On Medullation in the Pteridophyta.

BY

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With Plate XLVII.

I WOULD willingly have left the facts and reasoning detailed in the preceding paper to take their place without further remarks in the general sum of evidence, now so rapidly growing, which relates to the origin of the pith in Vascular Plants. And I should certainly have done so, had it not been that in a recent number of the *Botanical Gazette* (Dec., 1910, p. 401) Professor Jeffrey has restated his position on this question with increasing decisiveness. He first enunciated his views on stelar morphology at the meeting of the British Association in Toronto, in 1897. Speaking on the original paper, I then pointed out that, in my view, a fundamental fallacy underlay the whole of his statement, and that the fallacy arose from assuming that all Vascular Plants developed their tissues along the same lines. Dr. Scott, in reviewing Professor Jeffrey's three memoirs, in which his theory had subsequently been developed, wrote later in almost equivalent terms.¹ He remarked that 'The impartial critic will probably take the view that similar vascular structures have originated in different ways in various lines of descent, and that no one rigid scheme can be applied to all'. Now, after the lapse of thirteen years, Professor Jeffrey still maintains a rigid scheme, and as regards medullation affirms for Vascular Plants that 'the pith must in all cases be regarded as a derivation of the cortex, which has become more or less completely sequestered within the stele'.² In his summary he adds a saving clause, stating that 'the pith of the Vasculares, in all cases where definite evidence is available, is an inclusion of the fundamental tissues of the cortex on the part of the stele'.

In the years that have elapsed since 1897 I have seen no reason to alter my first opinion as to the invalidity of the views of Professor Jeffrey on stelar morphology, and especially on the origin of pith. But as the grounds for my dissent were not put into print at the time of his first statement, the present seems a suitable occasion for doing so, while certain facts will be added which bear upon the question. Primarily my objection is the out-

¹ *New Phytologist*, i, p. 212.

² *Bot. Gaz.*, Dec., 1910, p. 412.

come of general morphological experience. At once the words 'in all cases' and 'must' in his latest statement will attract the critical attention of morphologists. They can quote abundant cases of parallel development and homoplasy as shown in the external form of plants. There is no reason to hold that the evolution of internal structure differed in such respects fundamentally from that of form. We learn from comparative study that plants are opportunists in their internal as well as in their external evolution, developing along lines of least resistance, and dominated neither by logic nor by rule. Consequently, in the study of their tissues, strong and consistent antitheses are not to be expected, and so we shall, from prior experience, be prepared for divergences of detail and of method in the formation of such a tissue as pith in the several phyletic lines. Generalizations in terms of 'must in all cases' require to be based upon exhaustive knowledge of detail in order to meet this general probability, and will have to be reconsidered in the light of even a single discordant fact. Thus the mode of statement adopted by Professor Jeffrey, as a dogma rather than as a working hypothesis, at once challenges prior morphological experience.

We may, however, pass from this general objection to the statement itself. It must first be premised that there are those who hold that the limits of the stele are not constant; in fact that the endodermis is not an immutable phyletic barrier between the stele and the cortex. I have no wish to prejudge this question, and myself hold it as open to demonstration. But for the moment we may here proceed on the presumption that the limits of the stele have remained constant. For us the endodermis will be a convenient indicator of tissue-locality, and we may adopt 'without prejudice' the consequent terminology. There are, in that case, three possible sources of the pith, as it is seen in Vascular Plants at large.

(i) It may be always extrastelar in origin. Subject to the saving clause already quoted, Professor Jeffrey holds that this is the constant and only source of the pith in all Vascular Plants.

(ii) It may be always intrastelar in origin. With regard to the upholders of this view we learn from Professor Jeffrey,¹ that 'the English Anatomists . . . regard the pith as in all cases a specially differentiated portion of the fibro-vascular tissue itself'; but he adds that 'of late the extremity of the English view appears to be modified somewhat by the admission that in certain instances the pith may be derived from outside the stele'. Professor Jeffrey neither names these 'English Anatomists' who hold the extreme intrastelar view nor quotes from their works. As I do not share this view, it may be dismissed without further words from the present discussion.

¹ l. c., p. 402.

(iii) It may originate sometimes in one way, sometimes in another: indeed, it may be contemplated as possible that the pith may be partly intrastelar and partly extrastelar in origin in the same individual organism. This is the view which appears to me to be in accordance with the known facts. It commends itself as being in harmony with general morphological experience, and especially in that it provides for possible cases of parallel development, which on the experience of external morphology may be expected to occur.

As the extreme intrastelar view drops out of the discussion, the question which concerns us here will be whether the pith of Vascular Plants is constantly extrastelar or whether it originates in various ways. In discussing this alternative, it must first be remarked that Professor Jeffrey appears entirely to misapprehend what will naturally be expected of him in support of his assertion of a constantly extrastelar origin. For he says¹ that, 'although it is not possible to prove in all cases that the pith may be derived from outside the stele, it is fortunately only necessary to demonstrate this in a few instances, in order to invalidate the position of those who claim that the pith is differentiated from the stele itself.' This may be a satisfactory reply to such anatomists as are said to take the extreme intrastelar view, but it is no answer to those who are prepared to see a varied origin of the pith. To show that their position is erroneous and that Professor Jeffrey is right 'in all cases', the phyletic story of the pith must be known 'in all cases', and a single discrepancy destroys his generalization. He has made his statement in rigid and comprehensive terms, and the *onus probandi* lies with him. Nor will the establishment of the phyletic history of the pith in any one line of descent have any direct bearing upon that in any other, except as an interesting analogy, *unless it can be proved that the origin of the pith antedated the phyletic segregation of those stocks from a common ancestry*. As regards the Pteridophyta, it is not yet known for certain that any two of the recognized phyla, viz. Filicales, Equisetales, Sphenophyllales, or Lycopodiales, had an origin from a common ancestor, much less do we know whether that ancestor was pithed or not. But we do know that more than one of those phyla includes protostelic types, while comparison indicates that the vascular system in all of them is probably referable to protostely as the original condition. Moreover, protostely is present in examples which on other grounds are held to be relatively primitive. Such considerations clearly indicate that the pith in each phylum, where present, has originated phyletically distinct from that of the rest. Consequently, each separate phylum in which pith appears will present its own problem of medullation, which must be solved independently of the others. There is no common rule which can be established by observations made 'in a few instances'. Professor Jeffrey must

¹ l. c., p. 403.

be prepared to demonstrate the extrastelar origin of the pith in each phyletically distinct series of Medullated Plants if his statement is to hold. The plain fact is that a statement has been made 'for all cases' before 'all cases' have been adequately investigated, and it is not put forward as a working hypothesis, but as a rigid law. Whether Professor Jeffrey's generalization be ultimately substantiated or disproved, his handling of the origin of pith cannot be quoted as a model of scientific method.

I do not propose to enter here upon any critical examination of the facts for or against the stelar or cortical origin of the pith in all the several phyla of Vascular Plants which show medullation. This will be left to the professed anatomists. But two extreme examples may be taken from the Pteridophyta, which illustrate, to my mind satisfactorily, that the origin of the pith has not been uniform. The one case provides an example of extrastelar pith, the other of pith of intrastelar origin. The first example is taken from the Filicales. No one who has followed the evidence based upon the endodermal barriers would now deny that the tissue filling the cavity in rhizomatous solenostelic Ferns is of extra-endodermal, that is of cortical, origin, certainly in the greater part, and probably in most cases altogether. The suggestion of this came first from Van Tieghem in 1890, and the idea was taken up and amplified by Professor Jeffrey in 1897. But as Mr. Tansley pertinently remarks in his 'Lectures on the Evolution of the Filicinean Vascular System' (p. 132), 'Professor Jeffrey has nowhere discussed in detail the origin of the siphonostele (solenostele) from the protostele, though he himself stated the view of the primitiveness of protostely.' The most exact demonstrations of the steps of the progression in distinct phyla of Ferns, from the protostele to the siphonostele, and of the modifications which the latter undergoes, are due to Professor Gwynne-Vaughan, Mr. Tansley, and Mr. Boodle, while by far the best comprehensive account of the process and its results is that given by Mr. Tansley.¹ It may be taken that, speaking phyletically, the cortical origin of the pith in such cases has been demonstrated by these writers. It is, however, to be clearly understood, as pointed out by Mr. Tansley,² that such siphonostely is characteristic of Ferns belonging to the middle grades of evolution, though it also occurs in several of the lower and a few of the higher types. Stratigraphically it has repeatedly been found in the fossils of the secondary and more recent rocks, and persists in many present forms. It remains yet to be shown that this stelar structure figured largely, or even at all, in the really primitive types of vascular construction.

The second example, where the pith appears to have been clearly intrastelar in its origin, is in the Lepidodendreae. This is indicated by a comparison of early protostelic types such as *Lepidodendron esnostense* and *L. rhodumnense* from the Culm, with the condition seen in *L. vasculare*

¹ l. c., 1903.

² l. c., p. 56.

(= *L. selaginoides*) from the Coal Measures, where the centre of the stele is occupied by a 'mixed pith' composed of parenchyma and tracheides. A further step is seen in *L. Harcourtii*, also from the Coal Measures, where there is a bulky parenchymatous pith. It is true that Professor Jeffrey, in his Memoir on *Equisetum*,¹ states in connexion with his view of the extrastelar origin of pith, that where the pithed Lepidodendroid axis branches, the pith and the cortex are in continuity. But he does not appear to have gone further into detail on the question of the origin of the pith in the Lepidodendreae. It is to be remarked that such continuity, where it exists at the branchings, is only one condition necessary for the intrusion of the cortex into the stele. It does not demonstrate that it occurs, and it would be equally consistent with extrusion of the pith into the cortex, or with no such changes at all. In the absence of more cogent evidence than that which Professor Jeffrey has hitherto brought, the reiteration of the statement that the origin of the pith is extrastelar does not weigh against the comparison of the structure of forms in stratigraphical sequence such as those quoted. Palaeontological anatomists generally have accepted the stelar origin of the pith in the Lepidodendreae, which seems to me to be the only reasonable reading of the facts.

In presence of this evidence of the origin of an intrastelar pith in the Lepidodendreae, the next natural step in testing the truth of the conclusion should have been to see whether in their nearest modern correlatives there is any evidence of a like process, viz. in *Isoëtes* and *Selaginella*. I do not think that these comparisons have yet been made, though they would seem to be a necessary preliminary to any statement in terms of 'must in all cases'. In *Isoëtes* the anatomical and physiological conditions are so complicated and peculiar that it would not be well to lay much stress upon the structure of its primary stelar xylem. It appears to have the character of a 'mixed pith' with tracheides and parenchyma intermingled. But a better basis for comparison is in *Selaginella*, and it is not to be sought in the more specialized dorsiventral types of the genus, but in those of upright habit, with radial shoots, which comparison shows to be the more primitive, and therefore more directly comparable with the Lepidodendreae.² Such a species is *S. spinulosa*. Harvey Gibson³ has long ago described the structure of its stele, and shown how it is first centroxyletic, and that as it continues upwards the protoxylem strands pass to the periphery of the solid xylem-core. But he did not follow it upwards into the erect unbranched strobilus, and it is there that the point of structure appears which has a bearing upon our present question. If sections be cut through the axis below the strobilus, the stele may be found with a solid xylem-core as already described by Harvey Gibson, the protoxylem groups being peripheral.

¹ Mem. Post. Soc. Nat. Hist., 1899, Pl. XXVII, Fig. 3.

² Land Flora, pp. 300, 356.

³ Ann. Bot., vol. viii, p. 171.

But sections about the base of the strobilus show occasional thin-walled cells irregularly interspersed among the tracheides (Pl. XLVII, Fig. 1). The protoxylems are still numerous and peripheral and project slightly, while the xylems of the leaf-traces on entering the stele fuse directly, though often obliquely, each with a protoxylem which descends from a higher region of the axis. In sections taken at a higher level the thin-walled elements increase in number, forming a considerable though irregular tract towards the centre of the stele. This is, however, continuous outwards as irregular, thin-walled rays; these connect with the outer conjunctive tissue (Fig. 2). Occasionally an isolated tracheide may be found embedded in the soft central tissue (Fig. 4), or more than one of them (Fig. 6). Higher up (but still in a region where the tissues are already matured and the sporangia are in an advanced state, bearing megaspores with thick, dark-coloured walls) the central thinner-walled tissue predominates, and the xylem is divided into distinct strands, with broad thin-walled rays intervening between them. Figs. 3 and 6 show this. In Fig. 4 it is seen that the insertion of a leaf-trace impinges slightly obliquely upon one of the strands. Longitudinal sections show that the softer elements are elongated, with protoplasm and nucleus. Occasional transverse walls occur, but there is no conspicuous shortening of the cells, as is the case in the pith of most plants. This tissue may accordingly be held to represent degraded xylem.

It is thus seen in a living plant that a change of structure appears, involving the formation of a soft, pith-like intrastelar tissue, and it is to be noted that it occurs in a case where there is no branching of the axis, nor are there any foliar gaps to provide that continuity with the cortex without which cortical intrusion cannot take place. Moreover, the trabecular zone intervenes between the stele and the cortex uninterruptedly. It may of course be asserted that the softer central tissue is not really a pith because the cells are elongated. They are, however, thin-walled, and retain their protoplasm, and form a central living tract of tissue which is not vascular. These are the essential features of a pith. It may also be urged that the soft tissues are merely the result of imperfect development of tracheides, and that they would mature into tracheides later. Against this it is to be remarked that the tissues have the appearance of maturity, while the condition of the sporangia and of the strobilus as a whole shows that further development is not to be expected. This intrastelar tissue in *S. spinulosa* may in fact be held as comparable with the pith seen in certain *Lepidodendreae*. And a very remarkable parallel is seen between the slender cone of this *Selaginella* and the massive cone of *Lepidostrobus Brownii*, in respect of the internal structure.¹ I have shown elsewhere² how in this

¹ It may be noted also that a pith exists in the stele of the cone of *Spencerites* (Miss Berridge, Ann. Bot., xix, p. 274, Fig. 2). Doubtless other examples may be found in the cones of fossil Lycopodiales.

² Ann. Bot., vii, p. 347, Pl. XVI, XVII.

fossil there are air-spaces comparable with the endodermal space in *Selaginella*, though not in exactly the same place in the tissues. There is also a tendency to breaking up the xylem of the stele into separate strands, as in *S. spinulosa*, and, lastly, in both of them there is a mass of softer tissue occupying the centre of the stele. This I regard in both cases as an intrastelar pith, resulting from degradation of the central region of the xylem-core, a conclusion which is supported in both cases by the existence of intermediate conditions between the indurated tracheide and the thin-walled cell. Facts such as these seem to me to be incompatible with the statement of Professor Jeffrey that 'the pith must in all cases be regarded as a derivative of the cortex'. But, further, there is already at hand evidence that the formation of an intrastelar pith can be artificially determined by experiment. This has been shown by Flaskaemper in the roots of certain Leguminosae.

The medullation of roots has not hitherto figured in these discussions. But as a central medulla is frequently present in them, it would be interesting to see how it originates, and then to draw the analogy with what is seen in the shoot. No doubt the pith of the root may frequently be in continuity with the pith of the axis. It certainly is so in many seedlings, and in that case it would be open to those who hold that its origin is always cortical to regard it as a further involution from the pith of the axis, and thus be cortical in origin, though, in a sense, at second hand. But recently experiments have been described by Flaskaemper,¹ which demonstrate in the root that pith may be formed *de novo*, within the stele, where no possibility of involution exists. He found² that, if after a seedling of *Vicia* or *Phaseolus* had germinated and the radicle had begun to elongate the cotyledons were removed, the plant was checked, and the root, previously pithed, lost its pith in the parts subsequently formed. But when the plant had recovered strength by continued exposure to favourable conditions, the pith was reconstituted in the later parts of the same root. In a typical case, where the seedling had formed its root 6 cm. long, the cotyledons were removed: the seedling was then kept under careful cultivation for six weeks, during which time the root grew on to 26 cm. An examination of its stele from the base onwards showed in the first 5 cm. a normal tetrarch structure with many pith-cells. At 6 cm. the pith appeared reduced, and at 7 cm. pith was absent. The pithless state continued till about 20 cm. from the base, but in the distal part of the root, formed after the plant had recovered the loss of its cotyledons, pith appeared again in the transverse section. Here, then, is a clear case of the origination of an intrastelar pith in a root, without the possibility of any involution of the cortex from without. This analogy, which has a very close parallel with what has been described by Faull in his seedlings of *Osmunda*, and with my own observations on

¹ Flora, 1910.

² l. c., p. 205.

a weak *Botrychium* above, p. 548, has its value as bearing on the question of origin of the pith in the axis, and is a further indication of the invalidity of Professor Jeffrey's generalization.

It seems to me useless to bring forward any further considerations in order to rebut the rigid assertion of Professor Jeffrey that the pith 'must in all cases be regarded as a derivative of the cortex'. But criticism without construction is arid and unprofitable. Assuming on the basis of such examples as those quoted that the pith is not uniform in its origin, I shall now suggest a relation which appears to subsist between the form and position of the shoot and the type of its medullation, where that structure occurs. It is first necessary to show that such a relation exists, and the causes of it may be considered later. The two examples above, taken to illustrate respectively a stelar and an extrastelar origin of the pith, show strong antithesis to one another, both in the position and in the proportions of the shoot. The *Lepidodendreae* were upright, with columnar axis and relatively small, closely set leaves, as is also the cone in the living *Selaginella spinulosa*. On the other hand, the solenostelic, rhizomatous Ferns, such as the *Dennstaedtiinae*, the *Matonineae*, and certain *Pterideae*, are of creeping habit, with relatively large leaves, seated singly at intervals along an elongated rhizome. In the one case the upright axis is the dominant factor in the shoot, and the pith, where present, is intrastelar in origin. In the other the leaf is a dominant factor over the weak and prostrate axis, and the pith is extrastelar in origin. I suggest that *the position of the axis, together with the proportions of the appendages to the stem, at the time when the medullation was phyletically initiated, have been determining influences upon the method of origin of the medullation*. Once the method of the medullation was stamped in any phylum it might be continued on the same plan, with a high degree of conservatism, even though the position of the axis or the proportion of the parts might be altered. It is, in fact, suggested that in the first instance an upright microphyllous stock has favoured intrastelar medullation, while a creeping megaphyllous shoot has favoured extrastelar medullation. A test whether this relation is a real and valid one will be found in those plants in which mixed conditions occur; for instance, where the axis is and has phyletically been upright, but the leaves relatively large; or, again, where the stock is a creeping one, but the leaves only small. It will presently be shown that the mode of origin of the pith in cases where such mixed conditions occur accords generally with the suggestion, while they supply such various states of the tissues of the axis as may lead to a knowledge of the underlying principles which govern its structure.

In Chapter XVI of the 'Land Flora' I have advanced strong reasons for holding that the primitive symmetry of the Archegoniate sporophyte was radial. We know also for the *Lycopodiales*, *Equisetales*, *Ophio-*

glossales, and Marattiales, that the axis of the embryo is vertical, and that it grows directly into the upright seedling. But in the Leptosporangiate Ferns the embryo is prone at first. Nevertheless the radial upright stock is established at once in many Ferns. In fact, in plants which are radial in the mature state the initial condition of the recumbent embryo does not impress dorsiventrality on the seedling.¹ This is the case for *Osmunda* and *Todea*, so that for all practical purposes in the development of the stele these genera may be held to have had vertical axes from the start. It is uncertain what may have been the condition of other Leptosporangiate Ferns as regards their phyletic history, but it is significant that those great parent stocks, the Gleicheniaceae and Schizaeaceae, include prostrate forms among their most primitive types. This question will be discussed more fully on a later occasion.

It has been seen that those Lycopodiales which are pithed were upright microphyllous forms, with intrastelar pith. The same may be said for the Equisetales, though here the formation of pith and degeneration of the primary wood has gone much further.² But the Ophioglossaceae and Marattiaceae, together with the Osmundaceae, are megaphyllous forms with upright stocks. The question will be, What is the nature of their medullation? Of these the Marattiales, with their very complex dissolution of the vascular system into separate strands, present a peculiarly complex problem of their own, and may for the present be left on one side.³ The most interesting cases of megaphylly with a vertical stock among forms which may be held as primitively upright are then the Osmundaceae and the Ophioglossaceae.

The Osmundaceae are still the centre of keen discussion in respect of the source of their medullation. The one view is that the stelar condition seen in the living examples of the family is the result of reduction from a more complex condition, which was that of the 'amphiphloic siphonostele'. This view is based on the study of the current representatives of

¹ l. c., p. 214.

² For the conclusions of a discussion of the stelar condition in the Equisetales, see Land Flora, p. 391. I see no reason to change the opinions there expressed, though the subject has been again opened by Eames (Ann. of Bot., 1909, p. 587).

³ It may be noted that Farmer and Hill (Ann. of Bot., xvi, Pl. XVI, Figs. 11-13) have illustrated the origin of a pith, which can only be intrastelar, in *Angiopteris*. Brebner (Ann. of Bot., xvi, p. 550) points out that *Danaea* differs from *Angiopteris* and *Marattia* in not passing through a medullated stage. Further, since this paper was drafted, Miss Charles's paper 'On the Anatomy of the Sporeling of *Marattia alata*' has appeared (Bot. Gaz., Feb., 1911, p. 81). A comparison of her Fig. 8, Pl. IX, with my Fig. 8 for *Botrychium Lunaria* shows a substantial similarity. In both cases there is intraxyletic parenchyma, and apparent intrusion of parenchyma lying more externally. But after this the parallel seems to cease, and *Marattia* takes its own divergent way. Thus the evidence, so far as it goes, indicates that in the Marattiaceae a pith may be absent altogether: or it may appear temporarily before the peculiar break-up of the stelar system into meristeles. But in any case it is partly, or perhaps even wholly, intrastelar, and shows some analogy with what is seen in the Ophioglossaceae and Osmundaceae.

the family, together with reference to one relatively recent fossil. It is held by Professor Jeffrey and his pupils. But they have not advanced any evidence in support of it from early fossils. It would strengthen their case if they were to produce specimens of the reputed ancestors, showing the 'amphiphloic siphonostelic' structure, from early strata. But this has not yet been done. The other view is that the present condition shows the approximate limit of an up-grade development, which arose from a protostelic state, without the amphiphloic siphonostele having figured in the earlier stages at all. It has been based upon the study of a stratigraphical sequence of related fossil forms carried out by Kidston and Gwynne-Vaughan. This view would ascribe the origin of the pith to direct medullation of the protostele. The alternative view would be that the pith originated wholly by intrusion of the cortex through the foliar gaps, according to Professor Jeffrey's generalization. If the present Osmundaceous structure has really been reduced, the fossil correlatives should indicate progressively a nearer approach to a condition of amphiphloic siphonostely. But, with the exception of the relatively late *Osmundites skidigatensis*, the reverse has been shown to be their general trend. The facts and arguments of Kidston and Gwynne-Vaughan are now so well known that they need not be recapitulated here: nor yet the rejoinders with which they have been met by the other side.¹ It will suffice to consider the facts as stated by Kidston and Gwynne-Vaughan for the Osmundaceae from the point of view of the hypothesis above propounded. What we should anticipate, if it were true, would be that the stele should show intrastelar pith in accordance with the constant and phyletically erect position of the axis. Also that there should be some degree of formation of foliar gaps in accordance with the megaphyllous character. Kidston and Gwynne-Vaughan have shown, and illustrated by photographs of sections, and by diagrams, the existence of imperfect foliar pockets in *Osmundites Kolbei* and *skidigatensis*, two of the more recent fossil types. They are comparable in essentials with those relatively small pockets found in the

¹ The Fossil Osmundaceae: Parts I-IV, Trans. Roy. Soc. Edin., 1907-10; Jeffrey, Bot. Gaz., Jan., 1908, p. 67, and Nov., 1908, p. 395; also Bot. Gaz., 1910, pp. 401, 476; Faull, Trans. Can. Inst., vol. viii, p. 515, &c.; Sinnott, Ann. of Bot., 1910, p. 107. It is interesting to note how, in the last-named work, doubts of the accuracy of the observations of Kidston and Gwynne-Vaughan grow in the course of a few pages to full assurance of their error in the interpretation of a fossil which the critic has never seen. On p. 110 Sinnott, writing of *O. Dunlopi*, remarks: '*it seems entirely possible that very narrow rays . . . might have occurred.*' This suggestion is based on 'the present indifferent state of preservation' of a fossil he has never personally examined. On p. 111 his statement on the same fossil is strengthened thus: 'On the whole *it seems very probable* that we have here to deal with a form . . . where foliar gaps were *always* present.' At the conclusion of the paper the general statement which covers *O. Dunlopi*, together with the rest, is couched in still stronger terms (p. 116) thus: 'From such fossil evidence as is available therefore . . . *it seems quite clear* that the presence of foliar gaps is a primitive feature in the Osmundaceae.' The italics are mine. Readers will form their own estimate of the value of evidence thus accumulated in support of a favoured theory.

living genera of Osmundaceae. But such pockets are absent from the more ancient forms. This suggests that there has been a progressive formation of such pockets. On the other hand, in the earlier types there is merely a differentiation of the massive xylem-core into a centrally-lying region composed of short, thinner-walled elements, and a peripheral ring of firmer wood (*Thamnopteris*). In later forms, such as *Osmundites Kolbei*, the centre was occupied by a 'mixed pith', containing tracheides, while the remaining xylem consisted of separate strands.¹ This leads naturally to the condition of the modern types, with their central pith of parenchyma, but occasionally containing tracheides, as shown by Faull.² The intrastelar pith is foreshadowed in the earlier fossil types, and the stratigraphical sequence illustrates its origin along lines in accordance with the theory. Thus the actual structure of the Osmundaceae, ancient and modern, is such as to accord with what might have been anticipated, supposing the suggested relation of habit to internal structure to be valid.

Similarly, in the case of the Ophioglossaceae, probably their stock was primitively upright, and they are not only megaphyllous, but they develop commonly one leaf only in each season, and that of a large size (monophyllous). Supposing the suggested relation to hold, they should have an intrastelar pith in accordance with their upright stock, together with intrusive pockets in accordance with their megaphyllous character. Since in *Ophioglossum* the endodermis is less perfectly developed than in *Botrychium*, it is from the latter that the best evidence may be derived.

It has been seen in the preceding paper (p. 543) that a pith, which is at first entirely intrastelar, arises partly from the intraxyletic parenchyma, partly from intrusion of the conjunctive parenchyma. In weak plants this condition may be continued for some distance, and appears to correspond in origin and in structure with that demonstrated by Faull in young plants of *Osmunda cinnamomea*. But the intrastelar pith thus formed is liable to be encroached upon by intrusive foliar pockets, which become successively larger with the enlargement of the leaves. The endodermis, yielding

¹ Professor Jeffrey (Bot. Gaz., Dec., 1910, p. 476, &c.) meets the evidence adduced by Kidston and Gwynne-Vaughan from *Osmundites Kolbei* with the remark that 'the unprejudiced anatomist would scarcely admit the accuracy of their statements on the evidence they submit'. Doubtless the authors may have something further to say on this. Meanwhile, the 'unprejudiced anatomist', of whom we have heard so much in these discussions that we begin to doubt his existence, will draw his own balance between the criticisms of a writer at a distance from the specimens, who has a very rigid statement to defend, and the carefully considered conclusions of two experienced observers, whose study of the fossils themselves has been the basis of their statement. Moreover, he will take fully into account the coherent and consecutive features of their evidence, of which the facts for *Osmundites Kolbei* are only a fragment. Faull and Sinnott also take the same line of defence of their theoretical position as Professor Jeffrey by discounting the evidence from the fossils (which they have never seen) on ground of their imperfect preservation. Those who are accustomed to the interpretation of fossil structure will probably be able to assess at their proper value these criticisms *in absentia*. See Faull, l. c., p. 530, and Sinnott, l. c., p. 107, &c.

² l. c., p. 525.

apparently to encroachment of the cortex on the stele, projects convexly into the pith, and constitutes that internal endodermis recognized by Van Tieghem and Poirault. Thus the medullation in *Botrychium* corresponds to the theoretical anticipation, being both intrastelar and extra-stelar in origin. It arises from three distinct sources: (a) intraxyletic parenchyma, (b) conjunctive parenchyma (both of which are intrastelar), and (c) intrusive parenchyma of the foliar pockets (extrastelar).

The details as regards the origin of the pith in *Helminthostachys* are not yet to hand. It should afford an interesting example, being megaphyllous, but having a vertical position of its axis only in the earlier state of the individual. In its older stages the rhizome becomes prostrate, a condition which, on our hypothesis, should lead to the formation of large pockets in a plant with leaves of so large a size.

The Osmundaceae and Ophioglossaceae are thus seen to accord structurally, though in varying degree, with the theoretical anticipation. Both of them show an intrastelar pith in relation to their primitively vertical axis, and leaf-pockets may also be formed of varying size in relation to their megaphyllous character. The converse must now be examined. We shall inquire whether in any microphyllous shoots of rhizomatous nature there is evidence of a pith of extrastelar origin.

It may be said at once that the large majority of creeping microphyllous forms do not illustrate the anticipated structure. But this might be expected, for, judging from other experience, it is only in cases where the axis had already the creeping habit at the time when the medullation was phyletically initiated that the effect would be likely to appear. In cases where an intrastelar medullation preceded the adoption of the creeping habit of the axis, the course of medullation primarily initiated appears to have been continued, even though the creeping habit might subsequently be assumed. This may be illustrated by the Equisetales. In them the embryogeny is vertical and the primary shoot is upright. We may presume that an intrastelar pith was phyletically initiated in the primary axis, as it is structurally seen in the primary axis of the embryo to-day. The creeping habit being only assumed subsequently by branches of a higher order, these maintained, with the conservatism already recognized, their primitive type of medullation, that is the intrastelar. But in other cases medullation may be entirely absent, as in the creeping axes of the more advanced types of *Lycopodium*. This is also the case for the straggling species of *Selaginella*. But within that genus there is the well-known case of *S. laevigata*, var. *Lyallii*, which illustrates the point in question, though with details which plainly indicate homoplasy as compared with the Filicales. Considering the constancy of the vertical embryogeny in the microphyllous forms, and the fact that the upright radial axis is their primitive type, the rarity of the reaction in them cannot be held as a valid objection.

Selaginella laevigata, var. *Lyallii*,¹ has a short creeping rhizome, sharply differentiated from the upright 'foliage' shoots. The latter show a number of steles arranged with no definite order. But in the creeping rhizome the stelar arrangement closely resembles that of a typical Filicinean solenostele, with gaps formed here not by the departure of leaf-traces, but of the aerial branch-traces. Centrally there may be an accessory vascular strand, or more than one, behaving just as do the central strands in certain rhizomes of solenostelic Ferns. The similarity is so great that it has repeatedly been the subject of remark, and it has even been suggested that it might have a phylogenetic bearing.² This would seem to be an erroneous view, for *S. laevigata* is one of the more highly specialized and most definitely rhizomatous species of the genus, in which its type of structure is rare, if not actually unique. Moreover, the structural comparison is with such Ferns as the Pterideae and Matonineae, which are not specially primitive types among the Leptosporangiates, and phyletic comparisons can only properly be suggested between the most primitive types of such distant phyla, if indeed at all. It seems to be an example, and a very remarkable one, of homoplasy, of which the stimulating cause has been the horizontal position of the rhizome in each case. But the stelar gaps in the rhizomatous Ferns are foliar, in *Selaginella laevigata* they are ramular. In both cases the inserted organ is relatively large as compared with the rhizome itself, and this proportion has probably been also a factor leading towards the similar structural result. The existence of such a structure in a microphyllous type with creeping rhizome provides an example in accordance with our second theoretical anticipation. This plant, in accordance with the creeping habit of the rhizome, has by adjustment of the stelar masses enclosed a pith-like mass of ground tissue, which was plainly of extrastelar origin.

The structure thus seen in these converse test cases indicates that the suggested relation is really existent. It appears that the position of the axis and the proportion of the appendages relatively to the axis have been determining factors in the formation of the pith respectively from an extra- or an intrastelar source. It will, however, be at once objected that the Dicksonieae and the Cyatheae, and a host of other Leptosporangiate Ferns, are megaphyllous, have upright axes, and still their pith is of extrastelar origin. At first this would seem to be a fatal objection. But it is to be remembered that *according to the theory the determining influence is effective at the time when the medullation is first initiated, and once started, the same type of medullation is apt to be retained, even after a change of position of the axis has occurred.* At the British Association at Sheffield (1910) I brought

¹ See Harvey Gibson, Ann. Bot., viii, p. 187, Pl. IX, Fig. 76, and Pl. X, Figs. 77, 83-93; also Jeffrey, Mem. Bost. Soc. Nat. Hist., vol. v, No. 5, p. 160; also Tansley, Lectures, p. 135.

² Harvey Gibson, l. c., p. 192.

forward evidence to show that in the Cyatheaceae the erect habit is secondary, and that the family are derived from a rhizomatous ancestry, probably of near kinship with the creeping Gleicheniaceae. They appear to have become erect subsequently to the formation of a pith by intrusion through the leaf-gaps. The same is probably the case for the Dicksonieae and for *Plagiogyria*, and my own comparative studies already indicate that a like probability will emerge in the case of other upright Leptosporangiate Ferns. The point is that in such cases the extrastelar tissue had already penetrated through the foliar gaps into the stele of the rhizomatous ancestry before the erect habit was assumed, and that that type of medullation, once initiated, was perpetuated with minor modifications when the race later assumed the upright habit. It is this conservatism more than anything else which has concealed the factors that have been at work. Examining Ferns at large, without any clear phyletic ideas regarding them, we find the pith extrastelar in many upright as well as creeping forms. This apparent inconsistency has obscured the relation which seems to have subsisted in the first instance between the prostrate position and the initiation of an extrastelar pith.

Two leading factors have been mentioned in the preceding paragraph as influencing the medullation of Vascular Plants, viz. the position of the axis at the time when the medullation was initiated, and the disturbing influence of the insertion of the appendages. Other factors not yet recognized may also have had their effect. Pending their discovery, it may now be inquired what is the balance of influence of these two factors in cases where both may have been effective, and whether that balance is constant or variable. It is in such plants as the Osmundaceae and Ophioglossaceae, where the two factors are, in a sense, pitted against one another, that the striking of the balance may be witnessed in its structural results. For in them the axis is upright, which might be expected to encourage the formation of an intrastelar pith, while the relatively large leaves would encourage the intrusion of foliar pockets, leading to an extrastelar pith.

A further circumstance, which evidently had its effect (and may indeed be regarded as a mechanical consequence of the creeping or upright habit of the shoot), is the relative size of the axis compared with the area of the leaf insertion. Megaphylly is merely a term indicating vaguely a large size of the leaf. But the proportion of leaf to axis may vary even in types accepted as megaphyllous. And this fact is also illustrated by a comparison of the Osmundaceae and Ophioglossaceae. In the stratigraphically older forms of the Osmundaceae, which had a very bulky axis, but no leaf-pockets (e.g. *Thamnopteris*), the large xylem-core already shows differentiation at its centre in the direction of a pith formation. Leaf-pockets appear in the later forms of the phylum (*Osmundites Kolbei*), but being small they never seem to have influenced the general structure so greatly as did the intrastelar pith,

which appears as a 'mixed pith' in *O. Kolbei*. Finally, in the more modern Osmundaceae the pith is fully formed, while the leaf-pockets are never seen to be so large as in other Filicales. It is thus seen that where, as in the Osmundaceae, the axis is upright and relatively bulky, and the leaf insertion relatively narrow, the intrastelar pith is dominant, while the leaf-pockets remain relatively small. But in the Ophioglossaceae the proportion of the upright shoot is habitually different. They are commonly monophyllous, producing only one leaf in each season, but that leaf is larger proportionately to the axis than are the numerous leaves of a season in the Osmundaceae. We should then expect that the intrastelar medullation in them would be proportionally smaller, and the foliar pockets be relatively more prominent. This result is clearly indicated by the observations on the seedlings of *Botrychium* above detailed.

But if the balance of size of the parts really does influence the internal structure, as suggested, an interesting condition should be seen in the seedling of *Botrychium Lunaria*, where the first leaves are all minute scale-leaves. If the size of the leaf-pocket is in any way proportional to that of the leaf itself, the pockets of the earliest leaves of the seedling of this species should be small. That is exactly what is shown by the series of sections of the young plant of *B. Lunaria* described above. There is indeed no intrusive pocket at all in relation to the first minute scale-leaves of this seedling, and the barrier of endodermis is unbroken, so that there is not any communication at all between the cortex and the pith. The latter is present, however, though of relatively small dimensions, and is thus intrastelar in its origin. But in the larger leaves the endodermis curves convexly inwards, forming a pocket that encroaches on the pith. There is thus indication that in the Ophioglossaceae there is fluctuation of the balance between the two factors, and that it may even vary in the individual plant. The facts strongly suggest that the pith is here of two distinct origins, partly intrastelar and partly extrastelar, a condition which was contemplated as possible at the opening of this essay. But the original endodermal limit between the two constituent parts is often obliterated by the loss of its endodermal characters, partially or altogether. This is found in the upper regions of *B. Lunaria*, and it appears to be the constant condition in *B. ternatum* and *virginianum*, as it is also for most of the species of *Ophioglossum*. In this genus, however, the obliteration of the endodermis has gone still further, and involved commonly the external endodermis also. In the family as a whole the irregularity of occurrence of the endodermis is probably due to there being no physiological need for the maintenance of the barrier between the various parenchymatous masses, which are used for storage purposes. That being their prime function, the less the barriers to physiological transit the better. Thus the imperfection of the endodermis finds a physiological explanation. Nevertheless, the two components of the

Ophioglossaceous pith may have been, and probably were of distinct origin, and in the first instance have been regularly delimited by endodermal sheaths, vestiges of which were first recognized as present in them by Van Tieghem and Poirault. But these are more clearly seen in the seedling than in the mature state. Thus the ontogeny supports the conclusion.

In drawing this discussion to a close, its results may be briefly summarized as follows:—

1. The evidence, whether from anatomy of the mature plant, or from the development of the seedling with its ontogenetic bearings, or from the stratigraphical sequence of the fossils such as the Osmundaceae and Lepidodendraceae, converges in the support of the conclusion that the origin of the pith in the Pteridophyta has not been uniform. Its source may vary even in the individual according to its stage of development, or its physiological condition.

2. It may be derived in the following ways:—

- (i) Wholly from an intraxyletic source, by degeneration of the vascular tissue: as in the Lepidodendraceae, the primitive Osmundaceae, and probably also in the Equisetales:—or partly so, as in *Selaginella spinulosa*, the Ophioglossaceae, the modern Osmundaceae when young (Faull), and *Marattia* (Charles).
- (ii) The conjunctive parenchyma outside the xylem, but still intrastelar, may contribute to it: as in the Ophioglossaceae when young, and the seedling *Osmunda* (Faull). In *Selaginella spinulosa* also it appears to have played some part.
- (iii) The inner layer of the double endodermis may be a source of intrusive parenchyma: this appears to have occurred in the *Marattia* seedling (Charles), and possibly also in some other cases.
- (iv) The endodermis and cortex form intrusive leaf-pockets: as in the Ophioglossaceae after the first stages of the young plant are passed, and in the Leptosporangiate Ferns at large.
- (v) The steles may be adjusted so as to surround a centrally lying tract of cortical origin (*Selaginella laevigata*, var. *Lyallii*).

3. It has been possible to suggest hypothetically certain conditions which have been influential in determining from what source the medullation shall originate in any given case: viz. that in the first instance an upright microphyllous stock has favoured intrastelar medullation, while a creeping megaphyllous stock has favoured extrastelar medullation.

4. It has been found that in upright stocks which are megaphyllous, the medullation may be partly intrastelar, partly extrastelar, and that the balance between the two factors may be approximately forecast from a knowledge of the proportions and position of the shoot.¹

¹ Professor Gwynne-Vaughan suggests as a further factor the form of the leaf-trace itself.

5. It has been found that in a microphyllous stock which is of creeping habit an extrastelar medullation may be attained by adjustment of the stelar tissue, so as to resemble the condition seen in rhizomatous Ferns. This is the case in *Selaginella laevigata*, var. *Lyallii*.

6. Many facts are found to indicate that when once either intrastelar or extrastelar medullation has been initiated in a phylum it is apt to be retained, even after a phyletic change of position of the axis has occurred.

This account of medullation in the Pteridophyta is based upon such data as have been quoted in the text. Other factors than those recognized may emerge as affecting the origin of the pith, and the summary is open to amendment and modification. But it is believed that it more adequately expresses the essential features of medullation in the Pteridophytes than the rigid statement of Professor Jeffrey that 'the pith must in all cases be regarded as a derivative of the cortex'.

The work of the future relating to medullation should in the first place be to allocate among such sources as those named, or others that may be disclosed, the origin of the pith in any specific case; rather than to discuss whether or not the pith 'must in all cases be regarded as a derivative of the cortex'. It is high time that the study of medullation, and of stelar morphology, as a whole, should be freed from a form of controversy which has in its later phases resembled the contests of scholasticism rather than the more elastic discussions of modern biological science.

Tissues of various character and origin have been seen to contribute, either by degradation or by intrusion, to the central parenchymatous column commonly found in axes of the more advanced types of structure. We have seen that even the pith existing in a single individual may be referred to more than one distinct regional source. Its formation may be initiated by degradation only, without any intrusion at all, in which case it is strictly intraxyllic. Or the formation may be aided, or even initiated by intrusion from without: and according as the intrusion is less or more marked it affects first the more internal and later successively the outer-lying tissues. It is thus seen that the factor of involution from without is only one of those which contribute to the general result. In point of fact the pith column, with its chief function of storage of water and of nutritive materials, is not referable to any single source in the Pteridophyta at large.

It has been pointed out that the extent of the intrusion of more superficial tissues, whether intrastelar or extrastelar, is closely connected with the relation of the leaves to the axis in point of size. Where the axis is bulky and the leaves small there is no intrusion; where the axis is relatively less bulky and the leaves large there is apt to be intrusion, and it is more or less extensive according to the preponderant size of the leaf is greater or less. This balance of the parts of the shoot is, however, itself related to habit. An upright axis must for mechanical reasons be relatively short and

bulky to secure stability, and its leaves are crowded. This type of shoot favours intrastelar medullation, which is thus biologically related to the upright habit. In the creeping forms the mechanical requirements are not so urgent, and the axis may be long and relatively thin in proportion to the size of the leaves. It may be suggested, further, that the *causa causans* of the creeping habit itself is the weight of the relatively large leaves which the axis cannot itself otherwise support. This then leads to extrastelar medullation, which is thus biologically related to the creeping habit. According as the balance is struck between extreme conditions, the intrusion involves, it may be, only the more superficial tissues of the stele, as in the seedlings of *Osmunda cinnamomea* and weak seedlings of *Botrychium*; or the inner endodermis, as appears to be the case in the young *Marattia*; or the extrastelar tissues as well, as in the older Ophioglossaceae, and in Leptosporangiate Ferns at large.

But the most extreme state of involution hitherto recorded is that seen in certain Ferns, in which a basket-like structure is assumed. Here the involution has extended to the outermost tissues of the axis, and deep pockets, lined by the superficial tissue of the stem itself, burrow far into the central column of the pith. This has been described by Gwynne-Vaughan for *Onoclea*, *Cystopteris*, and *Aneimia*,¹ and it has been again referred to by Jeffrey, but without bringing any new instances.² A further example may be mentioned in *Plagiogyria*,³ though here the involutions of surface do not extend so deeply as to reach the pith. It may be remarked that all these examples come from Ferns which are closely related to forms with a creeping habit, and may be understood to have adopted relatively recently an upright habit with tufted leaves, and a massive axis for their support. Several of them indeed show the prior creeping phase and the later tufted state in their individual lives (*Onoclea*, *Plagiogyria*), while others belong to genera containing species with a creeping habit (*Cystopteris*, *Aneimia*). It may be that the basket-like structure of the stock in such cases results from the inability of the plant to meet the sudden demand of material for the construction of a more bulky axis, in species in which the adoption of an upright habit has made a broad and massive stock mechanically necessary for the insertion of the crowded leaves.

From the facts and comparisons above given, which thus lend themselves to a reasonable biological interpretation, the final result is that there is no rigid law of medullation, by which 'the pith must in all cases be regarded as a derivative of the cortex'. The only law appears to be that of organic life at large, that organisms accommodate themselves along lines of least resistance to their surroundings. That in so accommodating themselves their habit is seen to vary, and especially the proportions and attitude

¹ New Phyt., 1905, p. 211.

² Bot. Gaz., Dec., 1910.

³ Ann. of Bot., 1910, p. 429.

of the parts of the shoot. The consequences of this are reflected structurally even down to the pith itself, which, according to the habit and proportions of the shoot in question, may arise from more deeply seated, or successively from more superficial sources. That is the result which emerges from this study of medullation in the Pteridophyta.

The medullation of the Seed Plants, and ultimately of the Higher Flowering Plants, has not been touched upon here. But it is plain that any broad conclusion as to the origin of the pith in the Pteridophyta must affect the theoretical position as regards them. And those who hold that in the Pteridophyta the pith may be either intrastelar in origin or extrastelar will be prepared to extend such views to the Seed-bearing Plants. It has, however, been pointed out above that the establishment of the phyletic history of the pith in any one line of descent cannot have any direct bearing upon that of any other, unless it can be proved that the origin of the pith antedated the phyletic segregation of the stocks in question from a common ancestry. Applying this in the case of Seed Plants, the fact of solenostelic structure in such a Fern as *Pteris aquilina* can have no direct bearing upon questions of their medullation, unless it can be shown that the Pterideae had a common ancestry with the Seed Plants compared, and that that ancestry was already medullated and solenostelic before the two phyla were segregated. The present drift of investigation indicates that it is not in the direction of any solenostelic type of Ferns, as we now know them, that we shall look for the phyletic origin of any Seed Plants. It would be more to the point to inquire how the medullation was initiated in the Pteridosperms and other primitive Seed Plants, for their structure would throw a more direct light on the question. Moreover, what is required as a foundation for an opinion on the medullation of Seed Plants would be not merely the observation of isolated sections, but, so far as the material permits, a comparison of stems of different ages, in *Lyginodendron* for example, and of allied plants from different geological horizons. A knowledge of the origin of their pith arrived at in this way would provide a necessary test of the theoretical position of Professor Jeffrey on the stelar morphology of the Higher Flowering Plants.¹

Finally, it must be said again that there is no wish to prejudge the question whether the endodermis is or is not an immutable barrier between the external and internal systems of tissue. Certain examples of irregular, and even of sporadic development of endodermal characters in tissues apart from the usual positions for endodermis, would seem to indicate that endodermal structure may sometimes originate *de novo*. The whole discussion has proceeded on the understanding that this question is left open for future demonstration. Here the endodermis itself has served as a con-

¹ Jeffrey, The Morphology of the Central Cylinder in the Angiosperms. Reprinted from the Trans. Can. Inst., 1900.

venient indicator of tissue locality, and it has been seen that not only the tissues outside it, but also those interior to it may take their varying share in the process of medullation.

DESCRIPTION OF THE FIGURES IN PLATE XLVII.

Illustrating Professor Bower's paper on Medullation in the Pteridophyta.

Selaginella spinulosa, A. Br.

Fig. 1. Transverse section of the stele of *Selaginella spinulosa*, taken from the base of the strobilus, showing the central xylem-core composed of tracheides, with projecting protoxylem-groups. Occasional thin-walled elements are present in the xylem. $\times 72$.

Fig. 2. Transverse section from rather below the middle of the strobilus, showing the general arrangement as before, but there are now considerable but irregular tracts of thin-walled elements, especially towards the centre of the stele, which are connected irregularly by thin-walled rays with the outer conjunctive tissue. There is, however, no evidence of intrusion shown in the arrangement of the cells. $\times 72$.

Fig. 3. Transverse section from about two-thirds up the strobilus, showing the general arrangement as before, but the whole of the central region is occupied by thin-walled elements, constituting a massive pith. The xylem-core is now broken up into a number of separate strands, with broad parenchymatous rays intervening between them. $\times 72$.

Fig. 4. A stage corresponding approximately to that of Fig. 2, on a larger scale, and showing a single tracheide isolated in the centre of the parenchymatous tract. $\times 144$.

Fig. 5. A stage corresponding approximately to that of Fig. 3, on a larger scale, showing the relation of the isolated xylem-strands to the central pith. $\times 144$.

Fig. 6. Part of a stele from a level about half-way up the strobilus, showing isolated tracheides suggestive of the degradation of the xylem-core. $\times 325$.

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Bower, F. O. 1911. "On medullation in the Pteridophyta." *Annals of botany* 25, 555–574. <https://doi.org/10.1093/oxfordjournals.aob.a089343>.

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