On the Primary Xylem, and the Origin of Medullation in the Ophioglossaceae.

BY

F. O. BOWER, Sc. D., F.R.S.

Regius Professor of Botany in the University of Glasgow.

With Plates XLV and XLVI.

BOTRYCHIUM is the only genus of living Ophioglossaceae which shows secondary thickening of its axial stele. The greater part of the vascular tissue of the axis owes its origin to the cambium, so much so that in some cases 'the wood is practically all secondary, as may be learned from the radial arrangement of its matured elements'.¹ This prevalence of the secondary tissues has diverted attention from the primary tissues, which are apt to be ignored in the descriptions which are given of the structure of the axis. But for purposes of comparison with other genera of the family, and with other Pteridophytes, it is desirable that the primary tissues should be recognized, so far as they are present in *Botrychium*. It is the object of this paper to bring them more clearly forward than has hitherto been done.

In the mature axis of all the genera of this family there is a central pith, and the xylem as seen in transverse sections forms a more or less interrupted ring surrounding it. The interruptions are caused by the departure of the leaf-traces, each consisting of a single strand, excepting in the more specialized species of *Ophioglossum*.² In the pith an endodermal structure has been observed, but not with any high degree of constancy. This internal endodermis was first described by Van Tieghem,³ in young plants of *Ophioglossum vulgatum*: it was also seen in young plants of *Botrychium Lunaria*, and its origin traced by involution of the outer endodermis at the leaf-gap, the foliar strand being there detached with its special pericycle and endodermis. Van Tieghem described⁴ how 'the endodermis of the central cylinder, thus open, folds its two margins inwards, where they extend and rejoin around the pith, which is thus incorporated

¹ Jeffrey, Gametophyte of *Botrychium virginianum*, 1898, p. 22.

² Bower, *Annals of Botany*, vol. xviii, p. 215, and vol. xxv, p. 278.

³ *Journal de Botanique*, 1890, p. 405.

⁴ *Loc. cit.* p. 407.

with the cortex.' This was probably the first example of encroachment of the cortex upon the stele to be observed or described in vascular plants. The same author further pointed out that between the invaginated endodermis and the internal margin of the wood one or two layers of parenchyma intervene, which are continuous at their margins with the pericycle. So, according to his view, the pericycle is invaginated like the endodermis. Further up the axis the internal endodermis separates completely from the external, and henceforth there are two distinct layers of endodermis, one external, the other internal. This structure is continued upwards, but above the fourth leaf the internal endodermal characters were gradually lost, and in the adult plant there is only a single endodermis, i. e. the external. An internal endodermis was not found in *B. ternatum*, *virginianum*, or *daucifolium*, but it was clearly seen in *B. boreale*.

There were no illustrations of the data thus described by Van Tieghem, but subsequently M. G. Poirault, to whom the observation appears to have been in the first instance due, delineated the internal endodermis for *B. Lunaria*, and also for *Ophioglossum Bergianum*, in both cases finding it present only at the base of the plant.¹ An internal endodermis has since been found, and described in the old stocks of *Helminthostachys zeylanica*.² A current view which has been based upon these descriptions is that the pith of the Ophioglossaceae is to be ranked as intrusive cortex, with a lining of endodermis and pericycle. In the case of *Botrychium* the primary wood would then lie, such as it is, between the parenchyma which Van Tieghem described as internal pericycle and the zone of secondary wood.

It seemed desirable, in view of the advances in stelar investigation in other plants, to look again into the facts relating to the Ophioglossaceous stele. There is a general opinion that here, as elsewhere, the stelar condition has been ultimately derived from the solid protostele. Van Tieghem describes this structure for *Ophioglossum vulgatum* (loc. cit., p. 405) and *Botrychium Lunaria* (loc. cit., p. 407). In *Ophioglossum vulgatum* Van Tieghem states that 'in the whole region below the first leaf there is a central cylinder which is slender and without pith' (loc. cit., p. 405). I do not find this to be constant in plants sprung from adventitious buds on the roots. A pith may be present in these from the very first. The same medullated condition is found to be the case in some specimens of *O. reticulatum*, but others show a solid xylem up to a point immediately below the departure of the first leaf-trace. In *O. palmatum* such young plants as were observed were medullated from the first (Pl. XLV, Fig. 1). It appears, therefore, that variability exists within the genus *Ophioglossum* in respect of the medullation of the individual in the young state. There is some reason for believing that the existence or non-existence of a pith from the first

¹ Poirault, Ann. Sci. Nat., 1893, pp. 169, 170.

² Farmer and Freeman, Annals of Botany, vol. xiii, p. 421, Pl. XXII, Fig. 11.

depends upon the nourishment of the young plant. If it be well nourished the non-medullated phase is omitted, and pith is present from the first. But it is in ill-nourished or depauperate plants that the start is made with a protostele, which subsequently becomes medullated.

It will be important to observe the exact method of origination of the pith as it first appears in the protostele, in order to form an opinion on its morphology. The first appearance of the pith in a plant with a solid protostele at the base has been followed in *O. reticulatum*, and it is illustrated in the Figs. 2-5. At first the solid xylem-core is without parenchyma, being composed only of tracheides. But a little below the origin of the first leaf-trace, single cells, or small nests of them, retaining their thin walls and protoplasmic contents, appear among the mature tracheides (Fig. 2). Passing upwards, these merge into a central parenchymatous pith, which, however, at first has no clear limit from the xylem. Tracheides and parenchyma are intermixed (Figs. 3, 5). This continues only for a short distance, the pith consisting subsequently of pure parenchyma, which is then continued without interruption upwards. The surrounding ring of tracheides very shortly opens, throwing the pith into communication with the outer conjunctive tissue of the stele. This is the first step in the segregation of the leaf-trace (Fig. 4).

There can be no doubt that the parenchyma nests which precede the first establishment of the pith, and merge with it, are not only intrastelar, but also intraxyletic, in origin. A proportion of the pith may, however, owe its origin to an intrusion of the outer conjunctive tissue: but this source also is intrastelar. The similar origin of an intrastelar pith to be described below for *Botrychium Lunaria*, where the endodermis is clearly defined, confirms this conclusion.

The well-known imperfection of the endodermis in *Ophioglossum* is certainly a difficulty in the interpretation of the development of the young plant in most species of the genus. But on the other hand, the small species, *O. Bergianum*, has been quoted by Poirault (loc. cit., p. 170, Fig. 12), as having not only an external, but also an internal endodermis, the latter in the pith. I have cut the stock of my only specimen into transverse sections, but with negative results. No endodermis of the axis was found to take the safranin stain, though that of the roots, wherever present, showed up well in the same sections, with the same stain, and on the same slides. The structure was, however, conformable otherwise to that shown by Poirault, and I have no reason to doubt his observations, which were probably made on more favourable material. But it appears that the development of the endodermis is variable in the species. The above plant was sent to me by Mr. H. Bolus from the Cape in 1894. With it was sent a distinct plant, which I recognize as one of the small Cape forms of *O. lusitanicum*. This was also cut into sections, and showed the

disposition of its weak vascular system on the Ophioglossaceous plan, and with the endodermis variable in clearness of characters. Endodermal markings were seen outside the meristeles and also in the pith, in positions generally corresponding with what is shown in Poirault's drawing of *O. Bergianum*. Further, the outgoing leaf-trace was in some cases surrounded by a special endodermis of its own, as will be shown to be the case in *Botrychium*. These conditions are perfectly compatible with the arrangements more clearly seen in *Botrychium*, which will be described below. The conclusion which I draw from these imperfect observations is, that Poirault's observations are to be upheld; further, that the small species of *Ophioglossum* which show, however inconstantly, an internal endodermis, repeat on a reduced and incomplete scale the same type of structure as is seen more fully developed in *Botrychium*. It will be desirable that this be tested by some observer with more ample material at his disposal.

A similar variability to that found in the genus *Ophioglossum* in respect of the medullation of the individual in the young state, is seen also within the genus *Botrychium*. Already Jeffrey has shown that in *B. virginianum* the sporeling is medullated from the first, a fact which is probably in relation to its nutrition by the large storage prothallus, which serves as an effective nursing mother (loc. cit., pp. 21-2). The fact is corroborated by sections of my own sporelings collected in Jamaica. No internal endodermis was seen in them. In order to compare with this the sporeling structure in *B. Lunaria*, and at the same time to give the most pointed antithesis by selecting weak plants instead of those highly nourished by large storage prothalli, serial sections were cut from sporeling plants taken from the rocky ledges of the Breadalbane Hills, about 3,000 feet up. The plant most exhaustively treated bore one leaf, with a spike on which were only four sporangia. The axis was about $\frac{1}{2}$ inch in length, and very thin, with several roots. As sections showed, a number of leaves had preceded that which was expanded. Following the series of sections of this plant from below upwards, the stele appears from the first to be composed of tracheides with occasional parenchyma cells intermixed, while it is circumscribed by an endodermis, which is well defined considerably below the point of departure of the first leaf-trace (Pl. XLV, Fig. 6). Three roots were attached at this region. Already the cells around the primary xylem show activity of division, thus initiating the secondary development. At first the parenchyma cells in the xylem are not located specially at the centre of the stele; but as the level of departure of the first leaf-trace is approached, a concentration of the parenchyma occurs internally, and a central pith is thus formed. An essential point is that intraxyletic parenchyma exists before the appearance of a definite pith, and contributes to its formation. Very soon the pith is put in connexion with the outer conjunctive tissue by the opening of the xylem-ring. This

prepares for the departure of the first leaf-trace (Fig. 7), one margin of which is defined by the gap in the xylem-ring; but for some time the leaf-trace strand remains connected by the other margin with the xylem of the stele, as it is seen to be in Fig. 7. Meanwhile, the endodermis remains continuous all round, but it shows some irregularities in position of its cells in the neighbourhood of the leaf-trace. These lead to an involution, first on the side on which the opening of the ring began (this is indicated in Fig. 7), and subsequently on the other side. These involutions of the endodermis approach one another as the foliar strand moves outwards, and meet, as seen in Fig. 8. The endodermal limit of the stele is thus never interrupted, and there is no direct communication between the cortex and the stele. After a time the xylem-ring closes again, completely surrounding the central pith. But very soon it opens on the opposite side, for the issue of the second leaf-trace, which is also effected without any interruption of the continuity of the endodermis. The stele meanwhile assumes again a solid xylem-core, except for a few parenchyma cells irregularly scattered as at first among the tracheides. But soon the pith is reconstituted as before, and the process may be repeated at the exit of later leaf-traces. One point worthy of special notice is that as the leaves of the sporeling are successively larger, and their traces stronger, the incurving of the endodermis into the pith (which also becomes more massive as the plant strengthens) becomes more marked, indicating gradual steps towards that degree of encroachment upon the pith, and formation of that internal endodermis, which was first suggested by Van Tieghem. This is shown in slight degree in Fig. 9, and higher leaves of the same plant showed still deeper intrusion. Since, however, the degree of intrusion of the foliar pocket thus formed appears to depend upon the size of the leaf, it would not be expected to be large in so weak a plant as this sporeling from the Breadalbane Hills.

Another of the same batch of weak plants from the hills, which was cut into sections by Dr. Lang, showed the following interesting features. Passing upwards from the base, the vascular structure begins with a solid stele, in which, however, a distinct pith appears at the departure of the first leaf-trace. But there is no communication with the cortex, the endodermis being continuous, as in the previous case. The trace with its surrounding parenchyma is nipped off from the stele by involution of the endodermis, as in the specimen already described (compare Fig. 8). But the next two leaf-traces differ slightly in their behaviour, for in their departure they show the formation of a band of endodermis, which passes internally to the leaf-trace, before the actual separation takes place. The stelar sheath is thus completed before the outer band surrounding the stele and the departing trace is interrupted. This band of endodermis appears to be a new formation, not directly referable to involution, as in the case of

the first leaf: a similar origin applies also for the corresponding tissue opposite the later leaves of the plant previously described (compare Pl. XLV, Fig. 9).

At the departure of the next leaf-trace of the plant cut by Dr. Lang, which is the fourth leaf in succession from the base, scattered tracheides appear in the pith, as seen in Fig. 10. This leaf-trace, as well as those of all the subsequent leaves, departs, as was found by previous authors to be the case in mature plants, leaving an interruption in the external endodermis. But in this case it is plainly the result of that imperfect formation of the endodermal characters which is general in the older regions of these plants. The fading out of them may be clearly traced by passing upwards through the series of sections; for at the first separation of the strand from the stele the endodermis is complete: as the trace passes out the endodermis yields, and remains complete for a time, but the staining reaction of the radial walls fails, and the failure is first seen externally to the trace itself, as shown in Fig. 10 for the fourth leaf. No internal endodermis extending into the pith was observed in any part of this plant.

The structure thus seen in the two plants above described appears to be quite incompatible with any theory of intrusion of the cortex to form the pith, for the pith is present in both cases for at least four internodes below the first interruption of the internal endodermis, and structurally its origin is fully accounted for in relation to the intrastelar tissues. Moreover, the appearance of the scattered tracheides in the pith, at the level of the fourth leaf-trace in the second plant, appears to indicate a local reversion of the pith towards its original condition of xylem. This points to its phyletic origin having been, in part at least, by degradation of tracheides to parenchymatous cells.

An examination of other young plants of *B. Lunaria* shows that in respect of their medullation and in the behaviour of the endodermis in relation to the exit of the leaf-traces, they conform in essentials to what has been described; but there may be considerable variety in the exact details. The further elucidation of these will be necessary for a full understanding of the stelar condition of the genus, and of the family at large.

These observations on weak sporelings of *B. Lunaria* require comparison with Van Tieghem's results. They correspond in the main features. The chief difference lies in the question of the interruption of the endodermis. According to my own observations on young plants of *B. Lunaria* the endodermis is not interrupted at the exit of the traces of the lower leaves. It remains continuous, and all the changes seen are strictly intrastelar. In the stronger and older state the endodermis fades out. It is believed that greater reliance may properly be placed upon the earlier data, and especially those seen in weak plants, than on those derived from

old and strong plants. Accordingly it is not stated that Van Tieghem's observations of the interruption of continuity of the endodermis were erroneous, or that the endodermal connexions are always such as to constitute a complete barrier. What is stated is that such a barrier does occur in certain cases, and that still in them a stelar pith is present. Therefore, the establishment of the continuity between the cortex outside the endodermis and the pith within the stele is not a necessary condition for the formation of a pith in the Ophioglossaceae. Moreover, as the condition where the endodermis forms a complete barrier is the state of the young plant, the ontogeny indicates that this was the primitive condition in the family.

There remains the question of the real nature of the pith in these young plants where it originates without any direct connexion with the cortex, the stele being completely shut off by the continuous ring of endodermis. It appears to originate partly from the intraxyletic parenchyma, which masses together to produce it; partly from the conjunctive tissue outside the xylem (or xylem-sheath as it is sometimes called), with which the intraxyletic parenchyma is connected at the foliar gap. The arrangement of the cells as shown in Figs. 7 and 8 may be held to suggest intrusive growth of the conjunctive tissue. But the conjunctive parenchyma is itself of stelar origin, as is also the intraxyletic parenchyma. Thus the pith is in fact of intrastelar origin in these young plants, though there is some evidence of intrusion of an outer upon an inner stelar region.

Returning now to the examination of the primary xylem in *Botrychium*, an inspection of Figs. 6-9 shows that while there are in all cases signs of cambial activity outside the xylem-tract, and though some of the more peripheral tracheides may have had a cambial origin, this is certainly not the source of the majority of them, for their arrangement is not in radial rows. A comparison of these drawings with those of Professor Jeffrey for the seedling of *B. virginianum* (loc. cit., Pl. IV, Figs. 62, 63) shows clearly the difference. Whereas in that species primary xylem is virtually absent, here it is present in considerable quantity. It became accordingly a matter of interest to see the condition not merely at the base of the plant, as shown in Figs. 6-9, but also towards the apex, in a case where numerous leaves had been formed. This is shown in Fig. 11, which represents a section just below the apex of *B. Lunaria*, where the secondary thickening is beginning, but does not appear to have produced any tracheides as yet. All those here shown are regarded as primary xylem. It is to be noted that the tracheides are associated with parenchyma, which constitutes a pith at the centre. Some of the primary tracheides shown in Fig. 11 are seen to lie isolated in the pith. They may be held to represent vestigial remains of a more extensive primary xylem, which is in course of substitution by a development of secondary wood.

It becomes thus a question of interest to inquire what evidence there is of the existence of such vestigial remains of primary xylem in the genus, and what is its distribution in the different species. Frequently no such isolated tracheides exist in the pith of *B. Lunaria*. But where they do occur, they may be found to occupy positions which would be difficult to harmonize with a theory of intrusive origin of the whole pith. That is particularly the case in the section represented in Pl. XLV, Fig. 12. This shows in a weak plant the separation of a leaf-trace from the xylem-ring. The gap has opened, and parenchymatous continuity is established between the central pith and the outer conjunctive tissues. If the connecting tract were intrusive tissue of cortical origin, it should contain no tracheides. But here a tracheide is found occupying a central position in the connecting tract. A similar difficulty arises in the case of Fig. 10, where a great part of the medulla at the level of the fourth leaf takes the character of a mixed pith with scattered tracheides, though lower down it was purely parenchymatous.

Passing to *B. virginianum*, which has already been quoted as having virtually no primary xylem in the seedling, this condition is usually maintained in the older axis. But occasionally isolated tracheides occur. One of these is shown by Professor Jeffrey in his Pl. IV, Fig. 62, while Atkinson has also delineated two isolated tracheides in the pith of the same species ('Biology of Ferns,' Fig. 152), which can only be held as representing vestigial remains of a primary xylem. In my own sections, which were all from young plants, such a state is only occasionally met with in *B. virginianum*, but an example is shown in Fig. 13.

Very interesting conditions are seen, however, in *B. ternatum*. I have not had the opportunity of examining young sporelings of this species, but by cutting the base of the stock of fairly advanced plants collected in Jamaica, I was able to obtain results which show that the species retains the vestigial xylem more firmly than *B. virginianum*. Examples are seen in Figs. 14–16 of isolated tracheides, or groups of tracheides, lying in the pith: these, as they cannot be referred to a cambial origin, can only represent the vestigial primary wood. But since *B. ternatum* is thus seen to be more prone to such vestigial characters in its xylem, it was a matter of special interest to observe in one specimen of that species the consequences of an injury to the stock, brought about probably by the attack of some insect, or it may have been by some mechanical injury. Professor Jeffrey has lately brought forward evidence in support of the view that traumatic changes are apt to be reversionary, the tissues affected by the injury showing ancestral characters. This gives additional interest to the study of this case in *B. ternatum*.¹

The stock was cut into serial sections. The structure at the base of

¹ Wound Reactions of *Brachyphyllum*, Ann. of Bot., vol. xx, p. 383; Traumatic Ray-Tracheids *Cunninghamia sinensis*, Ann. of Bot., vol. xxii, p. 593.

the plant was found to be normal, and the stock of moderate size. Pl. XLVI, Fig. 17, shows its condition, with a large pith, slightly compressed. But quite suddenly, owing no doubt to the damage of which signs are seen penetrating deeply from the outside, the stele contracted to a much smaller size (Fig. 18), while the pith, which hitherto had been free from isolated tracheides, now showed many of them interspersed throughout the parenchyma. The central region of the stele is shown on a larger scale in Fig. 19, from which it is seen that tracheides lie at the very centre of the pith. Presently, as the damaged region was left behind, the stele again expanded, the pith enlarged and gradually became clear of tracheides. In fact a normal structure was resumed (Fig. 21), though of smaller size than that of the original stock. The interest of this case lies in the light it sheds on the relation of the primary wood of *Botrychium* to the pith. If by traumatic conditions the plant, as Professor Jeffrey holds, is liable to reversionary changes, then, since in this special case the parenchymatous pith has many of its cells replaced by tracheides right through to its centre, that would appear to indicate that the pith, right through to its centre, was originally of xylem origin.

The condition shown by the pith in this injured stock of *Botrychium ternatum* may be compared with that of the centre of the stele in a small rhizome of *Helminthostachys*, which was described by Farmer and Freeman.¹ The structure which is there shown follows naturally on that of the still younger stems represented by Lang.² A photograph of one of Professor Farmer's sections is shown in Fig. 22. In this, as in the injured stock of *B. ternatum*, the centre of the stele is occupied by a tissue composed of tracheides and parenchymatous cells. It has in fact the character of what is known as a 'mixed pith'. This condition is represented in greater or less degree in the young plants observed from the other genera of the Ophioglossaceae. It is shown in the young protostelic plant of *O. reticulatum* in Pl. XLV, Fig. 2, and for *Botrychium Lunaria* in Fig. 6. In each of these cases there is a tract of tissue where parenchyma and tracheides are intimately associated, though it extends only a short distance along the axis. But in *Helminthostachys* that condition may be continued for a long distance. Whether it be short or long, such a mixed condition exists as the progression takes place from the solid protostele to the medullated state. Thereafter, by gradual increase in the proportion of the parenchyma cells, and a decrease leading to complete absence of the tracheides, a substantial part, or it may be the whole, of the central medulla is established. It appears that owing to injury *Botrychium ternatum* has, in the case quoted, returned structurally to the phase of mixed pith commonly passed over rapidly in the individual life, but represented more effectively in young plants of *Helminthostachys* than in other members of the family. This interesting example of the principle of traumatic reversion, suggested by Professor

¹ Ann. of Bot., vol. xiii, p. 421, Pl. XXIII, Fig. 23.

² Ibid., vol. xvi, Pl. III, Figs. 65-70.

Jeffrey, has its important bearing as indicative of the intrastelar origin of a substantive part of the pith in the Ophioglossaceae.

Comparing the three genera of Ophioglossaceae, it is seen that the structure of all of them is referable in origin to the protostele, in which the xylem may be composed at first entirely of tracheides, as seen in the various species of *Ophioglossum*, and it appears to be the case also in some specimens of *Helminthostachys*.¹ Or a few parenchyma cells may be intermixed with the tracheides, as is more common in *Helminthostachys*, and in *Botrychium*. But, alternatively, in all the three genera the stele may be medullated from the first. In this respect there is inconstancy even in the single species. Whether initially medullated or not, a pith of some sort is formed in all cases before the departure of the first leaf-trace. Ontogenetically it is of intrastelar origin, and its source is by accumulation of the parenchyma of the xylem at the centre of the stele, added to, when the xylem-ring opens, by some degree of intrusion of the conjunctive tissue; but this is certainly not the only source. Its original source appears to be the former, and the occurrence of isolated tracheides, or groups of them, about the margin of the pith (Pl. XLV, Figs. 14–16), as well as the changes following on injury seen in *B. ternatum*, support this conclusion.

In *Ophioglossum* and *Helminthostachys* there is no cambium. But in *Botrychium* a secondary activity appears early, and most of the wood is so produced. The primary wood is accordingly vestigial in most species, though it may be fairly represented in *B. Lunaria*. The resulting condition may be compared with that seen in the fossil *Botrychioxylon*, recognized and briefly described by Scott.² The full description of this stem with figures will be awaited with increasing interest. Dr. Scott kindly showed me the specimens for the purpose of this comparison. The stele has centrally a core composed of tracheides scattered through a parenchymatous matrix. This represents the primary wood, and compares with that of the young stem of *Helminthostachys* (Pl. XLVI, Fig. 22), or of *Botrychium* (Pl. XLV, Figs. 10, 11). A broad band of secondary wood surrounds it, which corresponds to the secondary wood of *Botrychium*. The similarity between the fossil and the traumatic condition of *B. ternatum* (Pl. XLVI, Figs. 18–20) is specially striking, while, on the other hand, the comparison may be drawn with certain of the Botryopterideae, and especially with the stem of *Zygopteris*, which shows a central differentiation of the xylem along somewhat similar lines.

The course of development of the stock in the Ophioglossaceae shows a further factor, absent in the first steps of medullation, but increasingly important as the plant becomes established and the individual leaves attain larger size. It is the intrusion of foliar pockets. As Pl. XLV, Fig. 8, shows,

¹ Lang, Ann. of Bot., vol. xvi, p. 42: 'The xylem is in some cases a solid central strand.'

² Journ. Roy. Micr. Soc., 1906, p. 519; and somewhat more fully in Progressus Rei Botanicae, Bd. i, 1906, p. 181.

the leaf-trace in the young plant of *Botrychium* may pass off without intrusion of a foliar pocket, there being a clear demarcation by endodermis of the parenchymatous pith, which is already present, from the parenchyma associated with the leaf-trace. But at the insertion of the stronger leaves the endodermal barrier encroaches inwards, as suggested by Fig. 9, and it appears still more clearly in sections from other plants. Thus an addition may be made to the already existent pith. But as the plant becomes established, the barrier between the two components of the ultimate pith column is no longer maintained, for the intrusive endodermis is often imperfect, while there is also some evidence of formation of endodermis *de novo* in relation to the departure of the leaf-trace. It is probably this intrusive endodermis, whether originated simply by involution, or by formation *de novo*, which was observed by Van Tieghem, and the drawings of *B. Lunaria* and of *O. Bergianum* by Poirault apparently show the imperfect remains of that morphological barrier. The ontogeny is to be taken here as a true guide to the origin of the condition seen in the mature plant. From it we learn that an intrastelar pith was first initiated, and that subsequently foliar pockets, with ultimately a cortical intrusion, encroached upon the pith, and added to its bulk.

A comparison of the results thus obtained for the Ophioglossaceae with the description given by Faull for the seedlings of *Osmunda cinnamomea* shows an essential similarity.¹ In the first place he records (loc. cit., p. 525) the occurrence of isolated tracheides in the pith within the internal endodermis of *O. cinnamomea*. Unfortunately he does not figure them, but states that they are surrounded by a ring of endodermal cells, and suggests that they have been 'pinched off' from the stele. But are they not more probably to be compared with the medullary tracheides of *Botrychium*, and especially of *B. ternatum* (Pl. XLVI, Figs. 18-20)? In that case they would appear to be vestigial evidences of degeneration of the xylem. Their existence seems clearly to favour a view involving intrastelar medullation. All Faull's observations of medullation in the seedlings of *O. cinnamomea* up to the twelfth leaf deal with changes which are purely intrastelar. The ring fence of the outer endodermis is uninterrupted, and shuts off the cortex from any connexion with those parenchymatous tracts which occupy the stele. The twelfth leaf of the seedling (Faull's Fig. 14) still shows the barrier complete. In point of fact, his drawings and descriptions furnish a demonstration of the origin of an intrastelar pith, and would never have been recognized as anything else, but for the influence of Professor Jeffrey's comprehensive theory of intrusive pith, with which I propose to deal later.

The drawings and description of Faull show further in the seedling of *O. cinnamomea* that the pith originates partly from intraxyletic parenchyma, partly from the conjunctive parenchyma with which the intraxyletic pith

¹ Trans. Can. Inst., vol. viii, 1909, p. 515, &c.

unites at the leaf-gaps. The question may be raised, What is the real nature of that external conjunctive tissue? It is to be noted in *Osmunda*, as it is also in the Ophioglossaceae, that the connexion is not with the parenchyma immediately within the endodermis, which might be held to be really a sister layer with the endodermis, and so be ultimately cortical in its origin; but with the conjunctive parenchyma internal to the phloem, which is truly stelar. This being so, the origin of the whole pith in the Osmundaceous seedling up to the twelfth leaf (and even further, as shown by Faull's drawings, Pl. VI, Figs. 13-17) appears to be truly intrastelar, but derived partly from intraxyletic parenchyma, partly from the conjunctive tissue. Divested of all theory, this appears to be the actual fact.

Faull states specifically (loc. cit., p. 527) that in seedlings of *O. cinnamomea* 'internal phloem, and wide open leaf-gaps, through which cortex and pith communicate, were not found'. He goes on to suggest that 'their absence may be indicative of reduction expressed in the seedling stage'. But this seems an unnecessary perversion of the evidence from ontogeny in the interests of a favoured theory. It would seem better to question the truth of the theory of the reduction of the Osmundaceous vascular system from an 'amphiphloic siphonostele', than by its acceptance to be driven to construct a second hypothesis of 'reduction expressed in the seedling stage', in order to support it. If, however, the up-grade view of the structure of the Osmundaceae be accepted, the facts of the ontogeny will be found to run parallel with the facts for *Botrychium*. We may conclude from the ontogeny that an intraxyletic pith originated first in all these cases, and that it is subsequently put into connexion with the conjunctive parenchyma (or xylem-sheath) at the gaps in the xylem-ring.

Further, we may see from Faull's description of sporelings of *Osmunda*, and less clearly in my weak plants of *Botrychium Lunaria*, that the purely stelar pith, once established, is liable to be almost or even entirely obliterated as it passes upwards, and that it may be again reconstituted, until it finally settles down to permanence. This is to be compared with the behaviour of the intrastelar pith in the roots of certain Leguminosae, in which Flaskaemper was able experimentally to control the disappearance and reappearance of pith, and to show that the formation of an intrastelar pith depends upon nutrition.¹

A comparison of the structure of the sporeling in the two families suggests an interesting relation of it with the early nutrition. In the Osmundaceae the nutrition of the sporeling is by the green prothallus, which lives as it were hand to mouth. The sporeling which it produces is at first protostelic, and the vascular changes as described by Faull are entirely intrastelar for many internodes. In the Ophioglossaceae, on the other hand, there is a storage prothallus, which in *B. virginianum* is of

¹ Flora, 1910, p. 205.

large size and massive structure. It presents at once to the sporeling an ample supply of nutritive material. The sporeling in this species is, as might be expected, relatively complex in its early structure. The protostelic state is not represented in it, but it is medullated from the first. In *B. Lunaria* the prothallus is described by Bruchmann¹ as being 1 mm. to 2 mm. long, and 1 mm. wide. It is very much smaller than that of *B. virginianum*, and will offer a correspondingly smaller nutritive supply to the sporeling. We should expect from this that its sporeling would be structurally less complex. It is seen to be commonly though not always protostelic. The medullated state is certainly not the primitive condition. It may safely be concluded that the young plant of *B. virginianum*, like the offspring of the rich, is saved from early struggles. It omits the elementary structural stages, and springs at once into a condition of structural advance. If then we desire to see in their fullness the early steps of ontogeny, it is not to the plethoric sporelings we should go, but to those that are less well nourished, or it may be even starved. In them we may expect to see the steps of preliminary structure most gradually taken, and in extreme cases drawn out almost like the joints of a telescope. This was in fact found to be the case in the sporelings of *B. Lunaria* from the high ledges of the Breadalbane Hills. It is believed that in such depauperate plants the successive steps of the ontogeny serve as a safe guide in studying the origin of the vascular structure seen in the mature plant.

In the first place it is to be noted that in the early stages of these plants, though the external endodermis is well represented, an internal endodermis is absent. Sometimes it does not appear at all: in other cases it appears relatively late, in more or less direct relation to the intrusion of foliar pockets. But these are entirely absent from the first stages of the young plant. The medullation precedes them. Plainly, therefore, the pockets cannot cause the medullation. The converse is the more probable line of causality, viz. that the prior existence of soft internal tissue will favour the formation of intrusive pockets. From the study of these plants it is seen that the pith is in the first instance intrastelar, but it may subsequently be added to by the intrusion of foliar pockets. Sometimes the limits of these two components of the ultimate pith may be maintained, as shown by Pl. XLV, Fig. 9, and indicated by Poirault (Figs. 11, 12, p. 169, &c., loc. cit.). But, as is well known from the time of Van Tieghem's description of it, the endodermal limits become less definite in fully matured plants of *Ophioglossum* and *Botrychium*, while in *Helminthostachys* an internal endodermis is only known in strong and mature rhizomes.

It appears that a like condition has ruled in the Osmundaceae, but it is attained only in a more advanced state of the young plant. Here the sporeling is from the first less bulky, perhaps in relation to its assimilating

¹ Flora, 1906, p. 205.

prothallus, so different as a nursing mother from the bulky storage prothallus of the Ophioglossaceae. And the first ontogenetic stages are accordingly shown in more extended sequence. Faull points out the entire absence of foliar pockets in the young plants of *Osmunda cinnamomea*. Similarly Kidston and Gwynne-Vaughan have shown their absence from the earlier related fossils, such as *Zalesskya* and *Thamnopteris*.¹ But later in the development of the seedling of *O. cinnamomea* narrow foliar pockets make their appearance. And similarly in the later fossil forms, such as *Osmundites skidigatensis* and *Kolbei*, foliar pockets are found. Finally, in older plants of *O. cinnamomea* a continuity is established between the internal endodermis and phloem and the external, through the ramular, and less completely through the foliar gaps.² But this connexion only occurs in the mature plant. The ontogeny thus indicates that it is a late and derivative state. A like state is found in the relatively late fossil *O. skidigatensis*. The parallelism which thus rules between the ontogeny of the living forms of Osmundaceae and the story as based upon the study of the sequence of the fossils gives mutual strength and conviction to the evidence derived from each. From both sources the facts indicate that an up-grade development has occurred, involving a formation of intrastelar pith, and a progressive formation of leaf-pockets. But the latter seem never to have attained to a large size in the Osmundaceae, or to have contributed in the same measure as in the Ophioglossaceae to the sum of the central parenchymatous mass. This is the structural expression of the fact that in the Osmundaceae the leaves are numerous and individually smaller in proportion to the axis, while in the Ophioglossaceae, as a rule, only a single leaf is matured in each season, but it is of relatively large size.

SUMMARY.

1. The young plant in all the genera of Ophioglossaceae is variable in its state of medullation. In some cases there is at first a solid xylem-core ; in others the pith is present from the first.

2. This difference in medullation may be found between specimens of the same species, and there is reason to believe that it is determined by nutrition, the best nourished plants having a pith from the first.

3. Where the axis in *Ophioglossum* and *Botrychium* is at first protostelic, the pith is initiated below the departure of the first leaf-trace, and is referable in origin partly to intraxyletic parenchyma, partly to the conjunctive parenchyma of the xylem-sheath ; the two tissues being put into communication at the first leaf-gap. Meanwhile, in *Botrychium* the endodermis forms an uninterrupted barrier, shutting off the cortex ; thus the medullation is wholly intrastelar.

¹ Fossil Osmundaceae, Parts II and III.

² Faull, Bot. Gaz., vol. xxxii, p. 417.

4. Subsequently in *Botrychium* there is a further intrusion of foliar pockets, delimited from the primary pith by endodermis. The definitive pith column is thus derived from three distinct sources: (a) intraxyletic parenchyma, (b) conjunctive parenchyma, and (c) intrusive parenchyma of the leaf-pockets.

5. The endodermal limits in *Botrychium* are usually maintained in the lower part of the stock, and the inner endodermis may be held to indicate (as the internal endodermis of Van Tieghem and Poirault) the distinction between the intrastelar and the intrusive pith. But the endodermis is gradually obliterated in the upper region. In *Ophioglossum* the endodermis is less distinct from the first. The obliteration is probably connected with the fact that the whole parenchymatous system of the stock serves the function of storage, and physiological barriers are not required.

6. The primary xylem in *Botrychium* is in part or almost wholly replaced physiologically by the secondary xylem, which originates from the cambium. In the mature stock it is vestigial, and may be represented by the innermost tracheides of the xylem, together with occasional isolated tracheides, or groups of them, which are found about the periphery of the parenchymatous pith.

7. But in *Botrychium ternatum* a traumatic condition in a certain specimen showed tracheides scattered throughout the pith, even to its centre. If this be held to be a reversionary state, the facts would indicate that in this species the pith to its centre was originally stelar. A somewhat similar state has been observed in a sporeling of *Botrychium Lunaria*.

8. A comparison of this traumatic state of *B. ternatum* with the fossil named by Scott *Botrychioxylon* shows substantially the same structure. A close similarity exists on the other hand with young plants of *Helminthostachys*, supposing the secondary thickening of *Botrychium* to be absent.

9. The conclusion from these observations is that the pith in the Ophioglossaceae is primarily, though not always wholly, of intrastelar origin, and that the pith is in part at least intraxyletic in origin.

10. A comparison of the sporeling of *Osmunda cinnamomea*, as described by Faull, shows that, up to the twelfth leaf at least, the origin of the pith is intrastelar also, and corresponds to that of *Botrychium* before any intrusion of foliar pockets has occurred.

11. As the ontogenetic history for the two families runs parallel with the history of the fossil Osmundaceae, as disclosed by Kidston and Gwynne-Vaughan, it is concluded that an intrastelar pith was formed first in the descent both of the Osmundaceae and of the Ophioglossaceae, and that an intrusion of foliar pockets may have followed, varying in extent according to the proportion of leaf to axis in the individuals of the two families.

DESCRIPTION OF FIGURES IN PLATES XLV AND XLVI.

Illustrating Prof. Bower's paper on Primary Xylem, and the Origin of Medullation in the Ophioglossaceae.

PLATE XLV.

Fig. 1. Transverse section through the base of a root-bud of *Ophioglossum palmatum*, showing that the stock is medullated from the first. The elongated tracheides belonged to the parent root: the ring of tracheides marks the base of the axial stele. $\times 125$.

Fig. 2. Transverse section of the base of the stock of *Ophioglossum reticulatum*, showing a protostelic state. A few parenchyma cells are present in the otherwise solid xylem-core. $\times 144$.

Fig. 3. A section a little higher up, showing an initial state of a parenchymatous pith. $\times 144$.

Fig. 4. A section still higher, showing the xylem-ring open, and the pith in communication with the conjunctive tissue. $\times 144$.

Fig. 5. A drawing of the central region of Fig. 3 on a higher scale, showing that there is no exact limit between the parenchyma nests of the xylem and the pith.

Fig. 6. Transverse section of the base of the stock of a weak plant of *Botrychium Lunaria*, from the Breadalbane Hills. The endodermis is already well marked: a root is passing off to the right. The stele is a protostele, but parenchyma cells are scattered through the otherwise solid xylem-core. $\times 125$.

Fig. 7. Section of the same plant higher up, showing a pith connected through a gap in the xylem-ring with the conjunctive tissue. The endodermis shows irregularity of its cells, and a slight involution opposite the gap in the xylem-ring. The narrow arm of tracheides which projects outwards is the first leaf-trace, of which the gap defines one margin, while it is still connected with the xylem of the stele by the other margin. $\times 125$.

Fig. 8. Section of the same plant at the departure of the first leaf-trace. The xylem-ring is still open, and thus the pith communicates with the conjunctive tissue. But the endodermis, which is involuted but not interrupted at the passage outwards of the leaf-trace, still forms a complete barrier, shutting in the stele. The cells of the pith to the right are clearly sister cells with the tracheides surrounding them. $\times 125$.

Fig. 9. Departure of the trace of a larger and higher leaf of the same plant. The trace consists of more numerous tracheides, the xylem-gap is wider, and the pith more massive. But the endodermis is still a complete sheath, and has shown no interruption from the base of the plant. It surrounds still the outgoing leaf-trace, but a band of endodermis is seen internal to the leaf-trace, and it is specially to be noted that it arches strongly inwards into the wide xylem-gap. $\times 125$.

Fig. 10. Transverse section of the stock of a small plant of *B. Lunaria* from the Breadalbane Hills, from a series cut by Dr. Lang. It shows the departure of the fourth leaf-trace. Up to this point the endodermis has been a complete barrier, but now it appears interrupted for the first time, at points outside the departing trace. The pith contains scattered tracheides, showing the condition of a 'mixed pith'. It is to be noted that where tangential divisions have doubled the cells of the endodermis it is sometimes the inner, sometimes the outer of the sister cells that bears the characteristic marking. There is no internal endodermis. $\times 125$.

Fig. 11. Transverse section of the stem of a plant of *B. Lunaria* which has produced numerous leaves, cut at a level just below the apex. The secondary thickening is beginning, but the tracheides already matured are regarded as representing the primary wood. The limit of the pith is here very ill defined. $\times 125$.

Fig. 12. Part of a transverse section of a stem of *B. Lunaria*, showing the departure of a leaf-trace. An isolated tracheide lies in the middle of the parenchymatous tract connecting the pith with the outer conjunctive tissue. $\times 200$.

Fig. 13. The inner margin of the xylem in a sporeling of *B. virginianum*, showing two tracheides surrounded by pith, and almost detached from the xylem-tract. $\times 200$.

Figs. 14-16. Transverse sections of the inner margin of the xylem in plants of *B. ternatum*, showing isolated tracheides or groups of them lying free in the parenchymatous pith. $\times 200$.

PLATE XLVI.

Fig. 17. Transverse section of the stele of an injured plant of *B. ternatum*, in the region below the injury, showing the slightly compressed stele with a large parenchymatous pith. $\times$ about 50.

Fig. 18. A section from the same plant at the level of the injury. The stele is seen greatly contracted, with irregular xylem outside it. Internally the contracted pith contains isolated tracheides. $\times$ about 50.

Fig. 19. The central part of the above, showing more in detail the relation between the tracheides and the parenchyma cells. $\times$ 144.

Fig. 20. Another section of the same, showing isolated tracheides lying centrally in the pith. $\times$ 144.

Fig. 21. A section above the damaged region, showing the normal structure resumed, though the tissues are rather less bulky than those of the original stock below the injury. $\times$ about 50.

Fig. 22. Photograph of one of Professor Farmer's sections of a small rhizome of *Helminthostachys zeylanica* for comparison with Figs. 19 and 20 of *B. ternatum*. $\times$ 144.

1.

2.

5.

3.

6.

4.

7.

8.

11.

9.

12.

10.

13.

14.

15.

16.

2.

1.

5.

3.

6.

4.

7.

8.

11.

9.

12.

10.

13.

14.

15.

16.

Hutch, London.

17.

18.

19.

20.

21.

22.

Huth, coll.

Bower, F. O. 1911. "On the primary xylem, and the origin of medullation in the Ophioglossaceae." *Annals of botany* 25, 537–553.

<https://doi.org/10.1093/oxfordjournals.aob.a089342>.

View This Item Online: <https://www.biodiversitylibrary.org/item/239487>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089342>

Permalink: <https://www.biodiversitylibrary.org/partpdf/319850>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.