaf-sheath segments. In *Sphenophyllum tenerrimum* narrow, dichotomously branched leaves occur in whorls at the nodes. Such is also the arrangement of the linear leaves of those Devonian genera, grouped together by Hirmer[1] as the Protoarticulatineae. Their leaves stand alternate or superposed at successive nodes.

## Conclusion.

While Scott[2] and Lotsy[3] recognised the intermediate position of *Protocalamites* with reference to Sphenophyllales and Equisetales it was founded only upon the occurrence of centripetal xylem in the stem. As the result of this present investigation, this position is now more confidently established. Any reference[4] made to the course of the Vascular bundles in *Protocalamites* was to the effect that alternation occurred at the nodes, but while this has not been disproved, the contrary condition has been demonstrated in the Arran specimens.

*Protocalamites* shows affinity to *Sphenophyllum* and *Asterocalamites* in the occurrence of the leaves in whorls and their superposition - to the former alone in the presence of centripetal primary xylem and to the latter

[1] .- Hirmer(1927), p. 344.

[2] .- Scott(1908), p. 157.

[3] .- Lotsy(1909), p. 529.

[4] .- Scott(1920), p. 32; Hirmer(1927), p. 383.

in the branching of the stems and roots and in the more detailed structure of the xylem of the stem.

This genus thus links these two groups together, but that is not to say that they are in direct phyletic sequence.

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# EXPLANATION OF PLATES.

## *Protocalamites sp.*

### Plate 1.

Fig. 1. Transverse section of a primary stem, x 48.

Fig. 2. Transverse section of a stem at commencement of secondary thickening. x 40.

Note - large amount of centripetal and centrifugal primary xylem.

Fig. 3. Transverse section of an older stem. (From a peel off one of the Manchester blocks.) x 15.

Fig. 4. Transverse section of an older stem. x 34.

Fig. 5. Radial longitudinal section of an older stem, passing through a carinal canal. x 80.

p. = pith-
c.p.= centripetal primary xylem.
c.f.= centrifugal " "
p.x.= protoxylem canal.
s. = secondary wood.

Fig. 6. Drawing of tracheides in radial view, showing uniseriate pitting. x 410.

Fig. 7 Drawing of tracheides in tangential view. x 200.

m.= medullary-ray.
p.= pits in section.

Fig. 8. Transverse section of a stem, showing lacunar cortex. x 11.

## Plate 2.

Fig. 9. Tangential longitudinal section of the secondary wood. x 55.

x. = portion drawn in Fig. 8.

m. = long medullary-ray.

Fig. 10. Radial longitudinal section of a stem, passing through a carinal canal. x 172.

p. = special type of pitting in centripetal xylem.

Fig.11. Portion of Transverse section of a stem, showing leaf-trace departing from the protoxylem. x 82. Note - scalariform pitting in centripetal xylem.

Fig.12. Radial longitudinal section through a node. x 17.

l.t. = leaf-traces.

p.x. = protoxylem canal.

Fig. 13. Tangential longitudinal section of a stem, showing two adventitious roots. x 28.

l.t. = leaf-traces.

Fig. 14. A more external tangential section of same stem as in Fig. 13, showing exit of root. x 28.

## Plate 3.

Fig. 15. Transverse section of young triarch root. x 70.

Fig. 16. Transverse section of older root (tetrarch). x 40.

Fig. 17. Transverse section of root, showing clearly the four protoxylem angles. x 70.

p.x. = protoxylem.

Fig. 18. Transverse section of a root, showing cortex. x 15.

Fig. 19. Transverse section of a large root, showing exit of a smaller root. x 12.

Fig. 20. Transverse section of the smaller root, shown in Fig, 19, dichotomising. x 20.

Fig. 21. Longitudinal section of a bifurcating root. x 20.

## Plate 4.

Fig. 22 (a-f). Diagrammatic drawings of sections taken at the levels indicated in the node, shown in Fig. 25 (Pl.5).

(a) - l.b.= lateral branch, the primary bundles of which are indicated by dotted lines.
sh.= leaf-sheath of parent stem.
l.= leaf-segment.
(b) - p.= parent stem.
c.= carinal canal.
(d) - l.b.= lateral branch inserted in parent stem.

Nos. 1-5,1'-4' refer to the leaf-traces.

In (d),(e) and (f) the closely dotted lines represent the xylem tracheides of the parent stem.

## Plate 5.

Fig. 23. Transverse section of a lateral branch, showing leaf-sheath of parent stem attached. x 20.

l. = Transverse section of a leaf-segment.
l.t.,1',1 & 2 = leaf-trace bundles in the leaf-sheath.

Fig. 24. Transverse section of an isolated leaf. x 40.

pal. = palisade layer.

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pal. = palisade layer.

Fig. 25. Diagram of a hypothetical reconstruction of a node. Dotted lines represent level of the various sections in Fig. 22 (a-f).

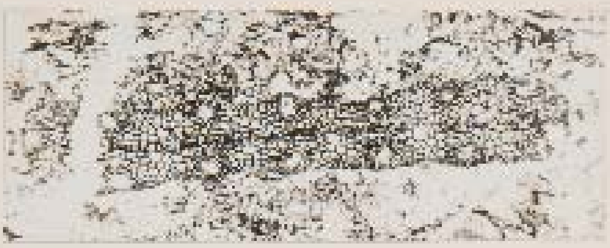
Fig. 26. Diagram of Vascular tissue at the node.

b. = that of branch.
s. = " " stem.
l. = " " leaf.

Fig. 27. Diagram of the course of the Vascular strands in the stem.

clear circles = position of leaf-traces.
black circle = position of lateral branch.

# PLATE 1.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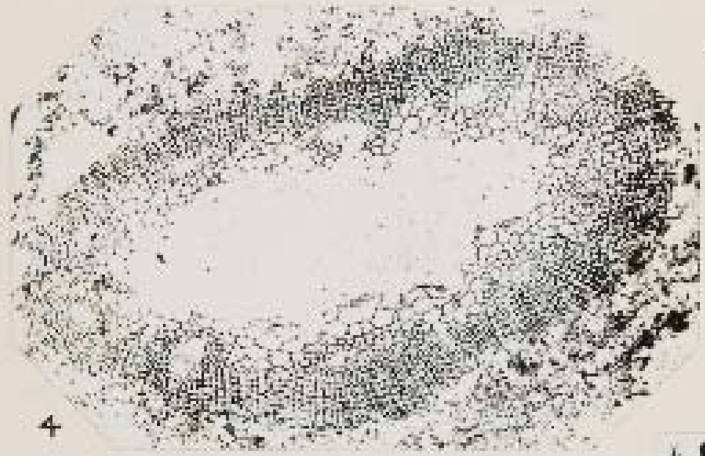
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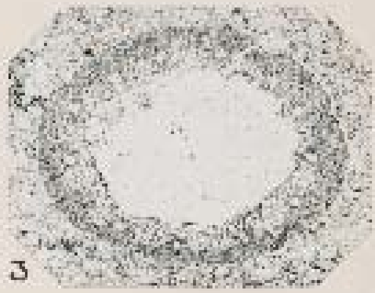
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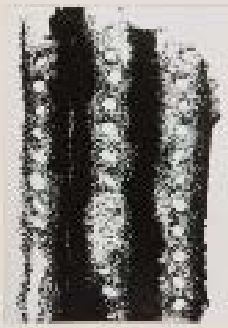
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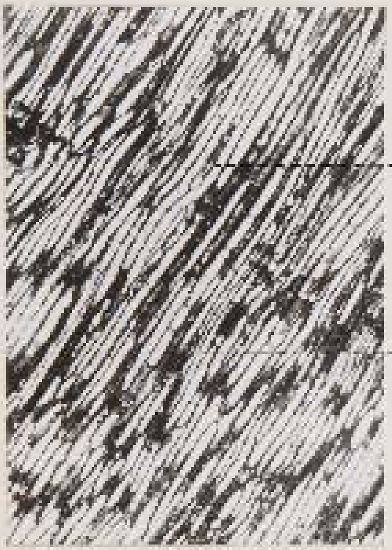

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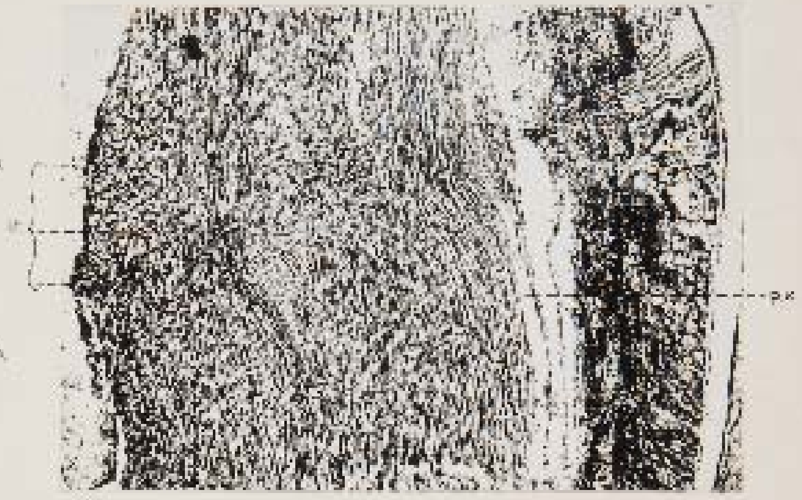

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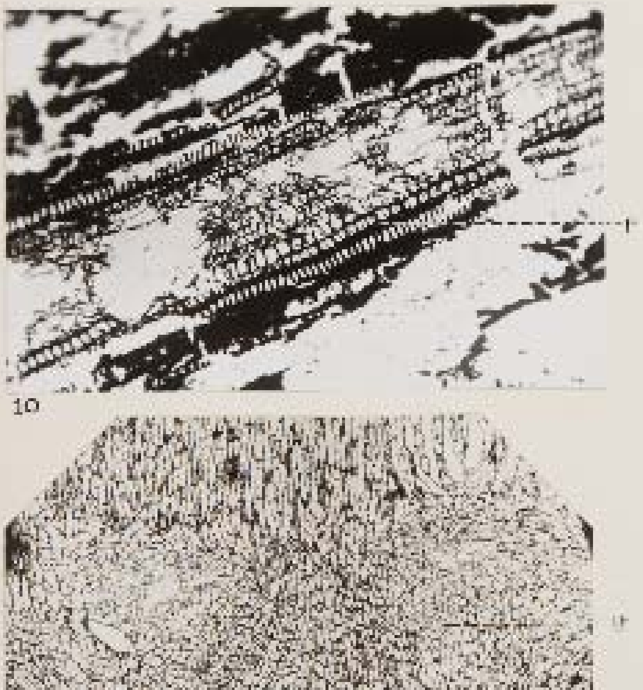

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# PLATE 3.


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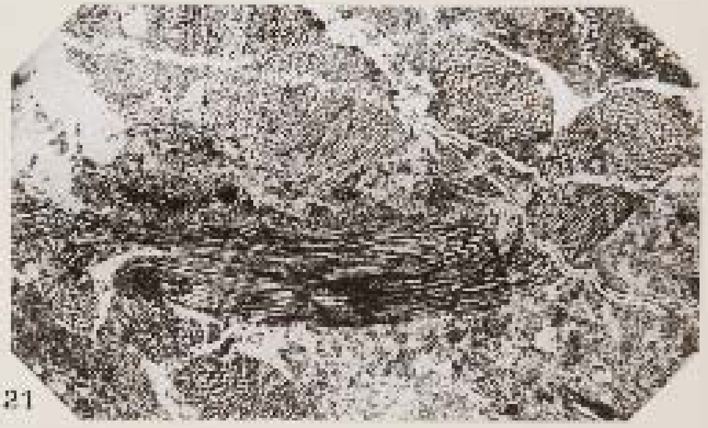
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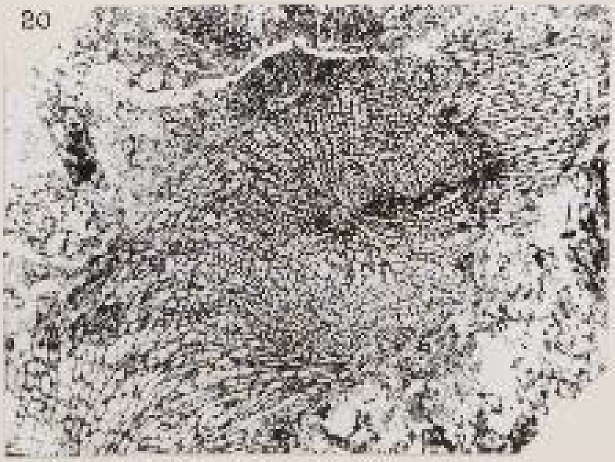


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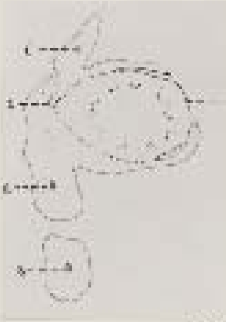

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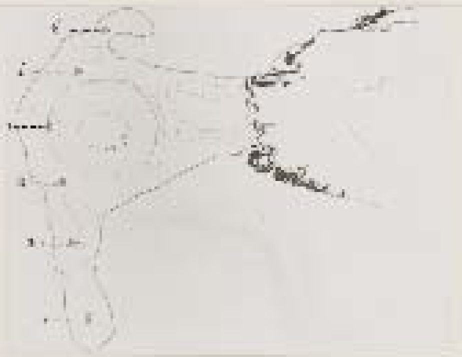

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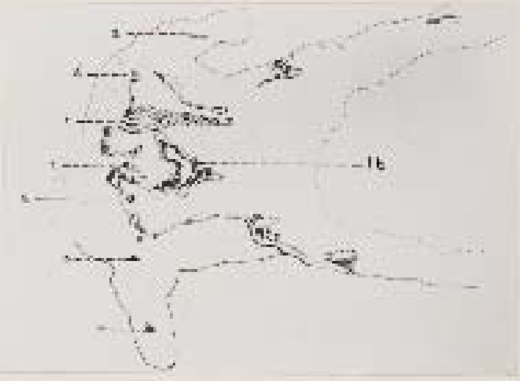

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e.

f.

# PLATE 5.

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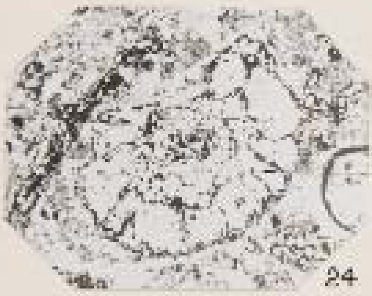

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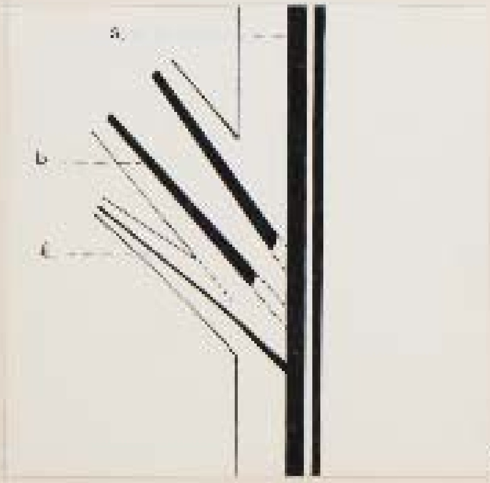

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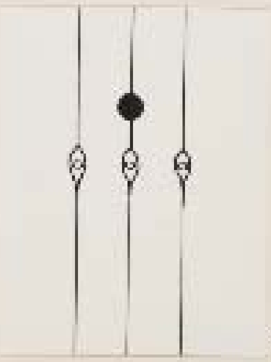

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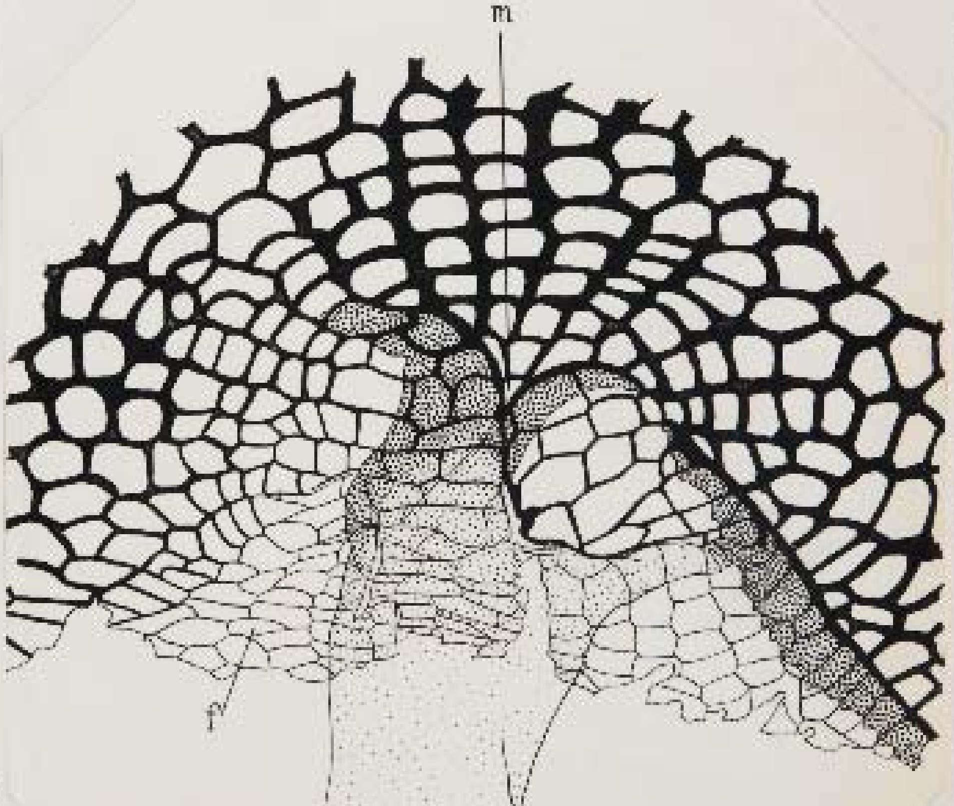
PLATE I.

Fig. 1.

Fig. 2.



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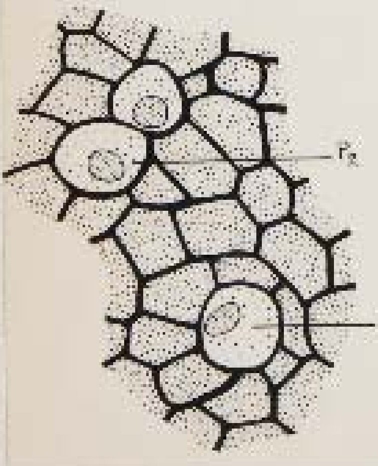


Fig. 4.

PLATE II.

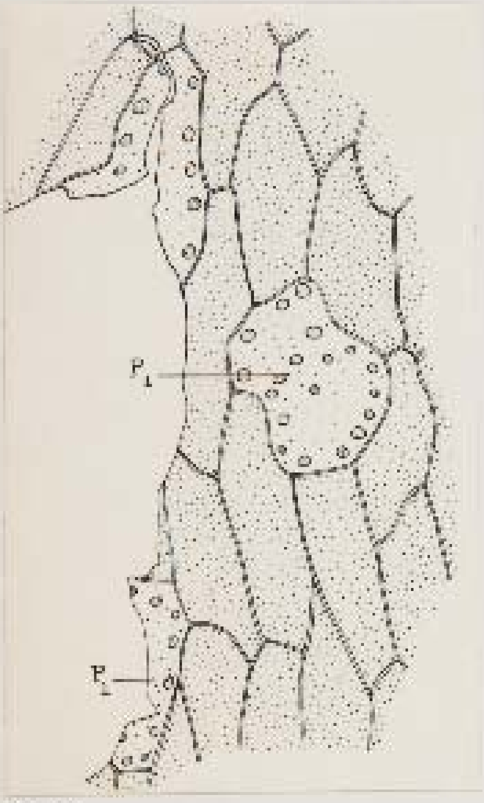


Fig 5.

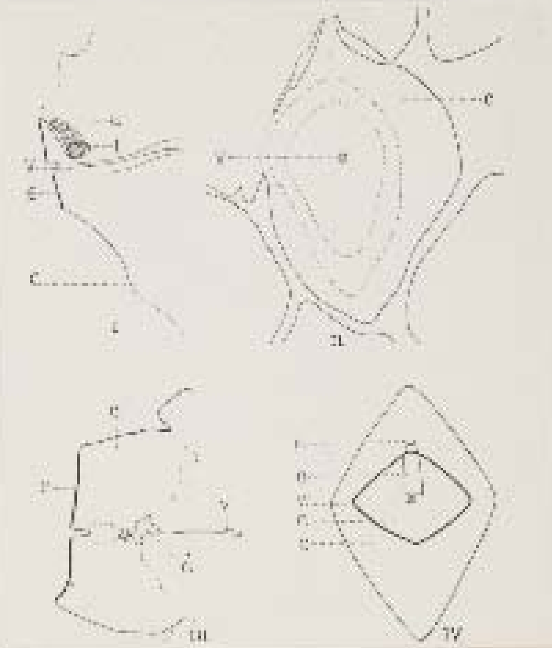


Fig. 8

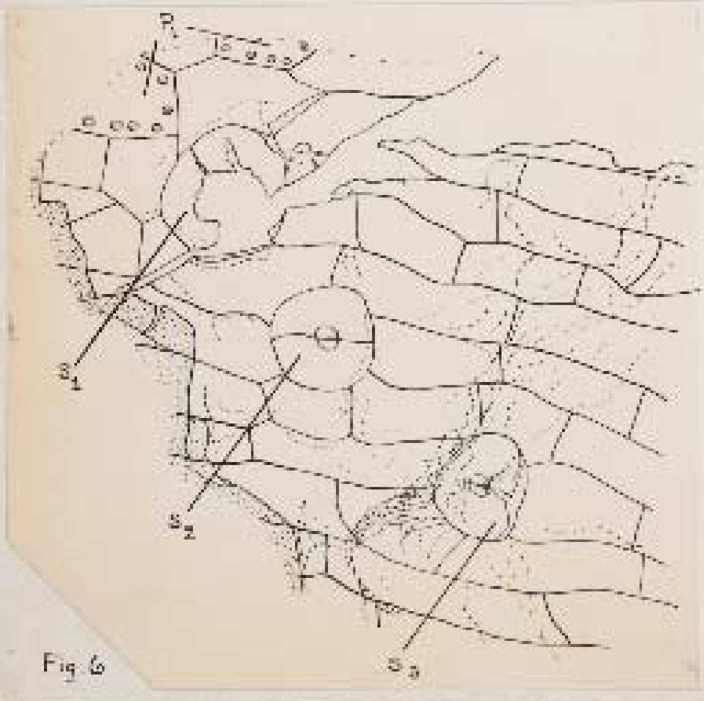


Fig 6

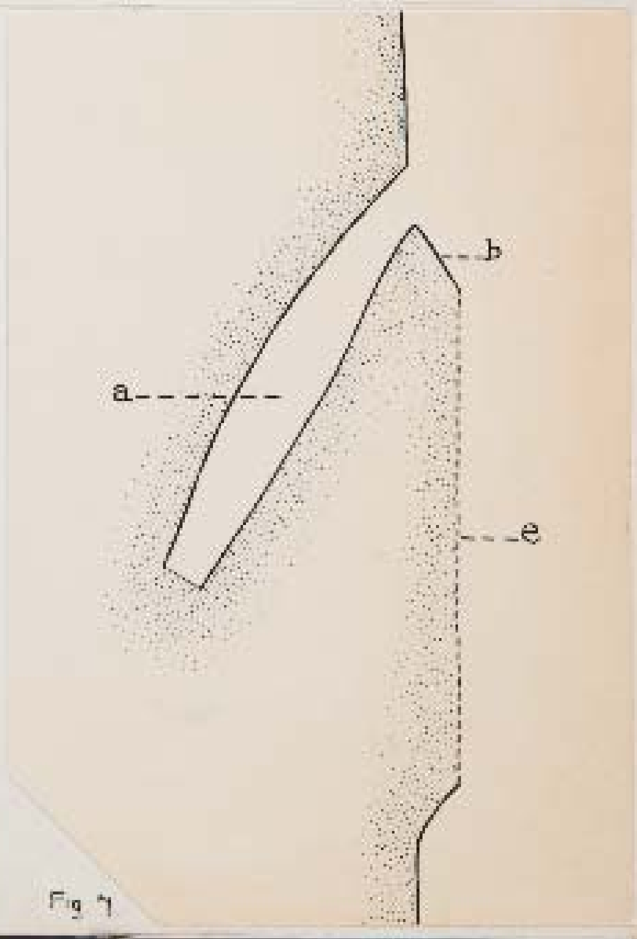
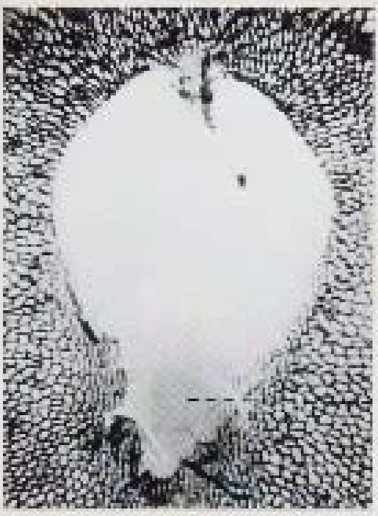


Fig 7

# PLATE III.



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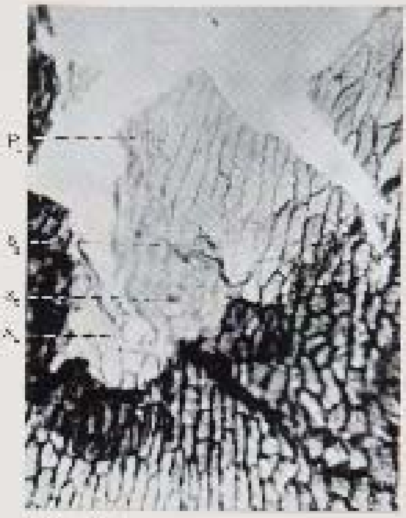

Fig. 10

Fig. 12.

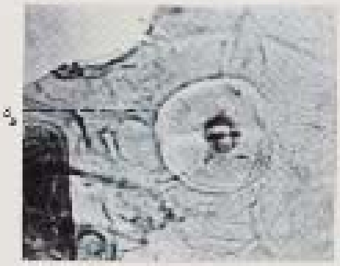

Fig. 11.

Fig. 13.