On the Presence of a Parichnos in Recent Plants.

BY

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With Plates XIX and XX.

THE term Parichnos was used by Bertrand [1] to designate the thin-walled parenchymatous strand of tissue, occurring in *Lepidodendron Harcourtii*, which accompanies the leaf-trace on the posterior side during its outward journey. It is described as originating in the middle cortex, and during its passage through the suberized zone—i. e. the outer cortex—the strand bifurcates, the two branches diverge, and eventually occupy a position one on each side of the foliar bundle, forming the well-known lateral prints on the leaf-scar, as seen on casts.

These facts were corroborated by Hovelacque [2] for *Lepidodendron Selaginoides* and by Williamson [3].

Essentially the same features occur in *Syringodendron*. Renault [4] has described the presence of two large lacunae, which accompanied the leaf-trace one on each side in *Sigillaria spinulosa*. He subsequently showed that these spaces were originally filled with a delicate tissue, traversed by secretory canals, and that each parichnos-strand was surrounded by a sheath of radially elongated elements.

Maslen [5], in his work on *Lepidostrobus oldhamius*, found that the parichnos was represented by an empty space of considerable size; there was no indication of branching, and, as regards this last point, he remarks that, 'this difference may perhaps be correlated with the small width of the proximal end of the pedicel, as compared with that of the leaf-base in the vegetative region.'

[1] Bertrand, Remarques sur le Lepidodendron Harcourtii de Witham. Travaux et Mémoires des Facultés de Lille. T. ii, 1891.

[2] Hovelacque, Recherches sur le Lepidodendron Selaginoides, Sternb. Mem. Soc. Linn. Normandie, xvii, 1892.

[3] Williamson, Organization of the Fossil Plants of the Coal Measures, part xix, Phil. Trans. Roy. Soc. Lond. B., 1893.

[4] Renault, Flore fossile d'Autun et d'Épinac.

[5] Maslen, The structure of Lepidostrobus. Trans. Linn. Soc. Lond., 2nd ser., Bot., vol. v, 1899.

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Scott [1] has called attention to the occurrence in the mature seed of *Lepidocarpon Lomaxi* of two gaps, one on either side of the bundle, which are strongly suggestive of a parichnos, and mentions that a really sharp differentiation of this tissue is only found near the base of the sporophyll. Further, when dealing with the structure of the axis of the strobilus, he remarks the presence in the sporophyll of a strand of large-celled tissue, which probably represents the parichnos of the vegetative leaf base of the Lepidodendreae.

Weiss [2] describes in *Lepidophloios fuliginosus*, a group of cells which, in connexion with each foliar bundle, passes through the outer cortex to the leaves where they form the so-called parichnos.

Thus it is obvious that the parichnos was a tissue of wide occurrence in the fossil forms of the Lycopodineae, and that it occurred both in the sporophyll and foliage leaf.

From a survey of the literature, still more so from the examination of the published figures, and from the actual preparations, one feature stands out with remarkable clearness, which is, that the different plants and specimens exhibit the parichnos preserved in very diverse conditions. At one extreme the tissue is represented by canals, as in the mature seeds and sporophylls of *Lepidocarpon* and *Lepidostrobus*; at the other extreme there is a very definite parenchymatous strand as described by Williamson, Bertrand, Hovelacque, Seward [3] and A. W. Hill [4], and others. In an intermediate position there are specimens showing the tissue in different stages of disintegration.

This feature is capable of a simple explanation, which is, that these seeming discrepancies are due, in many cases, to the fact that the parichnos has been preserved in different stages of development: the empty canal being the mature structure.

Whether this be true for all cases, palaeophytologists will be able to judge far better than the writer.

Turning to what has been termed [5] parichnos in recent plants, it may be seen best in *Isoetes Hystrix*.

The mature sporophyll of this plant exhibits two canals (Fig. 1) running longitudinally, and situated, one on each side of the sporogenous mass, in

[1] Scott, D. H. The seed-like fructification of Lepidocarpon, a genus of Lycopodiadaceous cones from the Carboniferous formation. Phil. Trans. Roy. Soc. Lond., vol. cxciv, 1901.

[2] Weiss, A biseriate Halonial branch of Lepidophloios fuliginosus. Trans. Linn. Soc. Lond., 2nd ser., Bot., vi, 1903.

[3] Seward, Notes on the Binney Collection of Coal-Measure plants, part i: Lepidophloios. Proc. Phil. Soc. Cambridge, x, 1899.

[4] Seward and A. W. Hill, On the structure and affinities of a Lepidodendroid stem from the calciferous sandstone of Dalmeny (Scotland), probably identical with Lepidophloios Harcourtii, Witham. Trans. Roy. Soc. Edin., xxxix, 1900.

[5] Hill, T. G., On the presence of Parichnos in Recent Plants. Brit. Assoc., Sect. K., Cambridge, 1904.

the lateral expansions of its base. The passages when mature (Fig. 4) contain mucilage, and, unlike the parichnos of fossil plants, they do not extend into the cortex of the stem, but are entirely confined to the base of the sporophyll, their limits seemingly depending on the extension of the sporangium.

Their development follows the normal course for lysigenous mucilaginous degeneration.

The first appearance is indicated by the swelling of the walls of the parenchyma, and the gradual disappearance of the cell-contents. This is shown by the marked density of the staining, as compared with the surrounding tissue (Fig. 2). The process of degeneration goes on rapidly, and lacunae appear, so that there is formed a central cavity (Figs. 3, 4, 15 and 17). This cavity gradually extends radially, ultimately resulting in an extremely well-marked mucilage-canal more or less circular in outline.

As regards the sterile leaves, *Isoetes Hystrix* does not form many, and, apparently, they do not possess the parichnos-strands.

Unfortunately it has not been possible to examine satisfactory material of any other species of *Isoetes* with the exception of *I. lacustris*, which plant does not show any sign of the structure in question.

Other living representatives of the Lycopodineae have naturally been examined.

In the case of *Lycopodium*, Hegelmaier [1] showed that the leaves of *L. inundatum* and *L. alopecuroides* are traversed throughout their whole length by a mucilage-canal, which enters the cortex of the axis where it ends blindly. In the young leaves, these canals are represented by thin strands of parenchymatous tissue somewhat merismatic in appearance. De Bary [2] draws attention to similar passages occurring in the marginal expansions, on the dorsally winged sporophylls, of *L. annotinum*.

Jones [3] corroborates Hegelmaier regarding the presence of the mucilage-canals in *L. inundatum*, and states that these structures were not observed in the vegetative leaves in the other species examined, viz. *L. alpinum*, L., *L. annotinum*, L., *L. cernuum*, L., *L. Chamaecyparissus*, A. Br., *L. clavatum*, L., *L. complanatum*, L., *L. Dalhousieanum*, Spring., *L. nummularifolia*, Blume., *L. obscurum*, L., *L. Phlegmaria*, L., *L. Selago*, L., *L. serratum*, Thunb., and *L. squarrosum*, Frost.

Many of these species have been examined by the writer, who corroborates the observations made by Jones regarding this point, with the exception of the case of *L. cernuum*. Although the mucilage-canals are frequently absent from the vegetative leaves, they are often present in the

[1] Hegelmaier, Zur Morphologie der Gattung Lycopodium. Bot. Ztg., 1872.

[2] De Bary, Comparative anatomy of the Phanerogams and Ferns. Oxford, 1884.

[3] Jones, The morphology and anatomy of the stem of the genus Lycopodium. Trans. Linn. Soc. Lond., 2nd ser., Bot., vii.

sporophylls. Thus it has been found that the following plants have more or less extensive mucilage-cavities in the strobili, but not in the ordinary vegetative parts :—*L. alpinum*, *L. annotinum*, *L. caroliniatum* and *L. clavatum*. On the other hand these passages have not been seen in any part, vegetative or reproductive, of *L. Phlegmaria*, *L. squarrosum*, and *L. complanatum*. *L. cernuum* has the structure particularly well marked both in the cone and vegetative regions (Figs. 12 and 13).

Taking for an example *L. clavatum*, it has been found that the development follows an essentially similar course to that already described for *I. Hystrix*, hence no detailed description is requisite.

A series of transverse sections through a young sporophyll (Figs. 5, 6, 7 and 8) demonstrate, that in the more distal regions the young parichnos consists of two rather ill-defined strands, which in passing towards the axis rapidly merge one into the other, so that when the stem is reached a broad zone of disorganizing tissue is produced. The examination of longitudinal sections shows that this lysigenous degeneration extends from the sporophyll into the cortical region of the stem downwards, almost as far as the insertion of the next leaf (Figs. 9, 10 and 11). When the canal is fully formed, the parichnos forms a single continuous structure, and it shows no signs of bifurcation ; indeed, it is only in the youngest stages of development that a double origin can be made out, and then only at its distal limits in the sporophyll. Thus a difference is exhibited between this plant and *Isoetes*, but it is to be borne in mind that the same dissimilarity occurs in different fossil plants ; for example, *Lepidostrobus* has a parichnos consisting of a single cavity, while *Lepidocarpon* possesses the more usual double arrangement.

A certain amount of variation is to be found in the strobili of different species of *Lycopodium*, more especially as regards the extent of the tissue-alteration. This, however, is a minor point of no consequence, and seemingly depends on the shape and other morphological features of the sporophylls.

The vegetative leaf of *L. cernuum* has a prominent canal, and contrary to what obtains in the sporophyll, where the cavity never, in any of the species examined, extends much beyond the region of the sporangium, it traverses the greater part of the leaf, and comes to an end in the cortex of the axis.

Owing to the lack of suitable material, the development of the parichnos of the vegetative regions has not been worked out : there is, however, no reason to suppose that it follows a course in its formation other than the normal.

As regards other genera of the Lycopodineae, many species of *Selaginella* have been examined, but in no case has anything approaching a parichnos been detected, nor has any reference to the existence of mucilage-ducts been found in the literature dealing with the structure of this genus.

This is a result which might have been expected on account of the relative smallness of the leaves. *Phylloglossum* also has given negative results.

The reasons for considering these canals as representing essentially the same structure as the parichnos of fossil plants are sufficiently obvious, and may be briefly enumerated :—

1. Both in recent and fossil plants they occupy the same relative position. On the one hand there is a double strand with the vascular bundle between and slightly above, as in *Lepidophloios* (Fig. 14) and *Isoetes* (Fig. 15); on the other, a single strand beneath the vascular bundle, as in the case of *Lepidostrobus* and *Lycopodium* (Figs. 12 and 13).

2. The appearance in section is frequently identical. The hollow canals of *Lepidocarpon*, for instance, may be compared with the mature structure in *Isoetes*. The parenchymatous strand in *Lepidodendron* is similar to some of the early stages in the development of the canals in *Isoetes* and *Lycopodium*. Thus Figs. 16 and 18, representing the parichnos of *Lepidophloios* and *Lepidodendron* respectively, may be compared with Figs. 15 and 17, illustrating a stage in the development of the mucilage-duct in *Isoetes Hystrix*.

The main point of dissimilarity lies in the fact that in *Isoetes* the parichnos does not extend into the cortex.

This may be considered an unimportant matter—that so ancient a feature should be altered somewhat in recent plants is to be expected, the surprising thing would be to find the tissue entirely identical both in recent and fossil plants.

Function.

It is manifestly a matter of no inconsiderable difficulty to assign a definite function to a tissue of so specialized a nature as the parichnos occurring in fossil plants. Consequently, it is not surprising to find that in this respect the authorities differ. Hovelacque considered the tissue as being glandular, with which view both Williamson and Bertrand disagreed. Renault regarded the tissue as representing gum-canals, Potonié as transpiratory organs. Scott [1], while admitting the possibility of the secretory function, points out that 'the persistence and enlargement of the parichnos on the surface of old stems suggests a respiratory function like that of lenticels.' This view is also held by Weiss [2], who suggests that the parichnos was probably 'a respiratory organ, allowing a passage of air from the leaves into the inner portion of the stem and down into the roots.' He compares the structure with 'the trabecular tissue of various species of *Selaginella*, which also accompanies the leaf traces, and probably has the same function as the middle cortex and the parichnos, but the persistence of the parichnos on the leaf scars of the old stems of *Lepidodendra* enabled

[1] Scott, Studies in Fossil Botany, London, 1900. [2] Loc. cit.

them also to supply the place of the lenticels of the recent dicotyledonous trees.'

As regards the parichnos of recent plants, I believe that it is primarily concerned in the production of mucilage, which would be of value to the reproductive organs in preventing their desiccation in times of comparative drought. And it is primarily for this reason that the structure has persisted.

The fact that the parichnos is chiefly restricted to the sporophylls of recent plants, as far as has been seen, bears out this opinion. If this view be accepted, it would explain why, in a plant like *Isoetes lacustris*, the parichnos does not occur ; for, of course, its presence would be quite unnecessary in a plant which leads a submerged aquatic existence.

It does not follow, however, that this was the function in the plants of past ages. In some cases this rôle may have been performed, more especially where the parichnos occurred in the strobili. But, on the other hand, it may not hold in those cases where the tissue occurs in the vegetative leaves. In some instances, the appearance of the parichnos does warrant the assumption that it was of a secretory nature; contrariwise the facts relating to their persistence, enlargement, and lenticel-like nature in many cases favour the views held by Scott and Weiss. It may be remarked that this latter opinion is not necessarily antagonistic to the former, for it is possible that a secretory function was first performed, and, when the leaves had been shed, was followed by a respiratory rôle.

It may be remarked that if any phylogenetic value be assigned to the parichnos, then its presence in *Isoetes* gives additional support to the view that this plant belongs to the Lycopodineae. The writer is of the opinion that the parichnos has a phylogenetic value.

In conclusion, I desire to express my thanks to Dr. D. H. Scott, F.R.S., Professor F. W. Oliver, F.R.S., Mr. E. C. Jones, F.L.S., and the Authorities of the Royal Gardens, Kew, for their kindness in supplying material. It should also be mentioned that this research was commenced in the Jodrell Laboratory, Kew, and finished in the Medical School of St. Thomas's Hospital.

EXPLANATION OF PLATES XIX AND XX.

Illustrating Mr. Hill's paper on the Parichnos.

Abbreviations :—*li.*, ligule ; *p.*, parichnos ; *s.*, sporangium ; *s. m.*, sporogenous mass ; *sp.*, sporophyll ; *t.*, trabeculae ; *v.*, velum ; *v. b.* vascular bundle ; L. S., longitudinal section ; T. S., transverse section.

Fig. 1. *Isoetes Hystrix.* Diagram of T. S. through the base of the sporophyll.

Fig. 2. *Isoetes Hystrix.* T. S. through the base of a sporophyll, showing the commencement of the mucilaginous degeneration.

Figs. 3 and 4. Later stages of the same.

Figs. 5, 6 and 7. *Lycopodium clavatum.* Series of transverse sections of a sporophyll through the region of the sporangium, showing the gradual increase in the mucilaginous degeneration as the proximal end of the sporophyll is reached (Fig. 7). The three figures do not represent sections in an uninterrupted sequence.

Fig. 8. *Lycopodium clavatum.* Part of Fig. 7 more highly magnified.

Figs. 9, 10 and 11. *Lycopodium clavatum.* L. S. sporophyll and stem. Parichnos in different stages of development.

Fig. 12. *Lycopodium cernuum.* T. S. stem, showing foliage-leaves with the parichnos.

Fig. 13. *Lycopodium cernuum.* L. S. sporophyll, showing dehisced sporangium and the parichnos below.

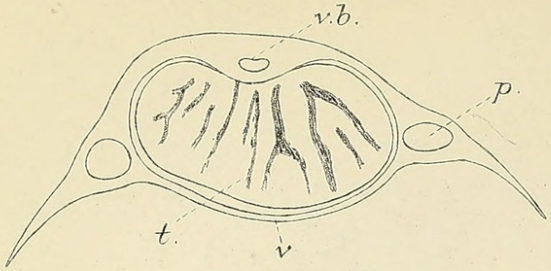
Fig. 14. *Lepidophloios* (Will. Coll., 1974 A). Photograph of part of T. S. of leaf.

Fig. 15. *Isoetes Hystrix.* Photograph showing many sporophylls in T. S. The parichnos is seen in various stages of development.

Fig. 16. Part of Fig. 14 more highly magnified.

Fig. 17. Part of Fig. 15 more highly magnified.

Fig. 18. *Lepidodendron.* T. S. leaf, showing parichnos.



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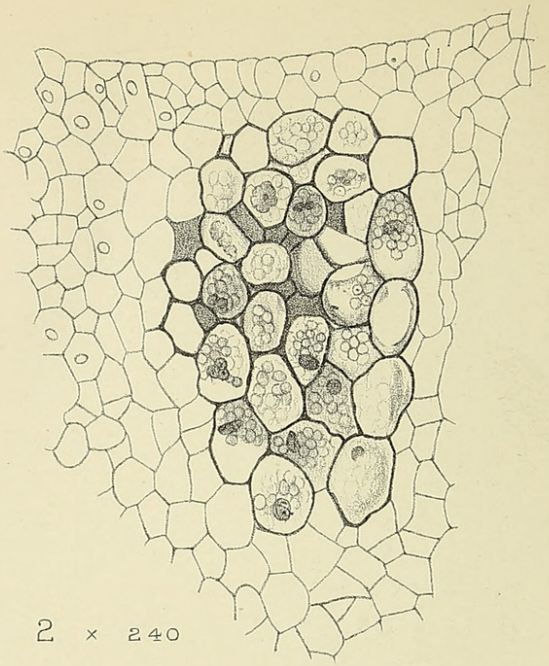

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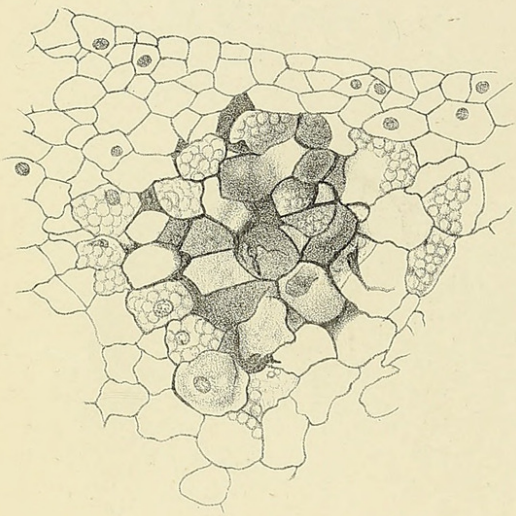

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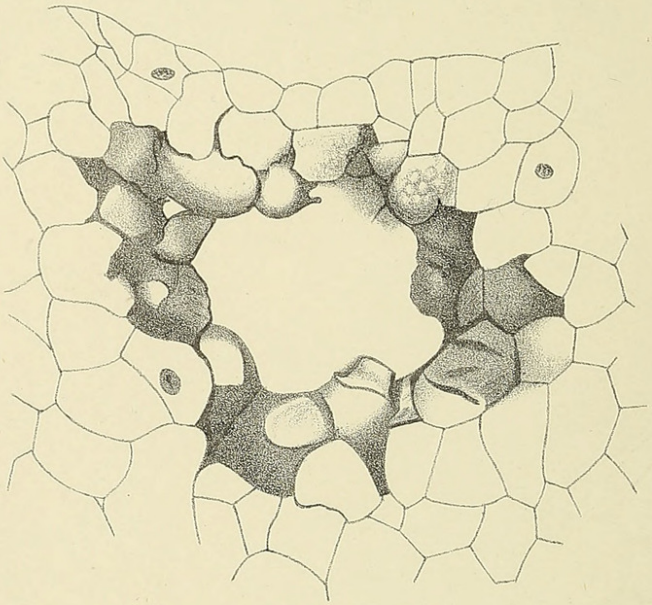

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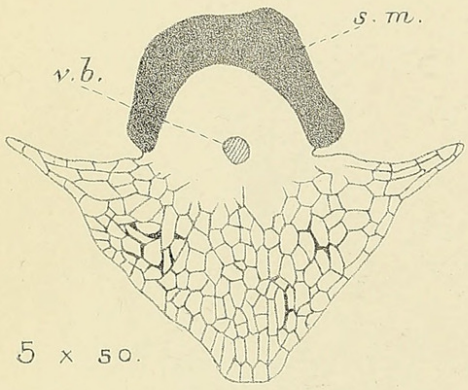

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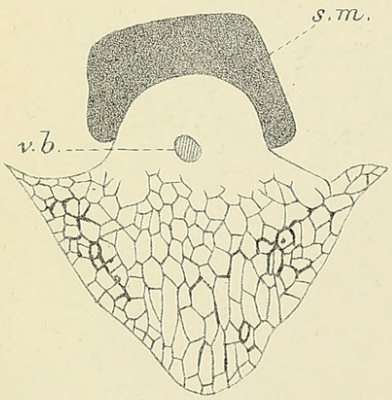

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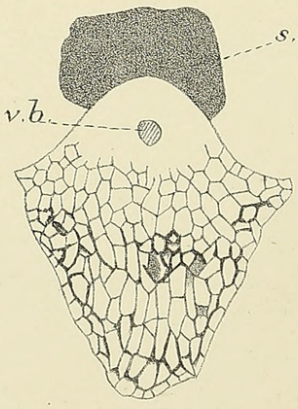

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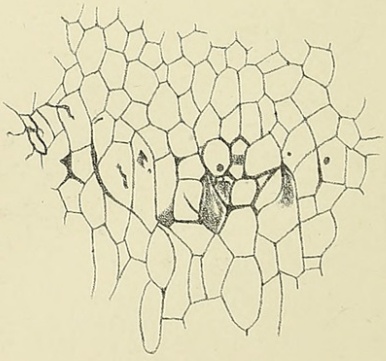

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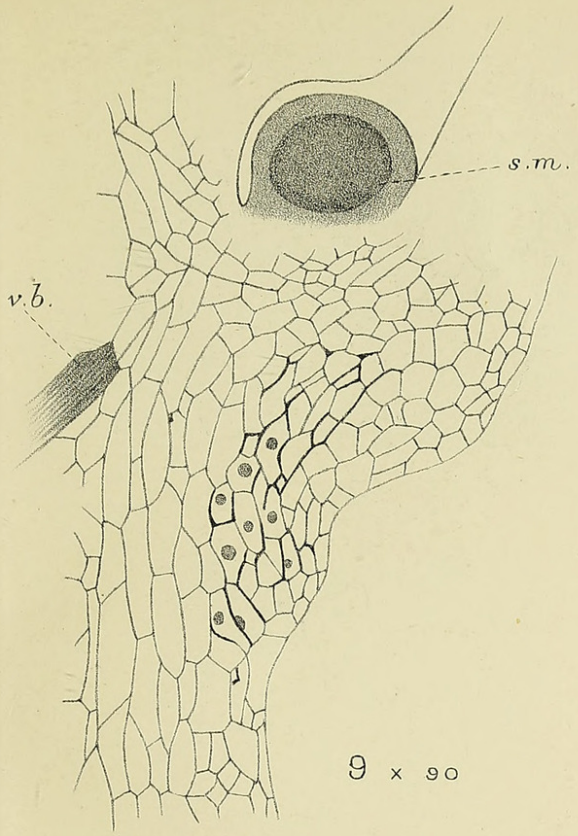

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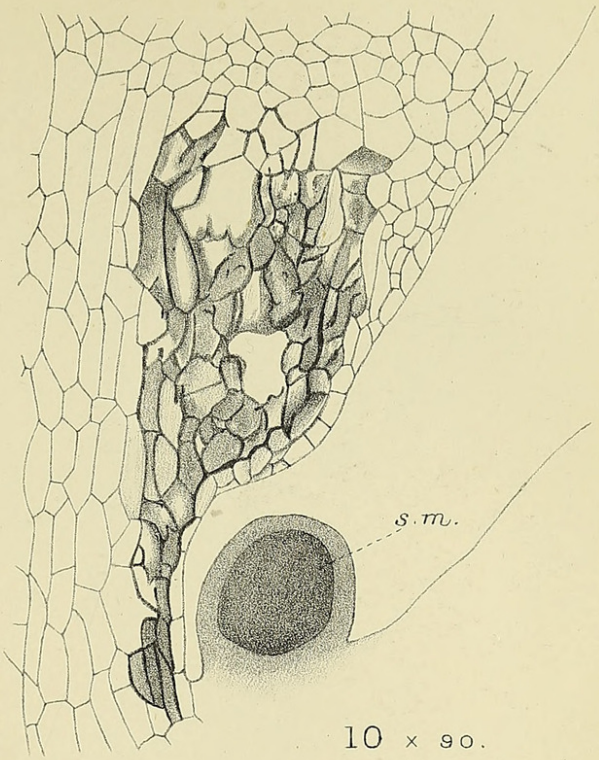

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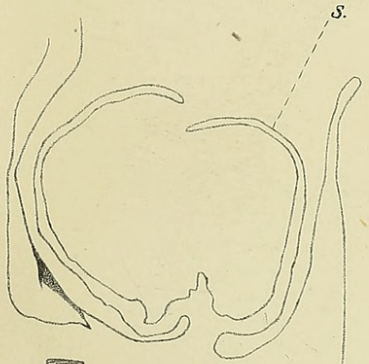

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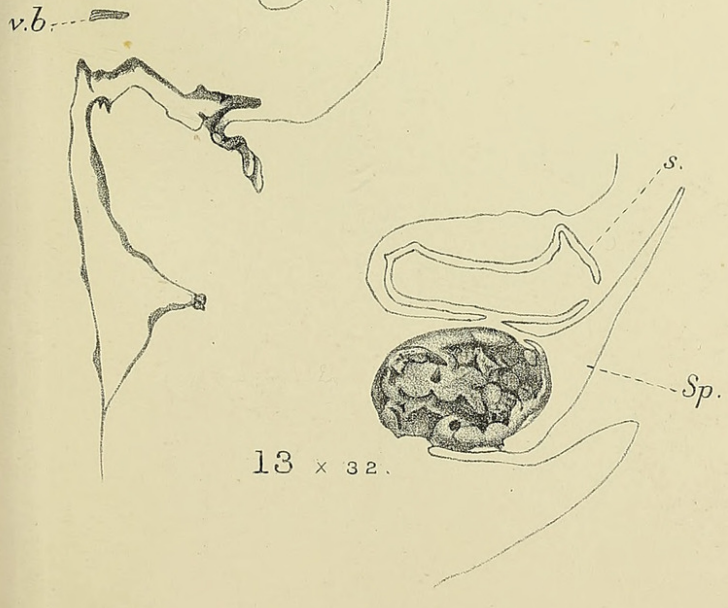

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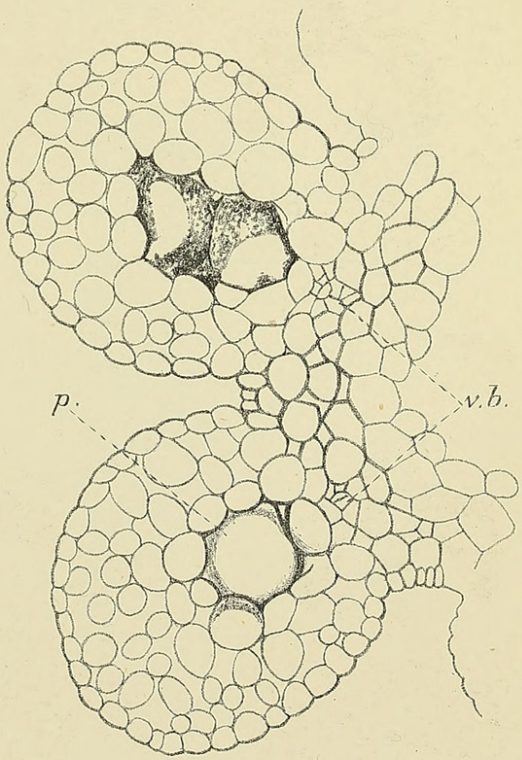

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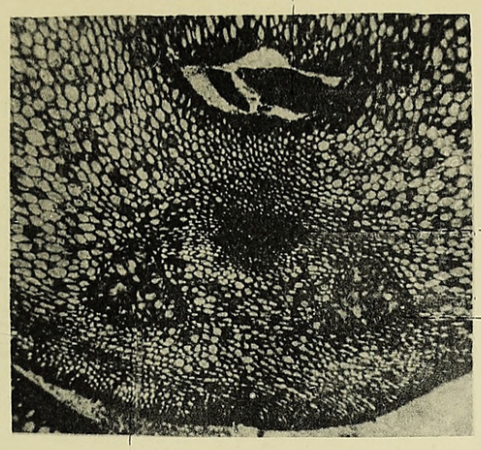

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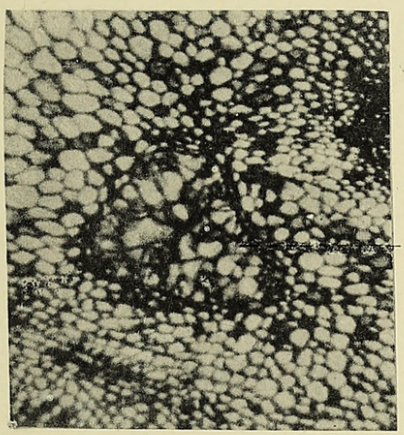

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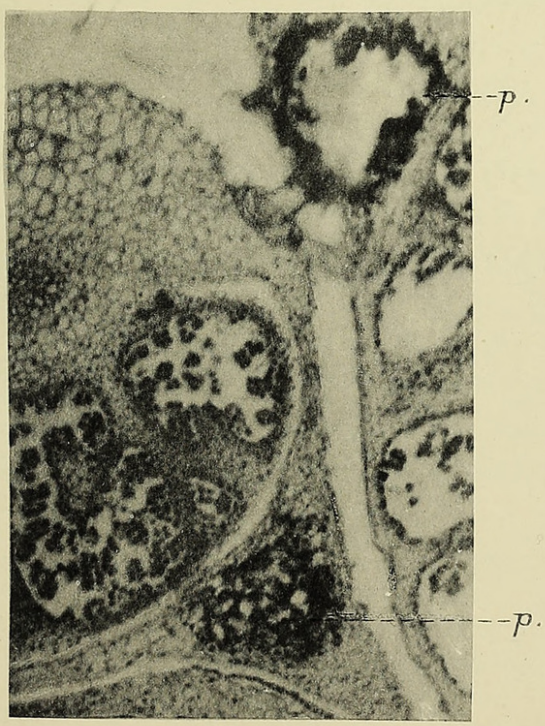

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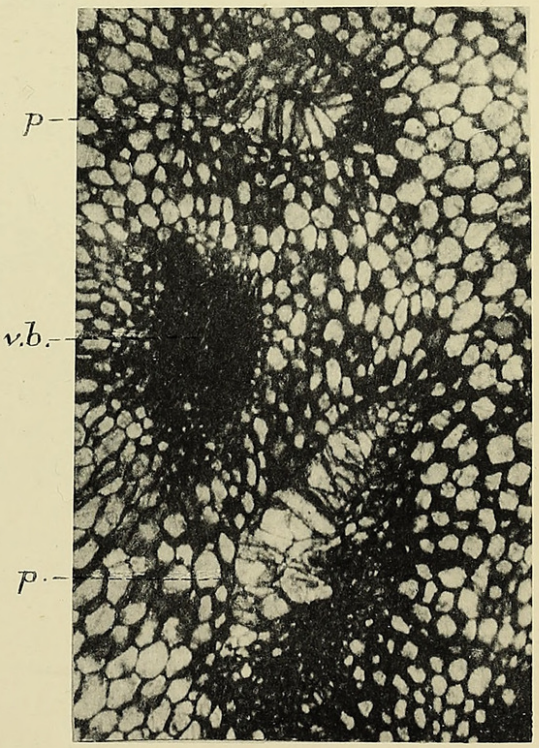

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