ON THE ANATOMY OF THE HYMENOPHYLLACEAE AND THE SCHIZAEACEAE AND SOME ADDITIONAL REMARKS ON STELAR MORPHOLOGY

by

O. POSTHUMUS.

(Botanical Laboratory of the Groningen University).

In a previous memoir 1) I have discussed some of the stelar morphological features in a number of groups of Ferns and Spermophyta. As the Hymenophyllaceae and the Schizaeaceae are not dealt with therein, I intend to give here some additional remarks on the anatomy of these groups from the above standpoint.

The supposition was made there 2), that the vascular bundle in the leaf and in the petiole is built up of a number of elementary bundles, which may be considered, as it were, as running to the axis and fusing laterally. These bundles, after having passed through the cortex, fuse with the vascular system of the stem. The mode of arrangement of the elementary bundles causes the different types of petiolar structure, which can be seen in transverse sections.

Each of these elementary bundles normally has one group of protoxylem; in transverse sections the bundles may be seen to be quite free from one another, or forming a strap of tissue with several groups of protoxylemelements, which may fuse, at a lower level, on the inner side. Adaxially to this protoxylem is an amount of thin-walled

tissue, which, in the less complicated forms, ends below as a funnel, each funnel being associated with a protoxylem strand, and mostly penetrating into the vascular system of the stem.

If one reads the descriptions, given by Boodle 3) of the anatomical structure in the Hymenophyllaceae, it seems very probable that this scheme may also be applied to this group. Some species, on the basis of these descriptions, will be discussed here.

Although, in the different species, the petiolar structure is liable to variation, it is, except in the lowermost part, collateral, the xylem in transverse section being arc-shaped with one median and two lateral protoxylems or with two lateral ones only.

In Hymenophyllum dilatatum 4) two lateral groups only are to be found. A short distance above the fusion of the petiolar trace with the axillary branch, the xylem is seen, in transverse section, to have formed a closed ring. The protoxylems are now internal, and intermixed with parenchyma 5). The phloem is now continuous all round the xylem of the bundle, which fuses with the bundle of the axillary branch.

In some species of Trichomanes similar structures have already been described. In T. reniforme 6) in transverse section of the collateral bundle two protoxylem groups may be seen at the inner side of the xylem, each with a mass of parenchyma, separated from each other by some metaxylem. Lower down these protoxylems fuse, the parenchyma is continuous; then the sides of the arc bend inwards, approach each other and fuse: the xylem now encloses a little parenchyma. Still lower down the phloem is to be found all round the xylem of the petiolar bundle.

The structure in T. radicans 7) is well shown in fig. 28—32 of Boodle's paper. In the petiole the wood is arc-shaped in transverse section. Lower down the two sides of the arc fuse, enclosing some parenchyma, which

diminishes in size lower down. The xylem of the bundle is now nearly solid and surrounded by phloem. The bundle then fuses with that of the axillary branch. The protoxylems of the petiolar trace and of the axillary branch may be traced distinctly for some distance in their downward course.

In T. javanicum Chambers described 8) similar features. In T. Prieurii one of the protoxylems ends blind in the stem 9).

When thus following the leaf trace in its downward course, we see at successive levels an endarch bundle with abaxial phloem; afterwards the inner margins of the xylem fuse at the inner side, thus enclosing some parenchyma, which diminishes in size lower down; the xylem is then wholly surrounded by phloem. This structure is essentially the same as that in the lower part of the leaf-trace in Thamnopteris and Cheiropleuria. It may be suggested that these structures in different species are homologous and that the reduction of the metaxylem of the leaf-trace has not extended so far as the insertion of the leaf-trace into the vascular system of the stem, and could not therefore act on the vascular system of the stem.

The structure of the latter is in accordance therewith. Though it is liable to variation, all different types may be described as derived from an originally solid xylem which has been reduced, perhaps owing to the habitat, but in its own way, not in consequence of the alterations in the leaf-trace. The phloem round the stem is always continuous. As in those Filicales, where a funnel may be found in the lower part of the leaf-traces, the xylem of the stem is not hollowed or pocketed.

It is also remarkable that in those forms where the reduction of the metaxylem of the leaf-trace has not gone very far, the leaves are mostly highly compound, as in the Hymenophyllaceae or much specialised in their venation, like Cheiropleuria. In some forms with simple leaves

(Monogramme linariaefolia, Asplenium Nidus, Elaphoglossum spec.) there is a dictyostele with well marked gaps. Solenosteles or dictyosteles, which are but little different from a solenostele, are found in the genera Adiantum, Hypolepis, Ceropteris, which for the most part possess compound leaves. In the Schizaeaceae too, Lygodium, which has the largest leaves, has the simplest structure.

The structure of the Schizaeaceae is well known through the investigations of Boodle, Tansley and others.

In Schizaea digitata the leaf-trace is collateral, 10) its protoxylems are perhaps lateral, but not distinct. The vascular system of the stem consists of a hollow tube of xylem, with parenchyma, which is often sclerified, inside of it. On the outer side it is lined with a continuous layer of phloem, pericycle parenchyma and endodermis. When the leaf-trace approaches the vascular system of the stem, the endodermis of both fuse and the xylem of the leaf-trace approaches that of the stem, which is now interrupted in the place opposite to the former. The sides of the leaf-trace fuse with the margins of the gap and the continuity is restored.

This collateral leaf-trace and the hollow cauline xylem tube are also found in the other species of Schizaea. One species, however S. dichitoma, 11) offers some points of interest. Here the xylem of the stem is also interrupted before its fusion with the leaf-trace, but the endodermis dips slightly inwards. The endodermis of the foliar bundle fuses with that of the vascular system of the stem on both sides of the groove, so that an endodermal pocket is formed, which can be traced for some distance downwards. In some transverse sections an internal endodermis is found, which, however, in successive transverse sections is seen not to be continuous with the outer endodermis, but wholly isolated. Some isolated tracheids occur in the pith. In S. malaccana Tansley and Chick 12) observed the

same features. In S. bifida Boodle 13) observed endodermal pockets, but no internal phloem and endodermis. The gaps in the xylem are here slightly longer than one internode, the xylen has the form of that of a dictyostele.

In the subgenus Anemiorhiza of the genus Aneimia the structure, as far as the xylem is concerned, is that of a solenostele. In A. coriacea 14) there is an inner endodermis too, but in the axils of the leaf-traces, figured by Boodle there is an endodermal pocket, which does not reach the inner endodermis so that at this level the inner tissues are not in continuity with the cortical ones. In A. aurita there is no internal endodermis or phloem, only some parenchyma is found inside the xylem 15).

In Aneimia Phyllitides 16) the stem-structure is wholly dictyostelic, with a simple leaf-trace, as in many Polypodiaceae. Mohria caffrorum shows the same structure 17).

The internal structure of Lygodium 18) differs much from that of the other members of this family. The xylem of the stem is solid; the xylem of the leaf-trace is triangular in transverse section with three protoxylems imbedded near the angles. Lower down the xylem is more rounded in transverse section and fuses with that of te stem. It was imposible to determine whether the protoxylems of the leaf-trace did fuse with those of the stem or not.

In Lygodium the leaf-trace is specialised in its own way, probably because of the climbing habit of the leaves, analogous to Odontosoria fumarioides 19). The alterations from the original structure have not yet reached the stem, and affected the structure of its xylem. In the other genera this has taken place and the wood of the stem is gapped and hollowed. But a funnel has never been found in the leaf-trace nor has an independent medullation been observed in the young plant 20). The inner side of the xylem of the leaf-trace passes gradually into the inner side of the xylem tube of the stem. The parenchyma, associated with

the leaf-traces, penetrates into the stem; that of successive leaf-traces unites and a pith is formed. In Anemia aurita this parenchyma is but scantily developed; in other species differentiation into endodermal cells was possible so that endodermal pockets and at last an internal endodermis could be formed.

The phloem, originally restricted to the outer side of the wood, lines in Anemia and Mohria also the inner side of the xylem tube. With larger development a dictyostelic structure is attained both in Schizaea dichotoma, without internal endodermis and in Anemia Phyllitides and Mohria caffrorum with internal phloem and endodermis; but the gaps do not reach any considerable length.

In the Gleicheniaceae and the Osmundaceae small funnels are found below the insertion of the leaf-trace; the medullation of the xylem of the stem is independent of this. In the Polypodiaceae, Cyatheaceae and Marsilia the medullation can be explained as the extension of the reduction of the adaxial parenchyma of the leaf-trace. The Schizaeaceae have a structure similar to that of the families last-named.

In my previous memoir I drew 21) a distinction between stem-xylem and leaf-trace xylem. This classification may be considered from two points of view; it may be a technical question or one of principle as e.g. the distinction between a main axis and branches in some inflorescences, e.g. a cyme.

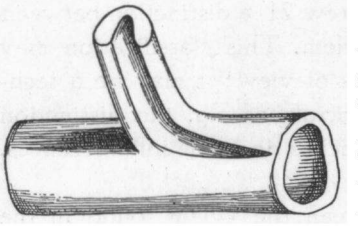
If we see a difference between the xylem found in the stem and that of the leaf-trace and its insertion into the vascular system of the stem, it will be necessary to indicate this difference in the description. When stress is laid on this fact, by giving names to both kinds of things, it is easier to form a mental picture of the vascular system.

But when we have distinguished between these two forms, the question of principle arises. Is the stem-xylem

(and surrounding tissues) independent of the leaf-trace xylem (and surrounding tissues), or are the leaf-traces branches of the vascular system of the stem or the vascular system of the stem formed by by the coalescence of the lower parts of the leaf-traces?

I have pointed out 22) that several facts do not favour the hypothesis that the leaf-traces are branches from the stem-system; so there remains only an alternative between the views: the stem-xylem is independent of the leaf-trace xylem or derived from the fusion of its lower parts.

The orientation of the leaf-gaps is dependent on the leaf-trace only. If the leaf-trace faces the apex of the stem it is quite symmetrical towards the plane, which goes through the leaf-trace and the axis of the stem. If the leaf-trace is obliquely inserted, the gap follows in its symmetry that of the leaf-trace. In some species the leaf-trace faces the medial plane of the rhizome. The right or left side of the xylem of the leaf-trace, which is now nearer to the top of the rhizome than the other parts, abuts on the xylem of the stem and there is no interruption in the latter above the insertion. The prolongation of the concavity of the gutter shaped strand curves round, not upwards, but towards the base of the rhizome. The xylem is interrupted for some distance below the insertion of the leaf-trace; the leaf-gap is, as it were, turned upside down. This is well shown in the figure of Odontosoria fumarioides (Davallia fumarioides) given by Gwynne-Vaughan 23) (see fig.) but it occurs also in other Ferns. If the stem-



Odontosoria (Davallia) fumarioides. Diagram of the vascular system, including a node and the base of a leaf trace, showing the position of the leaf gap. The top of the rhizome is to the left (after Gwynne-Vaughan, 1916, fig. 6, p. 502).

xylem is derived from the leaf-trace xylem, this must have taken place before the formation of the leaf gaps.

In most Ferns the differentiation of the stem-xylem is wholly independent of that of the leaf-traces. In a few Ferns only could the first formed elements of the leaf-traces be proved to be continuous with those of the stem. In the former they are endarch or mesarch, according to the condition of the parenchyma at the inner side, In the stem the first formed elements may be situated towards the periphery, inside the xylem or at the inner surface of the tube. If the stem-xylem may be considered as derived from the leaf-trace xylem, we may fairly assume that this process took place before any differentiation took place in the xylem tissue into proto- and metaxylem.

If we derive the stem-xylem from the leaf-trace xylem we must admit that this took place before the plant was differentiated, either in the symmetry of its elements or in the structure of the vascular bundles. But then we may also argue that both leaf-traces and stem system have arisen independently of each other, after these parts of the plants have been more clearly differentiated into these organs.

Either case is as likely as the other one and this side of the probleem is a different thing from the distinction between the stem-xylem and the leaf-trace xylem.

The critical moment deciding the predominance of the axis or of its appendages is only shifted to an earlier stage, where there is no control by any evidence.

In some articles, which I had previously overlooked, O. Lignier 24) discussed the relation between the axis and its appendages, especially in the Vascular Plants. He supposed that, in the Ferns, the leaves are derived from groups of branches, which have become dorsiventral; the lower parts of these groups form, according to his theory, the stem. The vascular systems of these "mériphytes" are

developed centripetally, and the vascular system of the stem is formed by the lower parts of these leaf-bundles.

In another article 25) he discusses the phylogeny of the vascular system and presumes, that after this dorsiventrality has been attained and under its influence, the bundles of the leaf-branches, which are originally solid and mesarch are opened at the upper side, forming an arc, with a billateral symmetry. „Cette transformation de la symétrie axiale en une symétrie bilaterale s'étendit de même que les adoptions précédentes des parties supérieures du mériphyte vers ses parties inférieures, atteignant finalement la tige elle même" 26). This supposition, for which he gives no arguments, is confirmed by the succession of the anatomical characteristics in the leaf-traces of Thamnopteris, Osmundites Dunlopi, Osmundites Kolbei and Osmunda regalis and by the structure in the leaf-trace of Cheiropleuria, when compared with that in the other Polypodiaceae, where the alterations may also be explained by a basipetal development of the reduction of the adaxial metaxylem of the leaf-trace into parenchyma.

Summary.

1. In the vascular system of the Hymenophyllaceae and of the Schizaeaceae the same characteristic features are seen as in other groups of Ferns.

2. In the Hymenophyllaceae the reduction of the adaxial metaxylem of the leaf-trace never reaches the xylem of the stem, which is often reduced in its own way.

3. In the Schizaeceae all grades of development may be observed but pith is never formed independently of the parenchyma of the leaf-trace.

4. The distinction between leaf-trace xylem and stem xylem is justified from a descriptive point of view; whether one of them is derived from the other, cannot be decided owing to lack of evidence.

5. Some theories of Lignier agree with views, formerly given.

---

1) Receuil des trav. bot néerl., vol. XXI, 1924, p. 111-296.
2) l. c., p. 147.
3) The anatomy of the Hymenophyllaceae, Ann. of Bot., vol. XIV, 1900.
4) l. c., cf. p. 466.
5) l. c., cf. fig. 6, 7 with fig. 9.
6) l. c., p. 470.
7) l. c., p. 471.
8) Ann. of Bot., vol. XXV, p. 1037, 1911.
9) Boodle, Ann. of Bot. XIV. p. 475.
10) ———, Ann. of Bot. XVI, 1902, p. 374, fig. 11-14.
11) ———, Ann. of Bot., vol. XVII, 1903, p. 514, fig. 24, 25.
12) Tansley and Chick, Ann. of Bot., vol. XVII, 1903, p. 495.
13) Boodle, l. c., 1903, p. 523.
14) ———, l. c., 1901, p. 386, fig. 41-43.
15) ———, l. c., 1901, p. 387.
16) ———, l. c., 1901, p. 379.
17) ———, l. c., 1901, p. 392, fig. 35.
18) ———, l. c., 1901, p. 361.
19) D. T. Gwynne-Vaughan, Ann, of Bot, XXX, 1916, p. 496.
20) Bower, Ann. of Bot., vol. XXXII, 1918, p. 4, 5, fig. 1-3; Boodle, l. c,. 1901, fig. 22-31.
21) Receuil des trav. bot. néerl., vol. XXI, 1924, p. 155.
22) l. c., p. 147
23) Gwynne-Vaughan, 1916, p. 502, fig. 6.
24) Lignier, Bull. de la Soc. Bot. de France, vol. LVIII, 1911, p. 7, 29, the older litterature is cited there.
25) l. c., p. 7, 8.
26) l. c., p. 29, 31.