The Ontogenetic Development of the Stele in Two Species of *Dipteris*.

BY

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With Plates LVII and LVIII.

THE material investigated was gathered by Mr. Tansley in 1901 on Mount Ophir in the Malay Peninsula. The amount of material available was not very large, and often the series of sections were not quite complete, so that not all the stages wanted were obtained; enough facts, however, were gathered to form some conclusions on the development of the stelar structure.

The plants investigated were *Dipteris conjugata*, Reinwardt, and *D. Lobbiana*, Moore. Both have a creeping rhizome with leaves going off in alternate rows. Fig. 3, Pl. LVII, shows a young plant of *D. Lobbiana*; the first leaves are divided once, in the latest formed a second dichotomy has taken place. The veins in the leaves branch dichotomously and anastomose, even in young leaves (*D. conjugata*, Fig. 5; *D. Lobbiana*, Fig. 6, Pl. LVII). In the adult stems of both species a solenostele is present. The anatomy of the stele of the mature plant of *D. conjugata* is fully described by Seward and Dale.¹

DIPTERIS CONJUGATA.

Endodermis. Surrounding the steles of the young plants we find, in the first place, a layer of endodermal cells easily to be recognized by the dark contents of its cells. An endodermis consisting of cells with dark brown contents is a very widely spread phenomenon among Ferns, and endodermal cells with similar contents are even found in the fossil solenostelic Fern described by Miss Kershaw.² In the regions near the growing point, however, and sometimes also in older parts, the dark secretion is either absent or, owing to bad preservation or other causes, is not apparent, and

¹ Seward and Dale: On the Structure and Affinities of *Dipteris*. Phil. Trans. Roy. Soc., London, B. 204, vol. cxciv, 1901.

² Kershaw: A Fossil Solenostelic Fern. Ann. of Bot., vol. xxiv, 1910, p. 686.

this makes the endodermis, especially in the young plants, often difficult to recognize.

Pericycle. The pericycle consists of one or two rows of cells, and these cells may have grey contents. The pericycle of the mature plant, as stated by Seward and Dale,¹ consists of two or three rows of cells.

Xylem. In the young plants the xylem is formed of scalariform tracheides, between which occasionally parenchymatous cells are found ; in older plants the parenchymatous cells are more numerous.

Phloem. The phloem consists of small elements, many of which often possess nuclei. In the older plants a pith is present, the cells of which have sclerotic walls ; they are very much like the cells of the inner cortex next to the stele.

Cortex. The cortex in the youngest stems is formed by uniform cells. In the older plants the outer layers of the cortex have cells with thicker walls than the inner ones, and in quite young plants this difference can already be noticed.

The Ontogeny of the Stele. The extreme base of the stem of *D. conjugata* was not present at all ; it is therefore impossible to be certain that a protostele is present, although it is highly probable. The stele of the young stem is often of the *Lindsaya* type² (amphiphloic protostele), and the ventral side of the xylem-ring is frequently much thicker than the dorsal, as in the adult stem of *Lindsaya* itself. This is not, however, a constant feature, as we may find young stages with a more equally developed xylem-ring. Near the base of the stem the tissue surrounded by the xylem has a parenchymatous structure. It is very difficult to tell in the early stages whether any of the cells of the central parenchyma are sieve tubes. Later on undoubted phloem is found, and only then can we say with certainty that the whole stele is of the *Lindsaya* type. A striking phenomenon is the appearance of cells with dark contents in the central tissue. Only a very few of these dark cells are formed at first. They do not form any regular layer, neither have they a constant position. They generally closely resemble the endodermal or pericyclic cells. The contents of the pericyclic cells are mostly not so dark as those of the endodermal ones. It is quite possible that the dark cells formed in the centre of the young stele should really be regarded as the common mother-cells of pericycle and endodermis.

The behaviour of these dark internal cells during the first stages is quite interesting. As stated, a few of these cells appear in the centre of the stele, but in the next sections their number decreases or they disappear completely. That they are really absent and not merely unrecognizable owing to the absence of their dark contents, is shown by the fact that when they disappear the whole central tissue is formed by a smaller number of

¹ Seward and Dale, loc. cit., p. 494.

² Tansley and Lulham : On a New Type of Fern Stele, &c. Ann. of Bot., vol. xvi, 1902.

cells. Some sections later the central tissue has again increased and dark cells are formed, but afterwards they disappear again. The position in which these cells appear varies a good deal. Sometimes they are formed when a leaf-trace is about to depart, sometimes just before the xylem-gap is closed, but they may be absent from both these positions. Fig. 13, Pl. LVIII, shows the stele of a young plant. The rhizome of this plant was 4 mm. in length and had formed eleven leaves. In this stage a leaf-trace has left the stele some little distance below, and the xylem is not yet quite closed. Two dark cells are seen in the centre surrounded by phloem. Fig. 14 is a section of the same rhizome after four more leaf-traces have gone off. No dark cells are present here. The xylem is much more developed on the ventral side. At the departure of the first leaf-traces there is no connexion whatever between the dark inner cells and the outer endodermis, but after some more leaf-traces have gone off, the dark inner cells come into connexion with the outer endodermis, when the leaf-trace separates from the stem-stele, and a real leaf-gap is formed for the first time. It may happen, however, that on the departure of the next leaf-trace there is again no connexion of the outer endodermis and the inner dark cells. The inner endodermis can now often be distinguished from the inner pericycle as a definite tissue, but it does not yet form a regular layer. The number of its cells constantly changes, and it may even disappear completely.

The presence of internal endodermal cells in the stele, before a real leaf-gap is formed and before any connexion has taken place between the outer endodermis and the inner tissue, shows that the inner endodermis is formed independently in the centre of the stele, and that the inner endodermal cells are not in any sense formed by 'intrusions' of the outer ones through the leaf-gaps.

In a series from an older stem we find a true solenostele, but the xylem-ring is still quite obviously thicker on the ventral than on the dorsal side. Protoxylems are apparently absent, as is generally the case in the first-formed stems of Ferns. The pith consists in the first section only of one cell (Fig. 1, Pl. LVII), and a few sections later no pith cell can be recognized. At the end of the series, however, the pith is quite a distinct tissue. Through the whole series the cells forming the pith and the internal endodermis are constantly decreasing and increasing in number; on the whole, of course, they increase. In the first appearance of the internal endodermis this fluctuation in development is already observed. It is seen in all the different tissues of the stele in the youngest stages, and here in the older stem it is again quite obvious, especially in the pith. The leaf-traces succeed each other in this stem very rapidly, and are rather small in comparison with the stele. They mostly go off with two xylem-strands.

In a still older stem the structure is much more like that of the mature

plant. The xylem cylinder is mostly uniform laterally and ventrally, but in some places the ventral side is still thicker than the dorsal one. The xylem consists of tracheides with rows of parenchymatous cells. Some of these have brown contents; probably this secretion is tannin, since in the mature plant the presence of tannin sacs is a constant feature. Mesarch protoxylems are perhaps present, but they are not very distinct. In the series described here the leaf-traces follow each other very quickly, and before a gap is closed the next leaf-trace is already prepared for by the part of the xylem-ring destined for the next trace becoming thinner and projecting outwards. The result is that a complete uniform xylem-ring is never present. The gap is, however, always closed before the projecting arc of xylem separates from the rest, so that the stele is still a true solenostele. In older stems the distance between two leaves is much greater, and there are long internodal stretches with an equally developed xylem-ring. An interesting fact is that the xylem at the margins of both sides of the gaps of this plant is distinctly thickened. The endodermis does not closely follow this thickening. In the mature plant, as described by Seward and Dale,¹ this thickening of the margins always occurs and is still more developed. Here all the other tissues have the same shape. In an old plant examined by me the closing of the leaf-gap was effected by these thickened gap-margins approaching each other on both sides till they fused. The stele had then the form of a ring whose xylem is much thicker on the dorsal than on the ventral side. Gradually this dorsal part becomes thinner till the tissue of the whole xylem-ring has the same thickness. This behaviour does not agree with the statements of Gwynne-Vaughan and Miss Kershaw. Thus Gwynne-Vaughan² writes of *D. conjugata*: 'The free xylem-strand has almost separated off from the solenostele altogether, being connected with it only at two points between which a tongue of ground tissue has inserted itself.' This statement may perhaps refer to the parenchymatous tissue which is formed in the abaxial part of the thickening, but this part belongs to the arc which goes off as the leaf-trace. The parenchyma separates the xylem of the limb of the horseshoe from its curved end. There is no sign whatever of a free xylem-strand nor of any thickening in the internodes. The figure of Seward and Dale³ of the mature stem shows an equally developed solenostele. Miss Kershaw⁴ writes: 'In *D. conjugata* the thickening of the margin of the leaf-gap extends through the internodes as well as the nodes, and this portion of the xylem has become almost completely separated off from the solenostele.'

¹ Seward and Dale, loc. cit., p. 499.

² Gwynne-Vaughan: Observations on the Anatomy of Solenostelic Ferns, Part II. *Ann. of Bot.*, vol. xvii, 1903, p. 700.

³ Seward and Dale, loc. cit., Fig. 8.

⁴ Kershaw, loc. cit., p. 687.

Nothing of the kind is figured by Seward and Dale, nor has it been noticed in the material examined by me.

As a result of the investigation of the different stages of the stem in regard to the development of the stele, we may say in general that probably first a protostele is formed, then the *Lindsaya* type occurs, and this then passes into a solenostele, which at first has thicker xylem on the ventral side, but afterwards comes to possess a xylem-ring equally developed on all sides. The xylem of the margin of the leaf-gaps becomes thickened, and higher up the stem this thickening is still more developed. There is, however, a great fluctuation in development in all the tissues. They may for some time go back again to the condition of a less developed stage. In one series a certain stage may be less developed than in another, or may last for a shorter period.

Roots. The roots of old plants in both species have triarch structure; but the first-formed roots of both species are probably diarch. In the mature plants roots are given off from any part of the surface of the stem (Seward and Dale¹) and independently of the leaf-traces. The same is the case in the young plants. In one case a root was even given off from the thinner and outwardly projecting part of the xylem-ring destined to form a leaf-trace.

Petiole. The first-formed petioles have a simple structure. The xylem forms a flattish arch and is surrounded by phloem. In petioles which are a little older the xylem is horseshoe-shaped. The xylem-arch is interrupted by parenchyma, as seen in Fig. 2, Pl. LVII, which shows the leaf-trace of a rather small plant while still included in the main axis. As already mentioned, the leaf-traces at this stage often depart with two xylem-strands. In petioles formed by an older plant the xylem is broken up into many more pieces. In the petioles which have already horseshoe-shaped xylem, the phloem surrounds the xylem, running in a straight line across the concavity from limb to limb of the horseshoe, but not lining the concavity. In Fig. 2 there is no phloem present at the adaxial side of the xylem. The part of the xylem forming the leaf-trace but still attached to the stele of the stem had here probably no lining of phloem on the inner side. In petioles formed later still we get the same characters as in the mature plants. The xylem is horseshoe-shaped, with the ends curved inwards, and the row of tracheides is interrupted by parenchyma. The phloem and also the endodermis follows the xylem-arch. Secretory sacs, which are absent in the young petioles, are present, and between them protoxylems are found. The investigation of the petioles of the different stages shows very distinctly that there is a gradual transition from the simple structure of the petiolar stele to the more complicated type of the mature plants. Thus we find some petioles which have at their base a horse-

¹ Seward and Dale, loc. cit., p. 495.

shoe-shaped stele, with the endodermis invaginated, while higher up the endodermis and pericycle form a straight line on the adaxial side. In some of the petioles of this stage a tissue of sclerenchymatous cells, surrounded by an endodermis, is found in the centre of the petiolar stele. These steles show a very close resemblance to those in the base of the petioles of *Matonia sarmentosa* (Compton¹), and of some species of *Gleichenia* (Poirault²). This structure is not found through the whole petiole but only in parts of it, and is not always the same in different leaves. In one petiole, e. g., the whole stele has horseshoe-shaped structure at the base. Then the ends of the limbs of the horseshoe approach each other till they meet. The endodermis of both ends joins together, and attached to it is a loop of endodermal cells, including a strand of ground tissue. The loop becomes detached from the outer endodermis, and thus a patch of sclerenchyma surrounded by a ring of endodermal cells is formed inside the stele. These endodermal cells are at first separated by only one layer of pericyclic cells from the endodermis surrounding the stele, but soon the patch of sclerenchyma with its endodermis is found more in the centre of the stele. This structure is reached at 0.5 cm. from the base. The resemblance to *Matonia sarmentosa* and some species of *Gleichenia* is now very striking. At a higher level more changes take place. The outer endodermis projects somewhat inwards, and the internal sclerenchyma changes its position more towards the adaxial side of the petiolar stele. Finally the inner and outer endodermis come into connexion with each other, and a normal horseshoe-shaped stele is again present at 1.5 cm. from the base. For a distance of 1.25 cm. this structure remains; then the ends of the limbs of the horseshoe approach each other again, and at 3 cm. from the base there is again internal sclerenchyma; but now only one cell, surrounded by endodermis, is present inside the stele. At 3.5 cm. the number of sclerenchymatous cells has increased to three. At a higher level it was impossible to tell if internal sclerenchyma or endodermis were still present, but the outer endodermis still formed a straight line at the adaxial side. Unfortunately the petiole was broken off at this point. At the highest level starch was still present in the stelar tissue.

At the base of another petiole, 5 cm. long, the endodermis and pericycle formed a straight line on the adaxial side. Inside the stele one or two dark cells were present which might be internal endodermal cells. Soon a whole group of these internal endodermal cells was formed, and in the midst of these one or two sclerenchymatous cells appeared. The sclerenchymatous cells surrounded by the endodermis come nearer to the outer endodermis and come into connexion with it. After some time they are separated again from the outer endodermis by a layer of pericyclic cells, and

¹ R. H. Compton: *The Anatomy of Matonia sarmentosa*, Baker. *New Phyt.*, vol. viii, 1909, p. 302.

² Poirault: *Recherches anatomiques sur les Cryptogames vasculaires*. *Ann. des Sciences nat. (Bot.)*, série vii, tome 18, 1893, p. 181.

then gradually the internal endodermal and the sclerenchymatous cells disappear.

Thus the behaviour of the petiolar stele was in this case quite different from the one described before. In the first one the internal sclerenchyma was at first in connexion with the cortex, and the internal endodermis was continuous with the endodermis surrounding the stele; in the second petiole the internal sclerenchyma and endodermis are formed in the stele itself, and have no connexion with cortical tissue and outer endodermis. In the last-mentioned petiole the stele was never horseshoe-shaped, for the endodermis is never invaginated on the adaxial side.

In a third petiole the different tissues behaved more like those in the petiole described first, but here the loop of endodermal cells surrounding the sclerenchymatous cells is never separated from the external endodermis. The two limbs of the horseshoe-shaped stele approach each other, separate, and approach each other again. The inner sclerenchymatous cells, or the ones in the curve or in the loop, have often thicker walls and are smaller than the cells of the cortex near the stele.

In many petioles of approximately the same age as the ones described, no internal sclerenchyma or endodermis was found. The changes described take place rather suddenly; it may therefore be that in some the structure was present in a small part, but not found. Seward and Dale¹ have found similar internal fibres in the stele of the main ribs of the leaf of mature plants.

As already mentioned, *Matonia sarmentosa* has in its mature petioles internal sclerenchyma at the base, while on a higher level a horseshoe-shaped stele is present. Perhaps some may think that the resemblance of the structure in some young plants of *D. conjugata* with the mature *M. sarmentosa*, and with some species of *Gleichenia*, must be regarded as an ancestral character, and that it adds support to the view that *Dipteris*, *Matonia*, and *Gleichenia* are related forms. But the irregularity of the behaviour of the internal tissues, the different ways in which they are formed, their rare occurrence and their presence in old leaves, are all facts which suggest to the writer that too much stress should not be laid on this character.

It seems to me possible to explain the facts as follows. When the petiole is getting larger and the limbs of the horseshoe become more divergent, the central tissue gets a tendency to form sclerenchyma. In connexion with this, endodermal cells are formed separating the sclerenchymatous cells from the other tissues. According as different parts of the stele are affected the different structures occur: i.e. the internal sclerenchyma is surrounded by an endodermis in the centre of the stele or is attached to the outer endodermis or directly to the horseshoe-shaped strand. In older petioles, in which the limbs of the horseshoe are more divergent, the stele has always the horseshoe shape. We find a similar case in different species of *Gleichenia*,

¹ Seward and Dale, loc. cit., p. 498, Fig. 38.

in which the centre of the petiole is often for part of its course sclerotic. In *Gleichenia dicarpa*, belonging to the sub-genus *Eugleichenia*, the central region, which Boodle¹ regards as being pericycle, consists partly of parenchyma, partly of sclerotic elements. No internal endodermis is present here, but it is found in other species of *Gleichenia*. The petiole of the sub-genus *Mertensia* has an invaginated endodermis. Boodle writes of it (p. 716): 'The central region is occupied by sclerotic tissue continuous with the cortex and apparently belonging to it instead of to the pericycle as in *G. dicarpa*.' In *G. pedalis* the endodermis is only slightly incurved, and here the pericycle is again partly sclerotic as in some *Eugleichenias*. We see, therefore, that in *Gleichenia* there seems likewise to be a tendency to form sclerenchyma in the central part of the stele, and this is brought about in the different species in various ways resembling the different structures of *D. conjugata*.

Often tannin sacs are not present at the base of the petiole, but appear at a higher level; this is also the case with the protoxylems. Division of the stele into two by constriction in the median vertical plain takes place only just before the lamina is reached and is soon followed by a second division. The veins of the leaf are collateral.

DIPTERIS LOBBIANA.

Stem. *Dipteris Lobbiana* has in many respects the same characters as *D. conjugata*. Fortunately the very first stages were present, but the series were more incomplete and broken than those of *D. conjugata*.

The diarch primary root passes into a protostele (Fig. 4, Pl. LVII). A part of the xylem projects and passes out as the first leaf-trace. The further stages often show the same types as are found in *D. conjugata*. The *Lindsaya* stage is passed through and a few dark cells are formed in the centre, and these disappear again afterwards. A xylem-ring is formed with unequally developed ventral and dorsal side, but the difference in thickness of the two sides is not so striking as in *D. conjugata*.

In one of the series we find the stage represented by Fig. 15, Pl. LVIII. The xylem has the appearance of not being fully differentiated yet, and the section looks as if it were near the meristematic region. Some sections nearer the stem apex, however, the xylem-elements increase very much, in connexion with the formation of a root (Fig. 16), and some sections further on still a complete xylem-ring is formed again. This ring is only one cell thick at the dorsal side and the xylem is much more developed at the point of insertion of the root. This series is again an example of the very irregular development which is so striking a character in *D. conjugata*. The increase of xylem-elements in connexion with root-formation is a very constant feature. When the meristematic region is reached, the xylem is

¹ Boodle: On the Anatomy of the Gleicheniaceae. Ann. of Bot., vol. xv, 1901, p. 714.

represented by a few scattered elements and a group of connected tracheides at one side. These connected tracheides form a fully differentiated leaf-trace (Fig. 8, Pl. LVII). This departure of a leaf-trace while the rest of the xylem is in the meristematic condition is found in all cases, and also in *D. conjugata*. It is a common phenomenon at the apices of Fern stems. But the local failure to develop xylem further back in the stem does not seem to have been described in other Ferns.

In an older stem a normal solenostele is found with an equally developed xylem-ring. The pericycle is formed by a row of 1-2 cells. The cells of the phloem have very thick walls. No protoxylems are apparently present in the xylem, which consists of scalariform tracheides with parenchymatous cells in between. A leaf-trace goes off with two separate xylem-groups. Still within the main axis it turns, ceasing to be opposite the leaf-gap. Fig. 7 is a section of the stele at this stage. The xylem-ring is still open and the internal endodermis is represented by a single cell only. The stele gradually increases in size and a pith is formed. The cells of the pith have thicker walls than those of the cortex near the stele. Near the growing point, when the xylem and phloem are already fully differentiated, the pith and cortex cells have still thin walls, and the endodermal cells have no contents and are not easily recognized. This shows that the xylem and phloem are sooner differentiated than the other tissues.

A still older stem is represented by Fig. 17, Pl. LVIII. On the whole it has the same characters as the one just described. The xylem consists of tracheides with dark brown cells in between. This brown substance may be a secretion of tannin. These tannin cells are represented in the younger plants by the colourless parenchymatous cells. No older plants of *D. Lobbiana* were available to enable one to form definite conclusions, but the structure does not differ very much from the one found in *D. conjugata* of approximately the same age.

A marked difference between the two species is that the leaf-trace in *D. Lobbiana* is given off as two separate strands, one after the other on the same side of the xylem-gap, as shown by the diagrams (Figs. 9, 10, 11, 12, Pl. LVII). No thickening takes place at the margin of the xylem leaf-gap in this species. On the whole, however, there is a great resemblance in the development of the stelar structure of the two species.

Petiole. The first-formed petioles have here also a simple structure. In a petiole 1 cm. long, the lamina of which divides twice dichotomously, the vascular strand is composed of a few xylem-elements forming a slightly curved arch and surrounded by phloem. Probably protoxylem is present. The pericycle consists of one layer of cells. The stele divides into two at the base of the lamina.

A petiole 3.5 cm. long had a lamina which showed three successive dichotomous branchings. At the base of the petiole the stele is formed by

two xylem-groups (Fig. 18, Pl. LVIII). Protoxylem is probably present. The phloem of the ventral side has joined that of the dorsal side and the endodermis extends somewhat inwards. The whole strand has the appearance of the beginning of a branching, but 1 cm. higher the strand has again single structure (Fig. 19). The tracheides form here an uninterrupted arch surrounded by phloem which does not line the concavity. Protoxylem is again present. At the distance of 1.5 cm. from the lamina the strand divides into two, and near the lamina a second dichotomy occurs. Four strands are thus formed, as seen in Fig. 20. Protoxylem remains visible. The veins in the leaves are eventually collateral; they are often surrounded by sclerotic tissue.

In the oldest plant the petiole has two separate strands. Only a very small part of the petiole was available, and in this part (3 cm. long) no change takes place, the two separate bundles maintaining the same distance apart. Each bundle is formed by a xylem arch surrounded by phloem. Endarch protoxylem is probably present. In the first section no tannin cells are found, but somewhat higher characteristic tannin sacs occur. They are not, however, always formed in the same tissue, for they may be next to the xylem in the conjunctive parenchyma, or they may occur in the phloem.

The petiole described first has a single stelar structure, and branching takes place only quite near the lamina; in the oldest plant the leaf-traces go off with a double strand from the stem stele. The transition stage between these two types is quite distinctly formed by the second plant with its double xylem-strand at the base, and again single structure afterwards.

In conclusion I want to express my thanks to Mr. Tansley for supplying me with the material and for all his kind help and advice throughout my work. The photographs were taken by Mr. Mangham, to whom I should also like to express my gratitude.

SUMMARY.

1. The evolution of the stele in the young plants of *Dipteris conjugata* and *D. Lobbiana* appears to be essentially similar. In *D. conjugata* the earliest stages were not available, but there is little doubt that a proto-stele would be found at the extreme base of the young stem, as it is in *D. Lobbiana*.

2. The central tissue formed in the middle of the xylem appears at first to consist largely, perhaps sometimes exclusively, of parenchyma. Later, sieve tubes appear and a typical *Lindsaya* stage is reached. In *D. conjugata* the ventral side of the xylem-ring is distinctly thicker than the dorsal.

3. Cells with dark contents, probably representing the beginning of an internal endodermis, appear isolated or in irregular masses in the midst of the central tissue (phloem or parenchyma). These cells may appear and disappear again several times as the stele is traced upwards, but make no connexion with the external endodermis at the leaf-gaps or elsewhere till after the departure of several traces.

4. Regular connexion of the dark cell-strand with the outer endodermis at the succeeding leaf-gaps occurs after some time; eventually pith cells appear in the centre of the group of dark cells and a normal solenostele is formed. The solenostele of *D. conjugata* frequently retains for some time the inequality of thickness of its xylem on the dorsal and ventral sides noticed in the *Lindsaya* stage, but the xylem-ring eventually becomes of uniform thickness all round.

5. The thickening of the xylem on the edges of the leaf-gap described by Seward and Dale in mature plants of *D. conjugata* occurs in the solenostele of quite young plants.

6. A feature of the steles of the young plants in both the species of *Dipteris* investigated is the irregularity of development in several of the stelar tissues. Thus the external endodermis is often irregularly arranged and is frequently double for part of its course. The pericycle sometimes contains similar dark contents. The dark cells which appear in the midst of the internal phloem or parenchyma in the young plants are generally regarded as being endodermal in nature, but they may be partly of pericyclic nature, or they may represent the common mother-cells of endodermis and pericycle. The development of the xylem is frequently irregular, the tracheides failing to develop in parts of the xylem-ring, which again becomes completely differentiated nearer the apex.

Local development of xylem in advance of the general development is often found in the neighbourhood of the apex of the rhizome at the point where a root or a leaf-trace is inserted.

7. In *Dipteris conjugata* the petiolar stele is always single, in the earlier leaf-traces a flattish arch of xylem surrounded by phloem, in the later a more strongly curved arch. Sometimes sclerenchyma surrounded by an endodermis is found in the centre of the stele of young petioles. These internal tissues differ very much in structure and are not formed in the same way in different petioles. Sometimes the internal sclerenchyma and internal endodermis are in connexion with the cortex and external endodermis; in other cases they arise and disappear quite independently. Dichotomy of the leaf-trace to form the main veins of the leaf takes place only at the upper end of the petiole.

In *D. Lobbiana* the petiolar steles of the first-formed leaves resemble those of *D. conjugata*, but in later-formed leaf-traces a double structure may be evident in the lower part of the petiole; this becomes single again

nearer the lamina and ultimately branches dichotomously before the lamina is reached. The latest formed leaf-traces investigated depart from the edge of the leaf-gap as two successively separated cylindrical strands. This phenomenon may be connected with the more thorough dichotomous division of the leaves of *D. Lobbiana*.

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EXPLANATION OF FIGURES IN PLATES LVII AND LVIII.

Illustrating Miss de Bruyn's paper on *Dipteris*.

PLATE LVII.

- Fig. 1. *D. conjugata* rhizome. Fairly young plant. Transverse section of the stele. Pith consisting of only one cell. $\times 340$.
 Fig. 2. *D. conjugata* rhizome. Fairly young plant. Transverse section of the leaf-trace still in the main axis. $\times 340$.
 Fig. 3. *D. Lobbiana*. Young plant. $\times 2$.
 Fig. 4. *D. Lobbiana* rhizome, just above primary root. Transverse section of the stele, showing protostelic structure. $\times 290$.
 Fig. 5. *D. conjugata*. One of the first-formed leaves, showing reticulate venation. $\times 8$.
 Fig. 6. *D. Lobbiana*. One of the first-formed leaves. $\times 8$.
 Fig. 7. *D. Lobbiana* rhizome. Fairly young plant. Transverse section of the stele. Only one internal endodermal cell. $\times 260$.
 Fig. 8. *D. Lobbiana* rhizome. Young plant. Transverse section of the stele near the apex. Stele in meristematic condition, except one part of it, which forms a leaf-trace. $\times 260$.
 Figs. 9, 10, 11, 12. *D. Lobbiana* rhizome. Older plant. Diagram showing the formation of the double leaf-trace.

PLATE LVIII.

- Fig. 13. *D. conjugata* rhizome. Young plant. Transverse section of the stele, showing two dark internal cells. $\times 156$.
 Fig. 14. *D. conjugata* rhizome. Same plant as Fig. 13. Section nearer to the apex. Transverse section of the stele, showing *Lindsaya* type and unequally developed xylem-ring. $\times 156$.
 Fig. 15. *D. Lobbiana* rhizome. Young plant. Transverse section of the stele. Xylem in scattered groups. $\times 156$.
 Fig. 16. *D. Lobbiana* rhizome. Same plant as Fig. 15. Section nearer to the apex. Transverse section of the stele. Xylem very much developed in connexion with root formation. $\times 156$.
 Fig. 17. *D. Lobbiana* rhizome. Older plant. Transverse section of the stele. $\times 100$.
 Fig. 18. *D. Lobbiana* petiole, 3.5 cm. in length. Transverse section of the stele near the base. $\times 156$.
 Fig. 19. *D. Lobbiana* petiole. Same petiole as Fig. 18. Section at 1 cm. from the base. Transverse section of the stele. $\times 156$.
 Fig. 20. *D. Lobbiana* petiole. Same petiole as Figs. 18 and 19. Section near the lamina. Transverse section of the bundles. $\times 156$.

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