ON SOME PRINCIPLES OF STELAR MORPHOLOGY

by

O. POSTHUMUS.

Introduction.

In the study of anatomical structures in Vascular Plants different ways may be followed, according to the problems the botanist may have to solve. For the study of the tissues attention will be given to the elements, their relationship and the structure of their wall and contents.

But for those, who study the distribution of the tissues in the stem and leaves, these tissues, if the true nature be established, will be choosen as the units, of which the structure is considered to be built up.

Both ways of dealing with the relationship of groups of plants must be taken into account, and if the results, reached by these different ways, be the same, we may expect to have formed an idea as clear as possible from the problem as is possible from the material.

If a structure be analysed, we form by combining its elements a mental picture of that structure. This picture, when compared with that obtained from other plants, gives us an idea of what we may fairly assume was the primitive form and thus we may follow the modifications of that primitive form that has come about.

In order to compare these mental pictures we look upon them as being built up of a complex of elements, the different arrangement of which gives the general characteristics. How far this conception may be generalised depends upon the suitability of its units.

This explains the numerous attempts that have been made since the appearance of the memoir of Van Tieghem and Douliot on Polystely, to consider the structure in the Vascular Plants from the same point of view. Each system consequently originated a nomenclature especially in accordance with the author's views. The older terminology was abandoned and replaced by another, the use of which was only justified when departing from certain theoretical considerations [1]). The meaning of these terms could not be constant and great confusion resulted.

The Stelar Morphology is the study of the anatomical structure, especially of the distribution of vascular tissues in the Pteridophyta and Spermophyta. It is not only studied in transverse sections, but the model is built up from successive sections. This model is studied as an object in three dimensions. Analogous points in the structures compared are sought for and differences are noted.

The structure of the tissues themselves is less important, they are considered to be homologous. Thus we have only to consider the distribution of the xylem, the phloem and their first-formed elements, the parenchyma between them and the endodermis. The position of the sclerenchyma and of idioblasts seems to be less important.

In this memoir I have tried to describe a number of structures from this point of view. I have endeavoured as far as possible to avoid "derived" terms and to use descriptive ones only, the meaning of which is independent of the views held by the author. My aim is to construct a scheme in which the different structures may be included.

---

[1]) cf. Brebner. 1902, p. 522; Schoute, 1902, p. 144, Fr. J. Meyer, 1916, p. 162.

CHAPTER I.

The Stelar Morphology of the Osmundaceae.

This family, which has nowadays a somewhat isolated position among the Ferns, is one of the oldest known. Fossil remains of this family are indisputably present in Palaeozoic strata. The recent forms, which belong to the genera Osmunda, Todea, and Leptopteris, agree in having a short erect or inclined stem, which is for the most part underground. The internodes are short; the leaves are crowded, spirally arranged and pinnate or bipinnate with a terminal leaflet. The older part of the stem, which is underground, is densely clothed with the persistent leaf-bases, so that, though the stem proper is small (only a few cM. thick), the rhizome may attain large dimensions. (J. P. Lotsy, 1909, p. 588; in O. regalis — 1 M. diam.). In Leptopteris Wilkesiana Brack. and L. Fraseri Presl (H. Christ, 1897, p. 334) the habit is that of a tree-fern; in the fossil forms Osmundites skidegatensis and O. Carnieri this was probably also the case. I have been unable to ascertain in the literature of the subject whether the stem in these recent forms consists of an axis without a sheath of leaf-bases as in Cyathea or whether it is constructed on the plan of the Osmundaceae.

Of the other characteristic features only the following need be mentioned here. The sporangia are large, globular with a short thick stalk. An annulus is wanting although a lateral group of thick-walled elements is present; the dehiscence is a vertical one. The spores are numerous.

An indusium is always wanting. The situation of the sporangia is different in the three genera.

In Osmunda the pinnae and sometimes the leaves are dimorphous; the fertile pinnae have their lamina reduced and the sporangia are placed on the margin. In Todea the sporangia are situated on the lower side of the pinnules along the veins. In Leptopteris there are only a few sporangia at the base of the lateral veinlets.

Horizontal rhizomes with long internodes as in the Gleicheniaceae or in Pteridium are not found in this family. The leaf is always symmetrically placed with regard to the axis of the stem; the leaf-trace always faces the apex. Irregularities in the structure such as occur in Dennstaedtia punctilobula and other allied forms, where the leaf-trace faces the medial plane, are unknown here. This absence of irregularities, combined with the fact that a relatively large number of the members of this family, both recent and fossil, have been investigated anatomically, renders the group a suitable one for comparitive study. The fossil species have been thoroughly investigated by R. Kidston and D. T. Gwynne—Vaughan (1908—1914). The agreement with the recent Osmundaceae is not only shown in their habit (they all have an erect stem with short internodes, clothed with the persistent leaf-bases) but there are a number of histological details which are common to them all, e.g. the occurrence of a sclerotic cortex, of "porose layers" and xylem consisting of tracheids only. The transverse section of the leaf-trace is characteristic in all: it is horse-shoe shaped with incurved margins. Thus the affinity of the fossil members with the recent forms is beyond question.

In the following chapter I will describe the structure of different members of the Osmundaceae. In order to make my theoretical conclusions more obvious I have arranged the types in a series beginning with the more elementary forms. The descriptions are taken for the most part from the authors cited and in some cases I have confirmed their results by personal observation. The structure in Thamnopteris will be dealt with in the first instance, since it is the simplest form known; next Osmundites Dunlopi, O. Kolbei and O. regalis will be discussed. From the latter type we may pass to O. skidegatensis and O. Carnieri in one direction and to Osmunda javanica in another.

The structure of the "seedling" will next be discussed, followed by a description of the structure of the petiolar trace. Finally a summary of the results with a statement of the theoretical conclusions will be given.

A. The stem.

Thamnopteris Schlechtendali (Eichwald) Brognt. (R. Kidston and D. T. Gwynne Vaughan, 1909, p. 601—657, f. 1—38). Only a piece of the stem of this plant has been found. It occurred in strata of Permian age near Bjelebei in the government of Orenburg. The length of the original stock was about 30 cM., its thickness 16 cM., the stem proper, which is densely clothed with the persistent leaf-bases, being only 5 cM. in diameter.

The internodes are short; the leaf-traces run radially but obliquely through the cortex, so that in a transverse section a number may be seen. The outer cortex is sclerotic, the inner part, which consists of parenchymatous tissue, has for the most part disappeared. The leaf-trace in the leaf-base is horse-shoe shaped in transverse section, with incurved margins. About 20 groups of protoxylem elements are situated on the concave inner side. Round the xylem a well developed continuous layer of phloem is situated; in it the first formed elements are situated on the outer side; the whole is surrounded by an endodermal layer.

At the insertion of the leaf-base in the stem the leaf-trace has diminished in size, especially in breadth; the number of protoxylem strands has diminished to 10, this reduction is continued, when following the course downwards, so that on reaching the inner cortex only 5 are present. Meanwhile the phloem and the endodermis disappear from the concavity of the xylem, the margins of which are no longer incurved. At the same time that the number of protoxylemstrands is reduced by fusion to one, the margins of the xylem approach and fuse. Thus a certain amount of parenchyma, situated adaxially to the protoxylem, is enclosed. At a lower level this is smaller in size, and at last wholly disappears. Below the latter level the leaf-trace has only one centrally placed group of protoxylem.

Meanwhile the endodermis of the leaf-trace has fused with that of the central system of the stem while the xylem of the leaf-trace, which has become more rounded in transverse section, approaches the xylem of the stem and fuses with it. For a short distance it can be traced as a ridge on the outer surface of the xylem, but at a lower level this disappears also. The protoxylem is only decurrent in the xylem-tissue of the stem for a short distance. The central xylem of the stem is cylindrical in shape; it consists entirely of tracheids, no parenchymatous elements being present. Those elements situated at the periphery are of a smaller size than the more central tracheids.

The phloem of the leaf-trace is continuous with that of the stem; in the latter no protophloem could be distinguished. The tracheids are pointed, with regular multiseriate pits, the outermost have the same pitting as the rest. The tracheids of the central xylem are different from those of the outer part; they are short and wide, with irregularly distributed pits.

The only protoxylem groups present in the stem are those decurrent from the leaf-traces; they consist of small tracheids with a single series of scalariform pits on their walls, and they die out gradually below without joining on to one another.

If we try to reconstruct the xylem of the stem without taking into account the arrangement of the other tissues, we see a central cylinder of wood, about 6 times as broad as the leaf-traces. The latter are solid at their insertion into the central xylem, each with a centrally placed protoxylemstrand, which is decurrent only for a short distance into the central axis. At a slightly higher level on the inner side of the protoxylem a small amount of parenchyma is found. This increases in size, so that the continuity of the metaxylem situated adaxially to the parenchyma, is interrupted. The parenchyma might be described as a cone of tissue, which follows the protoxylem and penetrates the xylem of the leaf-trace. The transitional part of the xylem of the leaf-trace thus possesses a funnel, decurrent into the xylem and into this funnel a cone of parenchyma fits.

It is my aim to demonstrate in this memoir, that such a funnel is present not only in Thamnopteris, but also in the other Osmundaceae. This formation of parenchymatous tissue at the adaxial side of the protoxylem is of a great importance in comparing the several members of the family, for a number of features can be more readily explained, when considered from this point of view. Yet this cone of parenchyma is not only present in the Osmundaceae, it occurs in other Filices, such as the Gleicheniaceae, the Dineuroidaceae, the Clepsydropsidaceae, the Polypodiaceae and the Cyatheaceae.

In the reconstruction of the vascular system in Thamnopteris (which we may consider as a starting-point in our examination) we can distinguish the following positions, as indicated in fig. 1:

um, the upper and inner margin of the funnel; above this level the xylem is horse-shoe shaped in transverse section; below this level it is annular.

lp. the lowest point of the funnel.
i. the insertion of the leaf-trace into the vascular system of the stem.
e. the end ot the protoxylem strand.
fp. the fusion between the two protoxylem strands which are found in the lower part of the xylem of the leaf-trace.

If these features are present in other plants, it may be possible to draw up a scheme for the comparison of such structures throughout the plant kingdom.

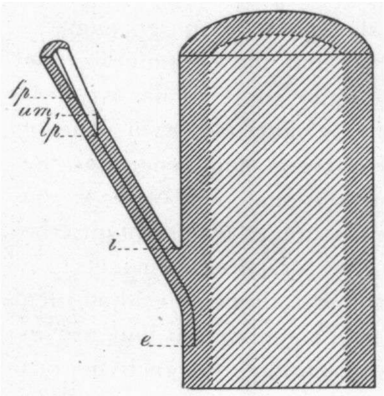

Fig 1. Thamnopteris Schlechtendali (Eichwald) Brongniart. Longitudinal section of a model of the xylem-tissue. Explanation in the text.

The interrelation of these points in Thamnopteris is not always constant as a consideration of the figures, given by Kidston and Gwynne—Vaughan will show. In most cases the fusion of the two protoxylem strands to form one, *fp.*, is at a higher level than the upper margin of the funnel *um,*. In such horse shoe shaped bundles only one protoxylem is seen (Kidston and Gwynne-Vaughan, 1909, fig. 23). If *fp.* is lower than *um,* there are always two such groups even in the annular stage (l.c. fig. 22). If *fp.* is lower than *lp.*, the bundle in a transverse section below the lowest point of the funnel is solid with two immersed protoxylem strands (Kidston and Gwynne—Vaughan, 1909, fig. 33—35). These 3 cases are shown in the figures given by the authors; it follows from the above that the fusion of the protoxylem strands is a process which is independent of the formation of the parenchyma of the funnel. It is possible, that the two protoxylem strands which are shown in figure 33, 34, 35, are each associated with some parenchymatous tissue, which is ending blind downwards.

Osmundites Dunlopi Kidston and Gwynne—Vaughan. (1907, p. 759—763, fig. 1—16). Of this plant, from Jurassic rocks in New-Zealand, a piece of the stem, covered with leaf-bases, is known. The specimen attained about 8 cM. in diam., while the stem proper was only 1.7 cM. thick.

In the leaf-bases the bundle is horse-shoe shaped in transverse section, with a number of protoxylem strands lying on the inner surface. At a lower level the transverse section is semicircular, while the number of protoxylems has been reduced. After passing inwards beyond the sclerotic cortex of the stem, the xylem of the bundle is reniform, with only one median protoxylem strand (l. c. 1907, fig. 3).

Meanwhile, as the bundle approaches the central xylem, a groove is formed in the latter just opposite the leaf-trace. The margins of the reniform foliar trace fuse with the margins of the groove, so that in a transverse section at this level an amount of softer tissue is seen to be enclosed on the adaxial side of the protoxylem strand (l. c. 1907, fig. 4) of the foliar trace. When traced further downwards this parenchyma diminishes in size and disappears; at this level also the protoxylem is no longer distinguishable.

The xylem of the stem forms an uninterrupted ring, consisting of tracheids without any intermixed parenchyma-cells. The outer elements are somewhat smaller than the inner tracheids. The central tissue of the stem has wholly disappeared. Though the ring of xylem is somewhat reduced opposite to the leaf-traces, no interruption of its continuity could be found.

Nothing is known of the other tissues which have been destroyed during fossilisation.

If the structure of O. Dunlopi be compared with that of Thamnopteris, some points of agreement are at once apparent. Parenchymatous tissue is present situated adaxially to the protoxylem and ending blind at a lower level, thus forming a funnel in the xylem. The lowest point of the funnel *lp.* is however not situated above the insertion of the leaf-trace into the tissues of the stem, as in the case of Thamnopteris, but lies below this point, so that the included parenchyma is yet visible after the xylem of the leaf-trace has fused with that of the stem.

The upper margin of the funnel which, in Thamnopteris, is at a level higher than the insertion of the xylem into the stem, is here lower, and the xylem situated adaxially to the parenchyma of the funnel is not only reduced, but has wholly disappeared, so that the parenchyma can affect the xylem of the stem, producing a groove in it opposite to the leaf-trace. Since the leaf-trace in Thamnopteris has lost its horse-shoe shaped character prior to its insertion in the axis of the stem, it touches the latter at one point on joining with it, In the case of O. Dunlopi however the petiole trace retains the arcuate form and therefore there are two points, one at each end of the trace, at which contact with the stem-xylem is made.

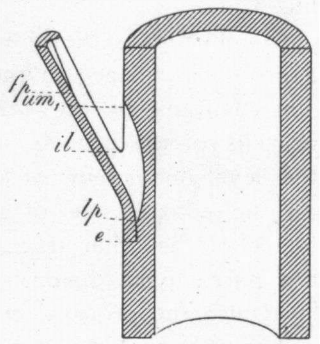

Fig. 2. Osmundites Dunlopi Kdst and Gw. V. Longitudinal section of a model of the xylemtissue. Explanation in the text.

The left point is indicated in fig. 2 by *il.* The upper margin of the funnel has disappeared at the point of insertion, but there is an analogous structure in the xylem of the stem, where a groove is present and reaches in an upward direction; this is indicated in the figure as *um,*.

A distinction between Osmundites Dunlopi and Thamnopteris is shown in the central part of the stem.

In the former the central tissues have dissappeared, but no doubt were parenchymatous, while in the latter they consisted of modified tracheids. Now the structure in Osmundites can readily be explained as derived from a stem similar to that of Thamnopteris by reduction of the central tracheids to parenchymatous elements.

The complete vascular cylinder as in O. Dunlopi can be explained as derived from a form with a medullated axis and mesarch leaf-traces, in which the tracheids situated adaxially to the protoxylem strands are not developed.

This zone of reduction, ending below as a cone, is prolonged downwards, so that it penetrates the stem-xylem and produces pockets in it. The leaf-trace now is endarch throughout its length and a groove is formed in the stem opposite to the leaf-trace. The medullation of the stem-axis is thus quite independent of the formation of pockets of parenchyma (funnels) in the periphery.

If this conclusions be correct, intermediate stages between Osmundites Dunlopi and Thamnopteris may be expected, especially as regards the leaf-trace. No such cases have been found in the Osmundaceae, except in the young plants. In the mature stems of Cheiropleuria bicuspis (Bl.) Presl, however, a pocket is found in the leaf-trace, with its lowest point below the insertion in the stem, so that a transverse section of the xylem of the leaf-trace, where it fuses with the xylem of the stem, has as annular shape. Simular features are found in Stromatopteris moniliformis Mett., and some species of Trichomanes. These forms will be dealt with later on.

Another interesting form from the present standpoint is: *Osmundites Kolbei* Seward (Kidston and Gwynne—Vaughan, 1910, p. 455—461, fig. 1—21).

This plant, of Wealden age, comes from South Africa.

Again only a piece of the stem is preserved. In it the leaf-bases, the outer sclerotic cortex and the vascular tissues are shown, but the inner parenchymatous cortex had wholly disappeared, as also the greater part of the pith.

The stem proper was rather thin (only 3,5 cM. in diam.), but it was densely clothed with the persistent leaf-bases, so that the rhizome as a whole reached a diameter of about 14 cM. The central vascular tissues were about 2 cM. across. The internodes are short, the leaf-traces pass through the cortex obliquely so that in one transverse section a number of them are seen.

In the leaf-base the trace in a transverse section is horseshoe shaped, with incurved margins, and about 12 groups of protoxylem elements are equally distributed on the inner surface. The xylem is surrounded by a continuous phloem and endodermis. When traced further downwards, the number of protoxylem strands in the leaf-trace diminishes, the incurved margins of the trace become straight, and thus the whole is semicircular in transverse section. In the lowest part it is reniform with only one protoxylem strand. As the leaf-trace approaches the central cylinder, a groove is formed in the xylem opposite the leaf-trace, this becomes deeper and disturbs the continuity of the xylem so that the pith is in communication with the parenchyma situated outside the xylem. At a somewhat lower level this interruption is closed on the inner side, the xylem of the leaf-trace fuses with the margins of the groove, so that an amount of parenchymatous tissue is inclosed, on the outer side with one strand of protoxylem. At a lower level this parenchyma becomes smaller in size and ultimately disappears. Still lower the protoxylem ends blind.

The outer tracheids of the stem-xylem are smaller than the inner ones; the tissue situated within this ring was no doubt of a parenchymatous nature, though it has for the most part disappeared during fossilisation. Some elements, however, which were more resistant, are still present (Kidston and Gwynne—Vaughan. 1910. fig. 4, 7, 14). These resistant elements are unmistakebly tracheal in form and appearence. They sometimes occur singly, but are often found more or less collected together into groups.

Their walls are well preserved and strongly thickened and show a well defined porose or reticulate pitting. They are very irregular in form but are all more or less elongated. These tracheal elements are imbedded in a cellular matrix which was too much distintegrated for any certain determination of its original condition.

There is no doubt, that they are real constituents of the central tissue. The supposition made by E. W. Sinnott (1914, p. 475) that they could be explained as intruded roots, which had entered the pith through the gaps, lacks confirmation.

As the xylemring in transverse section is interrupted in some places, while in other places it is only deeply grooved, it seems to consist of a number of laterally fused bundles. But from the description of Kidston and Gwynne—Vaughan it is clear, that this is not so, and that the axis is a hollow cylinder with interruptions above the insertion of the leaf-traces (Kidston and Gwynne—Vaughan, 1910, p. 457, fig. 1.)

Neither the phloem nor the endodermis could be distinguished in the stem. The protoxylem consists of tracheids with one row of pits. In the other tracheids the pits were multiseriate, even in the outer smaller elements.

The essential points in the structure of Osmundites Dunlopi can also be distinguished in O. Kolbei. Parenchymatous tissue, lying at the inner side of the protoxylem strand, is present as before, and dies out below, forming a funnel in the xylem-tissue. But O. Kolbei differs from O. Dunlopi in the greater development of this parenchyma which now penetrates the ring of xylem, thus connecting the pith and the tissues situated at the outer side of the xylem ring.

The gap however is rather small, and is closed before the leaf-trace fuses with the vascular system of the stem, so that where the leaf-trace is fusing with the stem the stem bundle has a U shape with the concavity turned outwards. Below this level it is of the same form as in O. Dunlopi.

Two new points thus appear in our scheme: (see fig. 3) *ur.* the upper part of the so-called „medullary ray", and *lr.*, its lower part. In O. Kolbei, *lr.* is situated above the fusion of the leaf-trace with the stem, (*il.* in our figures).

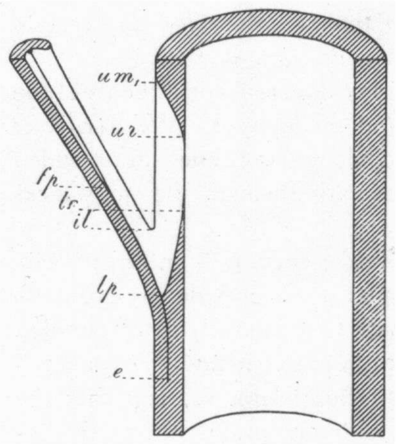

Fig. 3. Osmundites Kolbei Seward. Longitudinal section of the xylem tissue. Explanation in the text.

This scheme with some modifications is applicable to: *Osmunda regalis* L.

This plant has been thoroughly investigated by several authors, especially by P. Lachmann, (1889, p. 110), P. Zenetti (1891), J. H. Faull (1901). A description, modified for our purpose, is as follows.

The stem is erect or inclined, short, for the most part underground, and densely covered with persistent leaf-bases. The leaves, mostly 5—8 in number, form a crown; they are bipinnate, the upper part pinnate, with elliptical leaflets. The internodes are short, the leaf-traces pass obliquely through the cortex, so that in a transverse section several, cut at different levels, are seen. The outer cortex is sclerotic, while the inner cortex consists of parenchymatous tissue.

The structure of the vascular system is as follows: In a transverse section a number of xylem bundles are arranged round a parenchymatous pith, which sometimes contains some sclerotic elements (see fig. 4).

On the outer side of the xylem there is a layer of phloem.

This is continuous in front of the "medullary rays". The whole is surrounded by an endodermis. If the successive stages of a leaf-trace, passing the cortex, be studied, it becomes clear that opposite to the leaf-trace which has in the lower part only one protoxylem strand, a groove is formed in the xylem-bundle of the stem and at a lower level this breaks the continuity of the xylem. The margins of the reniform xylem of the petiolar trace fuse with the margins of this gap. Such gaps are so numerous that the ring of xylem is split up in into a number of bundles.

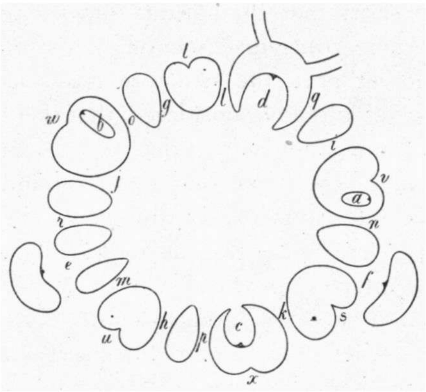

Fig. 4. Osmunda regalis Linn. Transverse section of the xylem of the vascular system in the stem. (Modified after Zenetti).

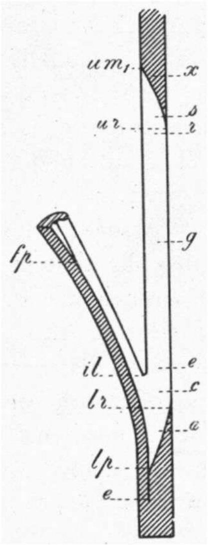

Fig. 5. Osmunda regalis L. Longitudinal section of a model of the xylem-tissue, built up from the former fig. (the letters on the right side indicate similar positions as in this fig.). Other tokens as in fig. 1—3.

At the level at which a petiolar-trace joins the stem, two of these bundles together with the leaf-trace appear to form a deeply incurved horse-shoe shaped strand with a median protoxylem. This horse-shoe shaped bundle however is not homologous with the horse-shoe shaped bundle in the leaf-base, but is formed, as stated above, by the fusion of the leaf-trace with the two bundles at each side of the gap. At a lower level the inner margins of the combined bundle approach and fuse. Thus a funnel of parenchyma is formed and it gradually dies out downwards. At a lower level the protoxylem also terminates. Thus in the lower part the structure is similar to that of O. Kolbei. (see fig. 5).

The internodes are so short that the various stages may be seen in one and the same transverse section.

We see that, in the lower part, the structure is essentially like that in the species already considered, that there is parenchyma situated at the inner side of the protoxylem penetrating into the xylem of the stem, and ending blind below. This parenchyma interrupts the continuity of the ring of xylem forming the "medullary ray" as in O. Kolbei. The dimensions of this interruption however are larger than in O. Kolbei so that it attains a greater length. The lower margin of the gap is here lower than the insertion, the xylem of the leaf-trace therefore does not fuse with a bundle which has a concavity on its outer side, buth with two distinct bundles which are united at a lower level, thus closing the horse-shoe (so characteristic in a transverse section of the stem of Osmunda regalis) on its innerside.

When the leaf-trace has fused with the two bundles on each side of the gap, and the trace is followed downward, a shallow groove, situated somewhat excentrically at the outer side, soon becomes visible. At a lower level, where the parenchyma and the protoxylems are already extinct, the groove is deeper, and gaps the xylem bundle. It is really the upper part of the gap from the leaf next below.

The phloem in the leaf-trace is situated on both sides of the xylem; but protophloem is only seen on the outer side. At a lower level it is absent on the innerside and the phloem on the outer side continues into that of the stem, this completely surrounds the xylem of the stem and is best developed opposite the leaf-gaps. It consists entirely of typical sieve-tubes; at the periphery a layer of tangentially elongated cells is present, the "quergestreckte Zellen" of Zenetti. They are elongated elements, devoid of nuclei and with terminal walls, more or less oblique and provided with sieve-plates. They are continuous with the protophloem of the leaf-trace and are considered as homologous with the latter. The phloem at the outer side of the leaf-trace increases in size opposite the groove on the outer side of the stem xylem, which is continuous with the gap of the leaf next below. Here it attains its largest development, and penetrates for some distance into the gap. The leaf-trace in entering the stem breaks the lateral continuity of the stem phloem, isolating an area of the latter in its axil and at a still lower level this phloem patch ends blind in the funnel.

In some specimens, which I investigated, the structure was less regular, owing to a variation in the size of the gaps.

In some specimens D. T. Gwynne—Vaughan (1914. p. 351, pl. XXI) noted the occurrence of tracheids dispersed in the pith; in some sections of the material I had at my disposal I observed a similar feature. The walls of these elements are lignified, and show a more or less regular pitting. Although usually lying near the xylem they often occur more centrally placed.

Osmundites skidegatensis Penhallow (Kidston and Gwynne—Vaughan, 1907, p. 770—777, fig. 22—28).

This plant occurs in lower Cretaceous rocks of Canada. Only the stem is known but it attained considerable dimensions. The vascular system alone has a diameter of 2.4 cM., and is surpassed in size only by O. Carnieri. In a transverse section the xylem ring is divided into 50 bundles, a greater number than is usual in the Osmundaceae. Very probably the stem was coated with persistent leaf-bases as in the other forms of this family. The leaf-traces run obliquely through the cortex, so that in one transverse section several different stages are visible. The outer cortex is sclerotic, the inner part consists of parenchymatous tissue; the preservation is excellent, so that numerous details could be observed.

The leaf-trace is horse-shoe shaped in transverse section, with incurved margins and a number of protoxylem strands dispersed on the inner side of the xylem. The phloem entirely surrounds the xylem, with protophloem elements at the outer side only. In the concavity of the foliar trace there is a strand of sclerenchyma. No distinct endodermal layer could be observed.

As the leaf-trace passes through the parenchymatous cortex this sclerenchyma persists, meanwhile, the number of protoxylem strands has been reduced to one, which is situated in the median plane. The reniform leaf-trace approaches the xylem of the stem and the margins of the leaf-trace fuse with the two bundles which are situated on each side of the gap opposite the approaching leaf-trace. Through this gap the sclerenchyma in the concavity of the leaf-trace is continuous with that in the pith. The phloem on the inner side of the leaf-trace is continuous with that at the margin of the leaf-gap, a marked distinction when compared with O. regalis.

At this level the xylem is crescent shaped in transverse section but at a lower level the inner margins of the combined xylem (petiolar trace + stembundles) approach and fuse. The phloem ends blind and at a somewhat lower level the sclerenchyma in the funnel also disappears. The funnel only contains some parenchyma, which ends blind below.

The protoxylem is now immersed in the metaxylem, but it also dies out downwards.

The phloem of the leaf-trace is continuous with that of the stem. In the latter no true protophloem could be distinguished but outside the metaphloem there follows a zone, 8—10 rows of cells deep, of elements, strongly elongated in a tangential direction. These layers of cells may be compared with the porose layers in Osmunda regalis. The metaphloem consists of distinct sieve-tubes which are separated from the xylem by a layer of parenchymatous cells. If the phloem be followed downwards it is seen to penetrate into a gap and communicate with an internal layer of phloem, which has no protophloem. At a lower level the sclerenchyma penetrates into the gap, so that the outer phloem now only communicates with the inner phloem by two bands, one at each side of the leaf-gap and separated by the sclerenchyma.

Osmundites Carnieri Schuster (Kidston and Gwynne-Vaughan, 1914. p. 475—477, fig. 35—40). This plant, of which fossil remains have been found in South Paraguay, is probably derived from Cretaceous strata, and attains larger dimensions than any of the other fossil Osmundaceae. It even surpasses Osmundites skidegatensis in size. The anatomical structure shows some pecularities which may perhaps be correlated with its larger size.

The stem attained about 9 cM. in diameter, and the stele alone is 3 to 3.5 cM. thick. The leaf-bases are not preserved, but the stem is covered with a thick zone of roots as is usually present in the lower part of the stem of recent tree-ferns. The cortex is composed of an outer sclerotic, and an inner parenchymatous zone. The leaf-traces are very large, with markedly incurved margins. Their fusion with the xylem of the stem is essentially similar to that in the other Osmundaceae. The gaps however are much larger than in the other forms, and so the xylem in a transverse section is divided into many distinct bundles (— 33 in all). The funnel is well developped, and is closed at the inner side as before, but the height of the funnel is small as is obvious from the small number of bundles which show the annular stage, most of the compound bundles showing only the horse-shoe shape in transverse section. The gaps are wide, and in the upper part, above the insertion of the leaf-trace, the endodermis penetrates into them, thus communicating with the inner endodermis. This endodermis is also continuous into the concavity of the foliar trace, and descends into the funnel, to a short distance above the formation of the annular stage (caused by the fusion of the inner margins of the bundles.) In the upper part of the gaps the endodermis has also died out, so that in the transverse section, figured by the authors, 8 xylem groups are visible, each limited by an endodermis, and some of them containing many distinct xylemstrands.

Osmunda Javanica	Blume. Synonyms are:
„ „	Blume. Enumeratio Plantarum Javae et Insularum adjacentium. fasc. II. Filices. p. 252. 1828.
„ „	(pars.) Greville et Hooker. Enumeratio filicum in Hooker botanical miscellaneous. vol. III. p. 231. 1833.
„ „	Presl. Supplementum Tentaminis Pteridographiae. p. 66. 1845.
„ „	G. Kunze. In Filices Javae Zollingerianus observationes. Botanische Zeitung. Bd. 6. p. 101. 1848.
Plenasium javanicum	Presl. Die Gefässbundel im Stipes der Farne. Abhandlungen der Böhmisch. Ges. der Wiss. Bd. 5. p. 325. 1848.
Osmunda javanica	G. Kunze. Die Farrnkräuter. Bd. II. t. CXI. p. 27. 1849.

Osmunda javanica (pars.) Hooker and Baker Synopsis Filicum. p. 426. 1868.
„ „ (pars.) H. Christ. Die Farnkräuter der Erde. p. 333. 1897.
„ „ L. Diels. Osmundaceae in Engler-Prantl, Natürliche Pflanzenfamilien. I. 4. p. 178. 1900.
„ „ C. Christensen. Index Filicum. p. 474. 1906.
„ „ E. B. Copeland. The Ferns of the Malay-Asiatic Region. The Philippine Journal of Science. Botany. vol. 4. p. 17. 1909.
„ „ (pars.) C. R. W. K. van Alderwerelt van Rosenburgh. A Handbook of Malayan Ferns. p. 756. 1909.
„ „ C. R. W. K. van Alderwerelt van Rosenburgh. A Handbook of Malayan Ferns. Supplement I. p. 440. 1917.

Osmunda javanica is the oldest known species of the section Plenasium of the genus Osmunda, which has been considered by Presl as a distinct genus. The section is characterised by its leaves, which are pinnate, with large, oblong-lanceolate articulate leaflets, the margins of which are entire or incised. The fertile pinnae are much contracted as in the other species of Osmunda, but confined to the lower part of the frond, though sometimes situated in the middle part. To this section belong the species O. Javanica Blume, O. banksifolia (Presl) Kuhn, O. bromeliifolia (Presl) Copel., and O. Vachellii Hook. There is no unanimity among these authors as to the exact delimitation of these species.

Osmunda javanica, as it has been described by Blume, is characterised by a larger size than the other species. The petiole and the rachis is very stout, the frond sometimes reaching a length of about 3 M., the larger leaflets are 30 or more cM. long, acuminate, the base cuneate, the edge entire or sligthly lobed, with adpressed teeth; the texture is coriaceous, as in the other species; the veinlets are dichotomously forked, and then run parallel towards the margin; the fertile pinnae are irregularly lobed. O. bromaelifolia differs from this form in having narrow linear leaflets and the fertile segments are more compound than in the other species, they are mostly pinnate, It is a native of the Philippines.

O. banksifolia agrees with O. javanica in the size of its pinnae, but differs very markedly in having prominent teeth in which the veinlets are more often forked than in the other species, and as these veinlets are no longer parallel, they appear pinnate. It occurs in the Philippines, Malacca, Southern China, Japan and Kamchatka. O. Vachelli Hook., (H. Christ, 1910, fig. 85) which occurs in Southern China, is the nearest ally of O. Javanica, the only important difference being its smaller size. There are differences in the venation of the several species, but these will not be dealt with here.

The confusion in the nomenclature of this section of the genus Osmunda has been caused by the fact, that a form, from the Lappas islands, showing some resemblance to the O. javanica of Blume, was named O. Vachelli by Hooker, and was later united with O. javanica together with a plant from Kandy in Ceylon. The latter was described by G. Kunze (1848—51, t. 121, p. 52) as Osmunda zeylanica, but proved to be identical with the Nephrodium banksifolium of Presl. In agreement with the views of Hooker these 3 forms, together with Nephrodium bromeliifolium Presl, were recorded in the Synopsis Filicum as O. javanica Blume. This opinion has been shared by Beddome (1887, p. 447) and H. Christ (1910, map II). They were considered by them as mere varieties of Osmunda javanica, which in that case has a distribution ranging from Ceylon Insulinde and the Philippines to South-China, Japan and Kamchatka. If this view be correct, the name should be altered in O. banksifolia on grounds of priority.

The species are regarded as separate by L. Diels (1899, p. 423), C. Christensen, (1906, p. 474) and by E. B. Copeland (1900, p. 15—17). The opinion of the latter is important in these questions as he has studied the different forms in nature, and not merely from herbarium sheets.

The material which I examined, consisted of 2 rhizomes of O. javanica Blume, and a number of leaves, which were partly attached to the rhizomes. The rhizome, as in the other Osmundaceae, is densely clothed with leaf-bases. Including this zone of leaf-bases, the thickness was about 8 cM., the diameter of the stem proper being only 1.5 cM. The length of the leaf-base was about 7 cM. The roots were about 3 mM. in diameter, strong and completely surrounded the lower part of the rhizome.

The leaves are simply pinnate, with a terminal leaflet; the length in my specimens was about 2.30 M. and the terminal leaflet was 30 cM. long. The pinnae were about 30 cM. long, 2.8 cM. broad, the upper and lower pinnae smaller in size. They are acuminate, the base is cuneate or slightly rounded, the edge is entire in all leaflets. The lower pinnae are nearly placed opposite one another, the higher are alternate. The texture is coriaceous, the surfaces naked on both sides. The midrib of the leaflet is prominent below, and strongly developed, the veinlets are close, dichotomously forked, and parallel in the outer part. The lower pinnae are fertile, in some leaves the 2 lowermost pinnae were sterile and had the usual form. Transitional forms between the fertile and the sterile pinnae as recorded by G. Kunze, (1848, pl. III.) did not occur in this material.

The outer cortex is darkly coloured and very hard. It consists of sclerotic cells of the form usual in the Osmundaceae. The inner cortex consists of thin-walled parenchymatous tissue, containing starch grains; at the inner side of the endodermis a few layers of parenchymatous cells occur and next follows a layer of tangentially elongated cells, closely resembling the same structure in Osmunda regalis. The metaphloem, which follows towards the inside, is easily distinguishable from the surrounding tissues by the larger lumens of its elements. Between the metaphloem and the layer of tangentially elongated cells elements with a dark content are present. The phloem is separated from the xylem by some layers of parenchymatous tissue.

Up to this point the structure of O. javanica is quite in agreement with that of the other Osmundaceae. The greatest difference is (see fig. 6) seen in the form of the wood, which will next be described. The leaf-trace in the lowest part of the petiole is similar in form to that in the other Osmundaceae. In transverse section it is horseshoe shaped with incurved margins, while a number of protoxylemstrands are dispersed on its inner surface. The phloem is present on both sides of the xylem, and the whole is surrounded by an endodermis. The bundle traverses the cortex in an oblique direction, the internodes are short, so that in a transverse section several leaf-traces are visible. When traced downwards into the stem the incurved margins of the petiolar trace disappear, as also the phloem on the inner side. In the outer cortex, as a rule, only three protoxylemstrands are present in the petiolar trace and by fusion this number is reduced to two, when the leaf-trace enters the inner cortex. Meanwhile the endodermis has disappeared from the concavity of the foliar trace. On the level, where the bundle fuses with the xylem of the stem, two protoxylems are still present in the foliar strand, and the latter is broader than in the other Osmundaceae. This strand fuses with two bundles of the stem-xylem, which as in the other Osmundaceae,

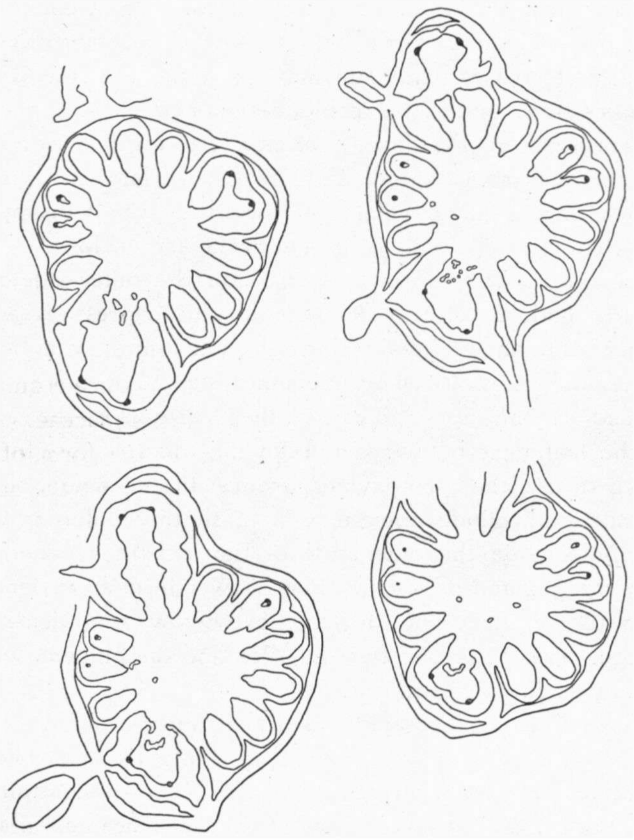

Fig. 6. Osmunda javanica Bl. Four successive transverse sections of the stem, showing the position of the xylem and phloem and the endodermis. The protoxylems are indicated by black dots. Isolated tracheids occur in the pith.

have no protoxylem, so that at first a broad horse-shoe shaped bundle is formed, with two protoxylem-strands in the two corners of the inner surface. At a lower level the xylem of the middle part of the bundle increases in size and is prolonged towards the centre, thus separating the two protoxylem strands and causing the neighbouring parenchyma to be divided into two. The amount of this parenchyma at the inner side of the protoxylem rapidly decreases, and adaxially of it the two metaxylem bundles fuse with this prolongation and so two pockets are present in the fused bundle. At a still lower level no parenchyma is found, and the protoxylems are wholly immersed in the metaxylem; still lower they totally disappear.

When the islands of parenchyma are enclosed at the inner side, a depression is formed on the outer side close to the middle of the xylemstrand. This depression grews larger and finally breaks through, sometimes even before the island is shut off at the inner side. The fissure thus formed is the upper part of the leaf-gap in the xylem of the leaf next below. On following this structure further downwards, the protoxylem groups in the neighbouring strands end blind. Sometimes at a sligthly different level the phloem on the outer side of the leaf-trace penetrates into the gap and persists for almost two-thirds of its length; then the leaf-trace of the leaf next below approaches, its margin fuses with the two bundles, and the phloem, which is now enclosed, soon ends blind.

The areas of metaphloem have only a slight lateral connection with each other; they could be described as separate phloem strands, and are really prolongations of the phloem on the outer side of the leaf-trace next above, which have become shut off from the outer tissues and end blind in the pocket of the lower leaf-trace. Thus the phloem on the inside of the leaf-trace, when it fuses with two bundles of the stemxylem, is not decurrent from the inner side of that leaf-trace, but from the outer side of the leaf-trace next higher in position.

The pith consists of parenchymatous tissue; in some preparations the presence of accessory tracheids, scattered in the pith, could be noted. Most of them were lying free in the softer tissue, but some were in connection with the inner side of the xylem bundles. They clearly showed scalariform walls and stained red with phloroglucine and hydrochloric acid.

The most striking difference between Osmunda javanica and the other Osmundaceae is in the structure of the lowest part of the leaf-trace and the adjacent tissues in the stem. The protoxylem strands, which in the other forms are reduced to one, are double here, and each of them is associated with a distinct mass of parenchyma. The lowest part of the funnel therefore is double. This feature can be explained on the assumption that the elementary bundles of the leaf-trace do not fuse completely in the lowest part of the trace, but that after being reduced to two they retain their individuality, and the associated parenchymatous areas act independently of each other in their lower part on the xylem of the stem. In the upper part of the space they form one funnel, the upper part causing the leaf-gap; in the lower part these areas are separate, each of them being represented in the mature stem by a separate funnel, which accompanies each protoxylem strand. The protoxylem strands themselves disappear as usual at a still lower level.

As *Osmundites Kidstoni* Stopes (1921, p. 55—61. pl. II) describes a fossil from Cretacous strata, consisting of a coating of Osmundaceous leaf-bases, and a small stem with a solid xylem. She considers it to be a missing link between the Osmundaceae with a solid xylem-bundle and the more specialised forms. It is shown, however, (O. Posthumus, 1924), that the stem and the petioles did not belong to one and the same plant.

Protothamnopteris Baldaufii Beck. (Beck, 1920). This name has been given by Beck to a silicified stem from the

Permian strata near Chemnitz in Saxony. Only the stem is known. It has a cylinder of xylem-tissue about 4 mM. thick, composed of scalariform tracheids of which those situated in the centre are of a larger size than the outer ones.

No protoxylem could be observed in the stem. The internodes are short. The leaf-traces are given off without any interruption of the stem xylem. In the cortex they are elliptical in transverse section, with the long axis set tangentially. Further outwards the leaf-trace is unknown. The stem was enveloped by a thick layer of roots.

The author compares the woody cylinder, of which he names the outer layers without any reason "Sekundärholz", with the structure found in Thamnopteris, which is only known to him by the figures given by Bertrand (1912). But neither the habit, the form of the leaf-trace, nor the histological details give any support to this supposition. The greatest resemblance is with Grammatopteris Rigolotti Renault.

Selenopteris involuta Corda. Corda (1867, p. 85, Taf. 53) describes, as Selenopteris involuta a bilateral petiole with a groove on its upper side. The petiolar bundle is horse-shoe shaped in transverse section and has incurved margins; the position of the protoxylem is not clear in the figure. This fossil, which by the form of the transverse section much resembles the petiole of an Osmundaceous form, is of Carboniferous age and thus older than Thamnopteris; further investigation would probably give interesting results.

Osmunda cinnamomea Linn. (J. H. Faull, 1901, p. 381 f. 1, 2, 6, 10—16, 21, 22) The structure of this plant is essentially similar to that of Osmunda regalis, especially as regards its woody parts. In details however, certain differences occur, the most striking being the presence of an internal endodermis, which is continuous with the outer endodermis through the ramular gaps and sometimes through the leaf-gaps also. The phloem penetrates relatively deeper into the leaf-gaps than in Osmunda regalis. In the neighbourhood of the ramular gaps inner phloem is present. The pith often contains sclerotic cells.

Todea. The anatomy of some species of this genus has been described by Seward and Ford (1902). The structure is essentially like that of the other Osmundaceae, but the gaps are relatively shorter than in the genus Osmunda, so that in a transverse section the ring of xylem shows a greater continuity. In Todea hymenophylloides the occurrence of an inner endodermis has been noted.

Leptopteris. Nothing is known of the structure of this genus. The tree-form of L. Wilkesiana (Brackenridge) Christ and L. Fraseri (Hook et Grev.) Presl suggests that the structure might resemble that of the extinct Osmundites skidegatensis and O. Carnieri which had a similar habit.

B. The "Seedling".

Young plants of this family have been investigated by Leclerc du Sablon (1890) (Osmunda regalis), Jeffrey (1902) (Osmunda regalis), Seward and Ford (1902) (Leptopteris hymnophylloides), Chandler (1905) (Leptopteris Fraseri), Faull (1909) (Osmunda cinnamomea), Gwynne-Vaughan (1911) (O. regalis) and Cribbs (1921) (Todea barbara).

In O. regalis the young plant gives off its first leaf from a point directly opposite to the "foot" of the embryo. The protoxylems of the diarch xylem of the first root lie in the plane running through the foot and the first leaf. The second leaf arises opposite to the first, but the following leaves are arranged radially. The anatomical structure of these young plants, however, varies slightly with the individual. The first leaf-trace departs in a perfectly "protostelic" manner, i. e. without leaving any depression in the xylem of the stem. In the fourth (sometimes in the third) and also in the fifth or sixth leaf, the parenchyma of the xylem sheath encroaches on the xylem of the stem in the axil of the leaf-trace. The first parenchyma to appear in the solid xylem of the stem is often due to the formation of such a pocket, but it is also possible, that the first parenchyma may be a true pith, and therefore quite independent of the departure of a leaf-trace. Also there are cases observed, in which the parenchyma in the axil of the leaf-trace and a pith appear practically simultaneously. In some rare cases this pith disappears again a sligthly higher level.

After the fifth or sixth leaf-trace the pith communicates with the xylem-sheath bay above the axils of every trace, forming the so-called medullary rays. Nevertheless the lower end of this pocket (which is also present in the younger parts), remains independent, as the parenchyma of this pocket is separated from the pith by a flange of tracheids. The level on which the communication between the parenchyma, enclosed in the axil of the leaf-trace, and the pith begins, depends on the varying height of the separating flange of tracheids; sometimes, and especially in the lowest leaf-trace, it is prolonged for some distance above the level of the leaf-trace departure, and the pocket opens in the xylem-sheath, or it reaches this level and opens in the medullary ray, or, as is usual in the higher leaf-traces and in the mature plant, it opens directly into the pith.

The leaf-traces vary in size, and the xylem of the first leaf-traces is particularly small. When a protoxylem could be observed, it must be noted that a number of them were unmistakebly mesarch. All these mesarch traces became endarch if followed far enough into the petiole, and the departure of these traces did not leave a pocket in the xylem of the stem because the latter was not hollowed out adaxially at the point of its departure. The other traces, which have a medullary ray or at least a parenchyma pocket in their axil, are endarch throughout their length.

The structure of the "Seedling" of Osmunda cinnamomea, described by Faull, agrees very closely with that of O. regalis. The most important differences are that the transitional region is more drawn out, (J. H. Faull, 1910, p. 519) that protostelic leaf-trace departure occurs often as high up as the seventh or eight leaf, and that a permanent pith is only attained about the level of the twentieth leaf. Here, too, more often than in Osmunda regalis, the xylem becomes solid after having formed a certain amount of pith.

These young plants thus show all the stages we have observed in the species discussed above. In the lowest part the stem is haplostelic and the leaf-traces are given off without leaving any interruption. It is remarkable that both authors state, that, when the leaf-traces are given off in this way, the bundle in the lowest part of the petiole is mesarch. A nodal pocket, if present, is always associated with an endarch leaf-trace bundle, so that the parenchymatous tissue is always situated adaxially to the protoxylem. A pith may occur independent of the pocket and it is not always in continuity with these pockets.

These characteristics are analogous to the features observed in O. Dunlopi. Continuity between pockets and pith is established at a higher level and the lower part of the former is still distinct as a funnel homologous with the funnel in the mature stem. The inner margin of the funnel may be at a higher level than the insertion of the leaf-trace, this stage resembles O. Kolbei, or at the same level as is sometimes the case in adult stems of O. regalis and O. cinnamomea; in the higher parts of the stem the upper margin of the funnel is situated below the insertion as is normally the case in O. regalis and O. cinnamomea.

Thus in one and the same young plant of O. regalis all possible conditions usual in the mature stems of recent and fossil members of the Osmundaceae may occur. It is not established, whether the transition from the mesarch to the endarch bundle in the lower leaf-traces is associated with a parenchyma-funnel, such as is found in Thamnopteris.

Whatever the value of this analysis may be for phylogenetic relationsships among the Osmundaceae, the facts show, that the structure in the lower part of the plant are the result of factors, which act throughout the whole ontogenetic development and cause a different relationship of the funnel and the pith at different levels. These differences can be paralleled in the mature stem of other species, recent and fossil.

C. The petiolar trace.

Before working out the comparison between the different structures in the Osmundaceae, it seems desirable to discuss the features in the petiolar trace in this group. Especially important is the fusion of the pinna-trace with the bundle of the rachis, since we can easily study here the mode of arrangement of the units, of which the vascular bundle in the leaf is composed.

The features, which occur here are so alike in the different forms that separate treatment is not necessary. In its strongest development, somewhat below its fusion with the lowest pinna-trace, the leaf-trace usually consists of a gutter-shaped bundle, which in transverse section is horse-shoe shaped with incurved margins. At the inner side of the xylem a number of protoxylemstrands are placed at regular intervals. The first formed elements in most cases have disappeared, the space being occupied by the outgrowing neighbouring cells.

When followed from below upwards, the fusion with a pinna trace may be described as follows: At the side of the bundle a piece of the vascular tissue, provided with some protoxylemstrands, bulges outwards. At a somewhat higher level this tissue separates from the remainder of the vascular bundle and this passes outwards into the pinna as a separate bundle. Thus in the vascular bundle of the petiole an interruption is present (E. W. Sinnott 1910, fig. 16). At a somewhat higher level the margins of this gap approach, first the endodermis fuses across the gap, then the phloem, and lastly the xylem. The former condition of the petiole is thus restored. Thus at the insertion of the pinna-trace a "gap" is present in the petiolar trace, through which the ground-tissue at the inner and outer side of the vascular bundle are continuous.

If the pinna bundle is somewhat smaller in size, the separating xylem-tissue is only accompanied by the phloem, the inner endodermis is merely bending out inwards, but never breaking through. Prior to the disturbance of the continuity between the pinna-trace and the remainder of the petiolar strand there is a fusion of the two margins of the interruption, which would be formed, and lie at the inner side of the sinus. In a transverse section it looks as though a certain amount of groundtissue is enclosed in the petiolar strand.

At a somewhat higher level, the pinna trace becomes free on the outer side. In this case no real "gap", is present, yet the ground-tissue at the inner and the outer side of the petiolarstrand is continuous. When we consider the form of the xylem only, a very distinct interruption is seen. 1)

If the bundle, which is given off, is still smaller in size, this enclosed part of ground-tissue is not present at all. The bundle, as limited by the endodermis, is nipped off

---

1) The same structure occurs in Dicksonia antarctica: C. Eg. Bertrand and F. Cornaille, 1902, fig. 35; Cibotium regale, l.c. pag. 82, fig. 85.

at the outer side of the strand; but there is however an interruption in the xylem tissue (D. T. Gwynne—Vaughan, 1916, fig. 17, 18).

In the upper pinnae or in the branches of each pinna, this form is still more reduced. The vascular bundle as a whole is never interrupted, as in the former case and neither is this the case when we look upon the xylem tissue as a whole. In the transitional stages the interruption in the xylem is very small and extends only for a short distance when traced upwards. In other case the continuity is not disturbed at all; the divergence of a vein being only indicated by a protoxylem group situated more deeply in the xylemtissue and becoming placed in a bay of parenchyma. The metaxylem then closes adaxially to this bay, and the protoxylem with this parenchyma, moves outward and becomes free. Still further it is nipped off and passes outwards into the stalk of a pinnule or into the mesophyl of the leaf. [1])

From the comparison of such stages with those present in other Ferns, conclusions may be drawn which give us an insight into the relation of the leaf-trace to the stem.

In the first place it becomes clear, that the size of the interruption which is formed, is dependent on the size of the pinna-trace. Where the interruption is marked, two positions may be recognized: I. The place where the pinna-trace fuses with the margins of the interruption; this position may be at different levels on the two sides of the trace, and II. the level at which the two margins of the interruption fuse together.

It is clear, that, when the interruption is wider, the latter point will be at a higher level, and this depends on the

---

[1]) E. W. Sinnott, 1910, fig. 13; D. T. Gwynne—Vaughan, 1916, fig. 6; cf. Microlepia platyphylla (C. Eg. Bertrand and F. Cornaille, 1902, p. 119. fig. 63).

size of the pinna-trace. When this latter point is situated at a lower level, the pinna-trace may not yet be free at both sides when the margins of the "gap" have already united. The bundle as a whole shows no interruption in a transverse section, though it is gapped and a connection occurs between the ground-tissue on the inner and outer sides of the petiolar strand.

If the interruption in the xylem is smaller than the distance between the endodermis and the xylem, which is nearly constant, the endodermis will not be incurved, but only nipped off at the outer side. Now we see the same succession of stages in the xylem, the interruption will be restored after the xylem strand of the pinna-trace has become free; the xylem-plate may or may not be interrupted, and lastly a protoxylem strand with parenchyma is enclosed in the metaxylem and nipped off at the outer side.

The veinlet bundle is very simple, consisting of a small amount of xylem, (with one endarch protoxylem on the upper side) and some phloem elements, the whole surrounded by an endodermis.

In the interpretation of the petiolar trace, which is best studied in successive transverse sections, one may start from two different mutually exclusive points of view. In the first place we may assume, as has been done by Schacht (1856, p. 307), that the vascular system in the plant is a continuous whole: „Die Gefäszbündel entspringen im Keime unterhalb der Stammknospe (Plumula), sie können sich fernerhin nur aus sich selbst durch Zweigbildung vermehren, und bilden deshalb ein zusammenhängendes System, welches die Pflanze von der Wurzelspitze bis in die Blätter durchzieht". The petiolar trace on this hypothesis is to be considered as a ramification of the vascular system of the stem and similarly that of the veinlets as the ultimate ramificacations of a foliar bundle.

If this interpretation of the vascular stucture be correct, the different types of branching of the petiolar trace must on the same principle be explained in allied forms.

To cite an example: In Dicksonia antarctica (C. Eg. Bertrand and F. Cornaille 1902, p. 46, fig. 23—26) e. g. the petiolar trace in a transverse section is shaped like a horse-shoe with incurved ends. In the middle part of both sides a sinus is present, called the „pli inverse" by the authors. The pinna trace is given off from the sides of the bundle on the anterior side of the „pli inverse".

In Cyathea medullaris (C. Eg. Bertrand and F. Cornaille, 1902 p. 66, fig. 34—39) the petiolar trace is similarly built, but the „pli inverse" is much deeper, so that its anterior and posterior sides approach each other. If the branch were given off as a part of the whole, it would be expected, that this occurred at the same place as in the former species. This is only the case with the anterior part of the pinna-trace, the rest fuses with the petiolar bundle at the abaxial side of the „pli inverse". The insertion of the pinna trace thus seems to be less dependent on the position of the bundle where it is given off in allied forms, but on the arrangement of the parts of the bundle itself in relation to the place of the incoming pinna-trace. Similar features are present in other Ferns as is described by the above mentioned authors.

A second point of view is that the petiolar trace has a certain degree of independence, not only as a whole in relation to the vascular system of the stem, but also that it is composed of a number of units, the arrangement of which, influenced by unknown factors, brings about the different structures. This possibility has been considered by Bertrand. He tried not only to look upon the petiolar trace as a whole, and to find homologies in the different regions which might be distinguished, but also to establish the nature of the units of which the foliar trace is composed. At the end of his book he says that there is no reason to prefer one point of view to another (C. Eg. Bertrand and F. Cornaille, 1902, p. 207).

The different pecularities in the structure of the petiolar bundle in the Ferns, and most probably those in the Spermophyta too, may be explained by the assumption, that the vascular bundle is composed of a number of units, resulting each from the differentiation of a procambium strand. Each unit corresponds to the „divergeant" of C. Eg. Bertrand and F. Cornaille. (1902 p. 16). It consists originally of a mesarch xylemstrand, surrounded by phloem-tissue and an endodermis. In the plants considered, this unit has been modified, the metaxylem situated adaxially to the protoxylem strands has not been formed, so that parenchyma, eventually phloem, takes its place. These units may fuse laterally; if two approach each ofter, the endodermis fuses first and then the phloem and the xylem. If the latter has fused, the two protoxylem strands may remain distinct or fuse also. In many cases these strands are but temporary united when only their endodermis or phloem has fused.

If the pinna-trace enters the cortex of the petiole, it enters into relation with the petiolar bundle, which goes downwards from the higher portions of the leaf. It is quite possible that the procambium strands of the higher parts are influenced in their course by the structure in the lower parts of the petiole. The mode in which the arrangement of these bundles is formed in relation to the other ones, determines the form of the transverse section of the petiolar strand. If the number is relatively large, they are not arranged in a simple horse-shoe shaped strand, as in Osmunda, but the lateral bundles move towards the centre of the petiole, and thus the so called „pli inverse" is formed. Now, if the pinna-traces pierce the cortex of the petiole or rachis, the arrangement is then as if the elementary bundles, which have approached the centre, were not present. The pinna trace fuses with the petiolar trace partly on the anterior and partly on the posterior margin of the "pli inverse", as is the case in Cyathea medullaris.

It is very probable that the differentiation of the petiolar traces extends from above downwards and that the factors which are decisive for the final form of the elements originate from a point situated in the higher parts of the leaf and extend in a downward direction. This assumption does not exclude the fact, that the lignification of the elements first takes place in the lower parts of the bundle, for this is but one of the latest of the many processes which take place in the differentiation of the meristematic cell into its final stage.

It is very probable that this rule governs also the Spermophytes, but that in these forms the reduction from the assumed mesarch to the endarch bundle has taken place in another way. Some pecularities which support this assumption follow.

Sometimes vascular bundles are to be found, which end blind below. Such bundles have been found e. g. in the lowest part of the lamina of the leaf in Alchemilla vulgaris L. (A. Rippel, 1913, p. 25), here the point of origin of the differentiation of this bundle, which is wholly isolated, must be at a higher level than the base of the leaf. Bundles which run into the stem and end blind there, have been found in a fasciation in Veronica longifolia (A. Nestler, 1894, p. 153), in the hypanthium of some Rosaceae (Hillmann 1910, p. 377), and in the corolla of Adenostylis (J. Briquet 1917, p. 23).

In the Ferns the occurrence of bundles, which end blind below, have been observed in the saddle of the dichotomous branching in Alsophila glauca, (J. C. Schoute, 1914, p. 61) and in the pith of some Cyatheaceae; in these plants some of the elementary bundles of the petiolar strand, which are free, are arranged towards the centre of the petiole and when traced downwards do not form an integral part of the normal curve, but remain separate, and pass through the gap into the pith, while the others approach the margins of the gap and are continued into the xylem of the stem. The presence of cortical bundles in some Cyatheaceae may possibly be explained in the same way.

That the petiolar trace as a whole is also independent of the tissues of the stem is shown from the investigation of the structure of the lower part of the foliar trace in Gleichenia pectinata. Here the margins of the leaf-trace are incurved, and not flattened, before the fusion, so that the leaf-trace fuses with the xylem of the stem on its outer surface.

The tubular form of the leaf-trace in some Gleicheniaceae may also be explained in this way: the elementary bundles approach each other at the anterior side in the medial plane, the endodermis fuses, and a mass of ground tissue is enclosed. This fusion however is not permanent, in the lower part the included tissues often communicate again with the cortical tissues. The closed petiolar trace is also found is some other Ferns e. g. in Cibotium regale (C. Eg. Bernhard and F. Cornaille, 1902, p. 60) [1]).

D. Summary of the results.

Before giving an opinion on the morphology the structures discussed above, I will mention the various views held by those, who have investigated the structures in this family,

De Bary was the first, who compared Osmunda with

---

[1]) For the different structural types, present in the foliar bundles of the Ferns the reader is referred to Colomb 1888; Davie 1917, 1918; P. Parmentier 1899; K. Thomae 1896.

other plants. In his Comparative Anatomy he describes the vascular system in O. regalis and compares it with the structure in some Conifers, where a leaf-trace enters into the cortex, runs through the stem for some internodes, and then fuses with the trace from the leaf next below. The number of bundles in a transverse section is equal to the number of internodes which have been passed. The fusion of the bundles is lateral; the two bundles approach each other and their sides fuse.

According to De Bary in O. regalis (1887, p. 289—291, fig. 128—130) the bundle runs through the stele for 13 internodes in the specimens he had seen. Then the leaf-trace fuses with the neighbouring strand. This statement however is incorrect; de Bary failed to see, that the incoming leaf-trace fuses with two of the bundles already present in the stem; thus the horse-shoe-shaped bundle which results from this fusion is not homologous with the reniform bundle in the cortex. Further he has not observed the splitting up of this bundle in the lower parts; he says: „Die Bündel sind an ihrer Austrittstelle aus dem Cylinder am stärksten, im Querschnitt hufeisenförmig, im Blattstiel behalten sie diese oder wenigstens Halbmondform bei. Im Stammcylinder nehmen sie nach abwärts zuerst allmählich, zuletzt rasch an Dicke ab, und erhalten keilförmigen Querschnitt. Sie werden hier durch schmale Parenchymstreifen (Markstrahlen) von einander getrennt." In the Conifers mentioned by him, the numbers of bundles on the same level is increased with one, by the entering of the leaf-trace; this increase is compensated by the fusion which occurs some internodes lower. In Osmunda, where the leaf-trace enters, the number is increased by one, but at the same time two of the bundles in the stem fuse with it, so that immediately below the insertion, the total number is one smaller. This is compensated by the splitting up of the bundle at a lower level.

In the Conifers and in all other Spermophytes the vascular system of the stem is composed of a number of foliar traces which are decurrent for some distance in the stem. The lower part forms a sympodium with the bundle of the leaf next below. In Osmunda however and in the other Filices the vascular system is a hollow cylinder and the leaf-trace fuses with it as soon as it has entered the stele, forming an interruption in it above its insertion. If these interruptions are large enough, the vascular system in a transverse section seems to consist of a number of bundles similar to those of the Spermophytes. I have discussed the mistaken view of de Bary at some length, because his explanation has been accepted by later authors who applied their deductions to the Phanerogams. This will be discussed later on.

Strasburger (1891, p. 448) comes to the same erroneous result, he finds even still greater resemblance with the structure in the Phanerogams, for he notes that the phloem is interrupted before the „medullary rays“.

v. Tieghem (1886, p. 27; 1891, p. 1373) agrees wholly with this view; he considers this plant to be monostelic as in the majority of the Phanerogams.

D. H. Scott (1895, p. 767) who held the same view, pointed to the great resemblance of the structure in Lyginodendron and in Osmunda. This resemblance together with the form of the leaves lead him to consider this as a prove of the affinity of the oldest Seed-plants to the Ferns; this supposition was the basis for the distinction of the class of Pteropsida, as defined by E. C. Jeffrey.

P. Lachmann (1889, p. 110) gives in his memoir on the origin of the roots in the Ferns, a description of the structure of the stem in Osmunda regalis. He points out that the bundle as a whole does not enter the leaf-base as de Bary (who had apparently not seen a series of successive transverse sections) believed, but that part of it remains in the stem. He describes the vascular system as follows:.... On peut dire que les faisceaux caulinaires de l'Osmunda regalis sont ondulés en sinusoides verticales très étirées et soudés par leurs convexités de manière a former un réseau dont les mailles étroites et très elongées correspondent aux feuilles''.

In 1895 P. Zenetti investigated the rhizome of O. regalis, especially the transition of the leaf-trace in the stem. He confirms the results of P. Lachmann and demonstrates that the protoxylems, which are decurrent from the leaf-traces, end blind and do not join together. Further he proves that Strasburger's opinion, that the phloem is interrupted before the leaf-gaps, is erroneous. He finds that there only seems to be a resemblance with the Phanerogams, there is more resemblance in the Sigillariaceae, where by the reduction of the central xylem the outer part is transformed into a number of bundles. He finds an anologous structure in the stem of the young plants of the Osmundaceae, where there is a solid central bundle of xylem.

Faull (1901, p. 409) and Jeffrey (1903, p. 123) came to other conclusions. In Osmunda cinnamomea the first author stated the occurrence of an internal endodermis, which enclosed a mass of brown sclerotic tissue. The branching is dichotomous, the xylem interrupted in the fork of this dichotomy, and through this "ramular gap" the phloem is decurrent on the inner side of the xylem-tissue. In Osmunda regalis and Todea barbara the pith sometimes contains sclerotic elements, as in the cortex, but the internal endodermis and phloem are wanting. The xylem is interrupted in the saddle of the dichotomy. This is not the case in O. claytoniana, where no sclerotic elements are present in the pith.

As Jeffrey stated that young plants of Osmunda regalis had a solid xylem strand in their lower parts, and assuming, that the structure in the young plant is primitive, he supposes, that the solid stele has been altered into a tubular stele by the penetration of cortical tissues through the ramular gaps and through the leaf-gaps above the insertion of the leaf-traces. From this form, in which the internal sclerotic tissues were in communication with those of the cortex, the recent forms might be derived by reduction. The structure present in O. cinnamomea is according to this hypothesis more primitive than that in O. regalis; the reduction has gone yet further in O. claytoniana and in Todea superba.

As Jeffrey thought the structure in Lyginodendron to be homologous with that in Osmunda regalis, he applied this hypothesis to the former plant, and as this was supposed to be an intermediate form between the Filices and the Spermophytes, this schema was accepted by him for the Spermophytes too.

These two groups of plants were included by him in the phylum of the Pteropsida, and separated from the Lycopsida. In a following chapter where the structure in Lyginodendron will be discussed, I shall draw attention to the essential points of differences between the structure in the Ferns and in the Seed-bearing plants, and show that this structural type, which shows a superficial resemblance, has come into being along quite a different way. Perhaps the nearest ally of the Seed-bearing plants must be sought in the Lycopodiales.

Kidston and Gwynne-Vaughan (1910, p. 467) came to the conclusion, by their study of the fossil forms in which they could establish the occurrence of forms with a solid central xylem, that in the haplostele the pith was formed by reduction of the internal xylemtissue into parenchyma. The internal tracheids in the pith of O. Kolbei in Osmunda regalis, (and in O. javanica) should then be an indication of this. An analogous case of the reduction of the central tissues to parenchyma is present in Diplolabis Römeri and in some Lepidodendraceae. In this the authors agree with Zenetti. At the same time or afterwards the xylem ring would be interrupted above the insertion of the leaf-traces, thus forming a communication of the tissues on the outer side of the xylem-ring with those within. Kidston and Gwynne-Vaughan point out (1908a, p. 435) that the horse-shoe shaped leaf-trace is derived from a formerly solid mass of xylem, with a central mesarch protoxylem. This mass becomes concave on the adaxial side by substitution of the centripetal elements of the xylem by parenchyma, the protoxylem becoming truly endarch. But they do not say how they think this process has taken place. Some years afterwards D. T. Gwynne-Vaughan (1911, p. 355), who had investigated the structure in the young plants, writes, that the outer tissues of the stem have in many cases a tendency to invade the central xylem in the axils of the leaf-traces, and the xylem sheath pockets represent the initial and simplest possible expression of this tendency. Thus Gwynne-Vaughan assumes that the formation of this interruption is connected with the insertion of the leaf-trace, but he does not lay stress on the structure in the simpler forms with the mesarch leaf-traces. He laid stress on the fact, that in the young plant the pocket in the axils of the leaf-trace and the formation of the pith took place independently of each other, which is an argument for its formation out of stelar tissue by reduction of the xylem to parenchyma.

Sinnott (1910, p. 110) objects to this explanation, and pleads for Jeffrey's hypothesis. As he derives his arguments chiefly from the mode of preservation of the fossils, and are of little value, they need not be discussed here.

When considering the structural peculiarities in the

Osmundaceae, I quite agree with the ideas of Kidston and Gwynne-Vaughan, that the pith has been formed by reduction of the xylem-tissue. The primitive form from which the Osmundaceae may have been derived was characterised by a solid mass of xylem, in which the mesarch leaf-traces were inserted. It is very probable, that the differentiation of the central xylem took place quite independently from that of the leaf-trace. Only in the downward extension of the leaf-trace, where the protoxylem is decurrent into the stem for a short distance, is there a differentiation dependent on that of the leaf-trace.

Thus the stelar structure is caused by the mutual relation of these two kinds of tissues, for which I suggest the name stem-xylem, and leaf-trace xylem. In the stem-xylem the differentiation of the internal tracheids was arrested, in the successive stages the tracheids being replaced by parenchymatous tissue. in which differentation to phloem, endodermis and sclerotic cells might have taken place.

The vascular system of the leaf is composed of a number of elementary vascular strands as are mentioned in the chapter on the petiolar-trace. These strands were mesarch, in the higher parts a number of them were at the same level, in the lower part of the petiole the number had been reduced by fusion so that only one was present near the insertion. In the course of the phylogeny the differentiation of the metaxylem situated at the adaxial side of the protoxylem in these elementary bundles was arrested. The factors causing the differentiation of the meristematic cells into tracheids lost their influence, so that at the adaxial side of the protoxylem only parenchymatous elements were formed. This reduction took first place in the higher parts of the bundle. No assumption can be made with any certainty as to the exact level. From this point the reduction gradually extended downwards, but in the lowest part it diminished in size. This reduction seems to be dependent on the presence of protoxylem elements, for, when the trace, as in Thamnopteris, is traced downwards, the parenchyma is at last formed in the neighbourhood of the protoxylem elements only, it diminishes in size and at last wholly disappears. Thus a funnel of parenchyma is formed in the xylem. In the course of the phylogeny this reduction took place at a lower level and at last it reached the insertion of the leaf-trace into the stem. The adaxial xylem of the leaf-trace had wholly disappeared, and the leaf-trace was endarch throughout its whole length. When the funnel increased in size, the xylem of the stem above the axil of the leaf-trace was reduced; thus a groove was formed opposite to the leaf-trace.

But meanwhile the central tissue had been changed into pith. The cylinder of xylem became perforated, since the parenchyma pierces the xylem, but not with its proximal end, but with its central portion. Thus the presence of a little funnel in the lower part of the leaf-trace can be explained. The size of the perforation varies in relation to the size of the reduction zone; if this is relatively small, the gap will, when traced downwards, be closed before the leaf-trace has fused. If it is larger, it will be still present when the leaf-trace fuses with the xylem of the stem; all these cases occur in the Osmundaceae and have been described in the previous chapters. When the gap is well developed, other elements such as sclerotic cells and an endodermis may be differentiated in it.

In O. javanica there is yet another modification. In the former case we have supposed, that in the lowest part of the leaf-trace only one elementary bundle could be distinguished. In O. javanica however, in the lower part two bundles of protoxylem are present, and some parenchyma is associated with them. This parenchyma ends blind and separate in each bundle, not always at the same level and the two protoxylem strands, which never fuse, end blind at a slighly lower level. This case demonstrates the independence of the elementary bundles even in the stem. Whether the occurrence of two elementary bundles at such a low level is correlated with the mode of growth or other external influences, or that it is a feature characteristic for its affinity and not dependent on ecological factors is questionable.

When the gaps have a relatively large size, so that the length is almost equal to that of the internodes which lie between two leaves situated on one and the same orthostichy, they will be placed at nearly equal intervals. Thus in a transverse section it seems as if there were a number of bundles, running down for some internodes in the stem. But the study of successive transverse sections and of young stems shows that it is really a hollow tube in which there are interruptions above the insertions of the leaf-traces. All that remains of the stem-xylem is here the lower part of the xylem bundles which border the leaf-gaps.

In the previous pages the hypothesis has been made that the parenchyma at the adaxial side of the protoxylem of the leaf-trace and in the central part of the stem has been formed by the reduction of xylem-tissue. This supposition has been made on the following grounds: If a meristematic cell is altered into a cell of a specialised form e.g. a tracheid, a number of influences must have been brought to bear on it during the processes which take place. The presence of these influencing factors is seen in their results, for it is very reasonable to suppose, that a cell, whose wall becomes lignified, has been exposed to other influences than those where the wall does not become lignified.

Now it is possible that, if the influence remains below a certain limit, then it may not be strong enough to have its optimal effect; it remains below the "threshold" value. If under anormal circumstances the nature of which is unknown, the "threshold" value of the factors which act during development, has been reached, elements may occur, where they would not have otherwise appeared normally. So the occurrence of the internal tracheids in O. Kolbei, O. regalis and O. javanica may be explained, just as in the case of the loose tracheids scattered in the funnel of Thamnopteris, This could not be explained by the supposition that the pith was formed by intrusion of the outer tissues into the stele.

A further remarkable point is, that not only in the Osmundaceae, but also in the other Ferns, the reduction of the metaxylem in the leaf-trace takes place adaxially to the protoxylem, that is at the side of the leaf-trace or pinna-trace directed towards the upper surface. There is a certain degree of "orientation" of the reduction towards the position of the leaf during life; the real nature of this fact however is hidden.

Only a guess can be made on the significance of the reduction of the elements situated in the immediate neighbourhood of the protoxylem elements. It is rather certain that the presence of living cells is necessary for the function of dead conducting elements. If the elements first-formed are situated centrally, they will, while becoming differentiated, only have in their immediate neighbourhood undifferentiated cells, which become tracheids. It is very probable that the reduction of some of these elements to ordinary parenchyma-cells will make the first-formed tracheids more suitable for function.

These types of structure as have been mentioned above do not form a phylogenetic series. They are to be considered as a series of structural types, which has been formed by the changing relation of the parts of the vascular system which compose the stele: i. e. the stem-xylem with its reduction of tracheids into parenchyma, the arrangement of the elementary bundles in the leaf-trace, and the size of the parenchyma situated adaxially to the protoxylem strands in that leaf-trace. O. skidegatensis and O. Carnieri are older, but more elaborate than O. regalis; O. javanica is more primitive than O. cinnamomea by the nature of its pith, but the presence of two protoxylem strands with adjacent parenchyma is a more advanced character, which is only found in this species.

CHAPTER II.

The Stelar Morphology of the Gleicheniaceae.

This family contains about 25 species, occurring in the tropics and in the temporate zone of the Southern Hemisphere. In the Northern temporate zone they are wanting, though in these countries the occurrence of Gleicheniaceae in strata from Liassic to Tertiary age, not only in Europe, but also in Greenland, has been established. Now they are wholly extinct here.

Their general habit is characterised by the possession of a horizontal rhizome; the internodes are of a varying length, in some species they attain a length of several centimetres. The leaves are petiolate, and highly compound. Their characteristic structure is, that the main rachis is not developed above the first pair of pinnae; this makes them easily distinguishable from other ferns, which are similar in growth. The pinnae have their rachises built in the same way. The branching thus seems to be dichotomous, but the prolongation of the main axis is in the axils of the pinnae, which form the fork of the dichotomy. The ultimate segments are close, oblong or semiorbicular; the texture is firm and leathery, the veinlets are flabellate or forked. The sori are usually placed on the backs of the veins; they are naked, and contain but few, large sporangia. These are sessile, or short stalked, with a complete horizontal ring, which shows a vertical dehiscence.

This is the general habit in the genus Gleichenia; the other two genera, which contain but one species each, are reduced in accordance with their xerophytic habit. In Platyzoma the unbranched leaves are dimorphous, those placed upon the sides and the lower part of the horizontal rhizome have lost their lamina, while in Stromatopteris the leaves are but very seldom forked and roots are wanting.

In their habit the species of Gleichenia show a close resemblance to Pteridium aquilinum. They occur associated in clearings in the woods or at the edge of the forests, covering whole surfaces; these formations, known as Gleichenietum (H. Christ, 1910, p. 38, fig. 3, 4), are analogous to the similar mode of growth of Pteridium, which is substituted for it in the Northern Hemisphere. It is very remarkable that, whilst the conditions of life are similar, the differences in internal structure are so considerable. In Gleichenia the structure is relatively simple, the stem possesses a solid mass of xylem, surrounded by phloem and an endodermis, but seldom with a central pith; while in Pteris there is a perforated stele with a complex internal system.

Gleichenia Boryi Kunze (Boodle, 1901, p. 723; G. Poirault 1893, p. 171, fig. 13). The leaf-trace bundle is, in a transverse section, horse-shoe shaped with sligthly incurved margins in the xylem; in the lower part it has the form of a C. The phloem is situated on the outer side of the xylem; it does not reach much further than the margins of the bundles towards the inner side; the endodermis does not pass into the concavity of the bundle.

When passing the cortex, the transverse section becomes semi-circular; the endodermis then fuses with that of the bundle of the stem. This has a solid mass of xylem, consisting of tracheids, intermixed with parenchyma and provided with some protoxylem strands, which stretch over the whole length of the node. The phloem is continuous on the outer side.

When the leaf-trace has approached the stele, the margins of its xylem, which has three protoxylems, fuse with the central bundle. Thus a mass of parenchymatous tissue with some phloem elements are enclosed. At a somewhat lower level this has grown smaller in size, and disappears; the 3 protoxylems, which were situated at the outer side of the parenchyma, now are imbedded; in the metaxylem they fuse with the other protoxylem strands decurrent from the leaf-trace next above. Thus the normal structure of the internode is restored.

Here a simple mode of the formation of a nodal island is present. The form of the xylem only is influenced by the action of the tissue of the leaf-trace. In the lowest part of the funnel there are 3 protoxylems. It is not clearly shown in Boodle's description whether the parenchyma associated with each bundle ends blind and separate in the lower part, or not. The structure in Osmunda javanica and in Gleichenia pectinata makes the former supposition very probable.

Gleichenia dicarpa R. Brown (G. hecistophylla Hooker). (Boodle, 1901, p. 724, fig. 12, 20—23; G. Poirault, 1893, p. 172—174, fig. 14). The internal structure of this plant agrees in the main with that of the former species. The greatest difference lies in the occurrence of a mass of sclerenchyma which is situated in the concavity of the leaf-trace and surrounded by an endodermis. The margins of the leaf-trace are much incurved and fused in the medial plane, the sclerenchyma thus being wholly shut off from the cortex; there is only a connection with the cortex at the fusion of the petiolar bundle with the stem bundle. This sclerenchyma with surrounding endodermis penetrates into the nodal island and ends blind there. One of the sides of the leaf-trace fuses with the stele before the other; thus the leaf-trace seems to have a slight torsion, for a short distance.

Gleichenia linearis (Bedd.) Clarke. (G. dichotoma

Hooker.) (Boodle 1901, p. 720, fig. 3, 6, 8—12, 14—19). In this plant the margins of the xylem of the leaf-trace near its insertion are fused at the inner side. The sclerenchyma included in the foliar trace is decurrent into the nodal island without having been in connection with the cortex. The parenchymatous tissue of the nodal island extends for some distance upwards along the protoxylem. In other specimens this was not the case. In some plants the sclerenchyma enclosed in the leaf-trace was continuous with that of the cortex; in others it was divided into three separate strands in the upper parts of the petiole.

Gleichenia circinnata Sw. var. *semivestita* Labilly. (Boodle and Hiley, 1906, p. 423, fig. 1—2). In this plant one of the protoxylem strands in the node ended blind below.

Gleichenia pectinata (Wild.) Presl. (Boodle, 1901, p. 728—731. fig. 24—27; Boodle and Hiley, 1906, p. 419—432, 7 fig.) This is the only known species of the genus Gleichenia in which a tubular stele is found. This "solenostele" however, is different in some points from that of the Polypodiaceae.

The cortex is sclerotic, especially the inner layers are much thickened. In a transverse section through the internode the phloem, which has continuous protophloem, is seen on both sides of the xylem. This consists of tracheids intermixed with parenchymatous elements. A number of protoxylem groups lie embedded in the xylem. Those on the lower side are in projecting ridges, near the surface of the xylem; they are continuous with the protoxylem of the roots. On the upper side they are clearly embedded; these are decurrent from the leaf-traces and continuous through the internodes, fusing with those of the leaf-trace next below.

When entering the cortex the leaf-trace is in section horse-shoe shaped with incurved ends and is endarch with several groups of protoxylem scattered on its inner surface. The phloem is continuous on the outer side of the xylem, but absent in the inner middle region. At this level the continuity of the annular central bundle in a transverse section is interrupted. The tissues situated at the outer side of the xylem, the ploem, endodermis and the sclerotic tissue of the cortex pass through the gap and communicate with the tissues within.

At a lower level the bundle becomes C shaped, with some (3—4) protoxylem strands. At its inner side, the lateral margins of the bundle fuse with the margins of the gap.

But the inner margins of the C shaped bundle of the stem fuse also; thus in transverse section a quantity of the sclerenchymatous tissue (which is the downwards continuation of that in the concavity of the leaf-trace) is not in communication with that of the pith, but is separated from it by a flange of tracheids. A funnel is formed here. At the outer side of this funnel there is some phloem too. At a lower level there is no longer any sclerenchyma, then the phloem disappears, at last there is only a little parenchyma left in the neighbourhood of the protoxylems. According to the description of Boodle and Hiley (1906, p. 421) groups of fibres arise independently (the structure being described in an acropetal way) of each other in the neighbourhood of the protoxylem strands, etc. This indicates the presence of a funnel near each protoxylem strand. In each funnel the different tissues end blind without any relation to those of another funnel.

Below this point the protoxylem strands are wholly embedded and have no parenchyma. These groups are prolonged into the stem, and further downwards they fuse with those of the leaf next below.

Another interesting feature is that the petiolar trace was not flattened before its fusion with the xylem of the stem but its outer side fuses with the xylem of the stem.

Thus the incurved hook of the vascular bundle has not a free connection with the inner tissues, but, when traced downwards, ends in a funnel of its own. This has been drawn by Tansley (1908, p. 142, fig. 41); in his figure the sharp distinction between the middle and the lateral parts of the leaf-trace at this level is clearly shown.

Platyzoma R. Brown. Only one species, Platyzoma microphyllum R. Br., (Thompson 1916, p. 631-656, 3 pl., Thompson 1919 p. 571-596, 3 pl.) belongs to this genus. This plant is found in Australia. It has a horizontal rhizome, densely covered with gold-brown hairs. The roots are placed on the lower surface, occasionally on the sides of the rhizome. The internodes are short and the leaves crowded. They are dimorphous, some of them are pinnate, with small round leaflets; others are filiform, without pinnae. Those of the first group are placed on the upper surface of the rhizome, the filiform leaves are placed on the sides and on the lower surface. Sporangia only occur on some pinnate leaves, the fertile leaves closely resemble the sterile ones. The veins are sympodially arranged. The two forms of leaves are united by transitional stages. In habit and mode of growth it greatly resembles the genus Jamesonia. (H. Christ, 1910, p. 180, fig. 80).

The cortex is broad, and developed peripherally as a strong zone of sclerenchyma and more centrally as a mass of storage parenchyma. The leaf-traces pierce the cortex obliquely; thus in a transverse section a number is cut, and are seen placed around the central bundle. These leaf-traces are unequal in size, the larger bundles originating from the pinnate leaves, the others from the filiform leaves. In the former the xylem is crescent in transverse section with incurved margins and with 2 lateral and one median protoxylem-strand. Traced downwards the protoxylem strands fuse together till there is only one, lying in the median plane. In transverse section the xylem is then crescent only, and with the phloem situated on its outer surface. The endodermis does not dip into the concavity of the xylem of the leaf-trace.

The xylem of the stele is composed of tracheids intermixed with parenchymatous elements, and is surrounded by a continuous phloem zone, a pericycle and an endodermis and there is in most cases an internal endodermis.

When the leaf-trace approaches the stele its endodermis fuses with that of the central bundle. On the same level the phloem in the latter opposite to the leaf-trace is wanting, somewhat lower the xylem is hollowed, thus a sinus is formed, the margins of which fuse with those of the leaf-trace. By this process an amount of parenchymatous tissue is enclosed, which ends blind at a somewhat lower level. The protoxylem of the leaf-trace looses its individuality some distance above its insertion into the central xylem.

The phloem of the leaf-trace fuses with that of the central bundle, which is interrupted above the insertion of the leaf-trace.

In the xylem of the stem, in which there is no protoxylem, two zones can be distinguished according to the characters of the tracheids and the distribution of the parenchyma: an outer part, composed of small tracheids with relatively few parenchymatous elements, and an inner part, consisting of wide short tracheids, intermixed with a rather large amount of parenchyma-cells.

At the inner side of the xylem ring there is no internal phloem; only a few parenchymatous layers separate the inner endodermis from the xylem-tissue. The tissue enclosed by the endodermis is sclerotic as is also the tissue of the cortex, but nowhere is it continuous with the latter.

The parenchyma of the pocket is never connected with the pericycle. In some transverse sections the continuity of the xylem seems to be interrupted by a chain of parenchyma cells, but these are normal xylem parenchyma only, and not the basal extension of the parenchyma decurrent from the leaf-trace into the pocket.

The structure of the central bundle is not homogeneous. Mostly the xylem is thicker in its ventral part than on the upper side. In a specimen, investigated by Thompson, the structure was partly as above mentioned, but when traced downwards, the sclerotic inner tissue was reduced, and disappeared as also the endodermis. The inner pericycle now formed an intrastelar pith, which was very reduced in size, the inner xylem was better developed here. At a somewhat lower level the pith became bigger, an endodermis enclosing sclerotic tissue was formed de novo, but disappeared lower down. Thus an amount of tissue similar to that of the cortex was found inside, wholly included by an internal endodermis. It was completely shut off from the external endodermis, and included in the xylem.

This plant is not only remarkable by having this character, but also by the difference in size in its sporangia, part of which are large, containing about 16 spores; the others are smaller, the number of spores produced reaching 32. Between the smaller and larger spores transitional forms may be found. Thus a certain degree of heterospory occurs, but it is not known, whether the gametophyte which grows from these spores, shows any difference.

Stromatopteris Mettenius. This genus is like Platyzoma monotypic; the only known species, Stromatopteris moniliformis Mett. (Thompson, 1917, p. 132—156) occurs in New-Caledonia. Like Platyzoma it has a xerophytic habit (H. Christ 1910, fig. 39, p. 204). The rhizome is short, inclined or erect, thin and quite devoid of roots. The leaves are pinnate, very seldom dichotomously branched. The pinnae are small, adnate, rounded at the top, leathery with involute margins.

The cortex is sclerotic and composed entirely of brownwalled fibrous elements, bearing many large oval pits on their thickened walls; they seem to be devoid of protoplasts. No intercellular spaces are found in the mature cortex.

The internodes are rather long, thus in a transverse section only one leaf-trace is seen. The leaf-trace is round in transverse section, and its xylem horse-shoe shaped, with narrower elements situated on the inner side; the phloem is situated on the outer surface of the xylem.

When traced downwards the leaf-trace approaches the central bundle of the stem. This consists entirely of tracheids, intermixed with parenchyma and surrounded by a layer of phloem and an endodermis. Further, the endodermis of the leaf-trace fuses with that of the stem. In the concavity of the xylem of the petiolar trace a number of tracheids are formed; and then the petiolar trace, which has become solid, fuses with the xylem of the stem. The downward continuation of the petiolar trace is seen a somewhat lower level as a continuous band of tracheids on the outer side of the xylem.

The apex above the insertion of the leaf is sometimes somewhat arrested; the leaf, which is well developed, then seems to be placed terminal; the relation of the leaf-trace to the bundle in the stem is less clear in this case.

In this plant thus there is a stele with a solid xylem bundle consisting of tracheids intermixed with parenchymatous elements, and surrounded by phloem and an endodermis. Into this bundle a leaf-trace is inserted, the xylem of which is gutter-shaped; a distinct protoxylem strand can not be distinguished (in fig. 17 however 2 lateral groups of smaller elements are seen, which are medial in fig. 13 and fig. 56). In connection with the habit, etc. this plant may be considered as a reduced form, in which the bundle of the stem has preserved its solid xylem and the parenchyma in the leaf-trace has its extension nearly to the stem-bundle without having an influence on it.

Ontogeny. Of the structures in the young plants in this family only those of Gleichenia pectinata (Thompson, 1920, p. 724) will be mentioned here. It is the most interesting one in this respect, as only in this plant a pith is found, connected with the cortex.

In the base of the young plant, there is a solid bundle of xylem-tissue, surrounded by phloem and endodermis. The leaf-traces fuse with it, without causing any interruptions. The upper portion of this stem bundle has a mixed pith with large tracheids, scattered through thin-walled parenchyma; at a higher level a central parenchymatous tissue is present.

The leaf-traces in this stage fuse with the xylem of the stem without causing any interruption above their insertion. At a higher level there is an interruption, and the endodermis dips slightly inwards,

Next, the phloem appears in the pith as an indefinite and incomplete ring of sieve-tubes lining the xylem internally; and then endodermal cells appear in the pith. They mark the base of a tube of inner endodermal cells closed below and widening upwards into pith, it is in fact the increase of the endodermal area of the endodermal pocket of the leaf next above. This endodermis is continuous through the leaf-gap with the outer endodermis.

Thus it is shown; that the medullation and the pocket formation are distinct phenomena; that in the centre of the stem the differentiation of the xylem-tissue is arrested; and independent of this process a pocket is found in the insertion of the leaf-trace formed by the downward extension of the parenchyma which is situated adaxially to the protoxylem in the leaf-trace. This brings about an interruption of the xylem-tissue, through which at a still higher level the endodermis is decurrent. The nodal island, the lower end of the pocket in the xylem, which is found in the mature stem, no doubt will be found here also, though it is not given in the diagrammatical figures, given by Thompson.

CHAPTER III.

The Stelar Morphology of the Dineuroidaceae.

To this Family belong the genera Dineuron, Diplolabis, Metaclepsydropsis and Etapteris.

Dineuron B. Renault. Two species of this genus have been described. One of them, Dineuron pteroides, occurs in the Permo-carboniferous strata of France; the other, Dineuron ellepticum, has been found in the Pettycur Sandstone of Culmian age in Scotland. Of both of plants only the petioles are known. They are thinner than in the other genera, e.g. in Dineuron ellipticum only 2.25 mM. in diam. The cortex consists of an outer sclerotic part, about 0.6 mM. broad; the inner parenchymatous cortex was very narrow, only 0.1 mM. broad. The petiolar bundle, which had a diameter of about 0.7 mM., was surrounded by a distinct endodermal layer.

In *Dineuron pteroides* (P. Bertrand, 1909, p. 216, fig. 104, 105) the pinnae were placed in four rows in alternating pairs on both sides of the petiole. The pinna-traces are of a very small size, with only one median protoxylem strand; on entering the cortex of the petiole they approach each other and fuse. The petiolar bundle at this level is elliptical in transverse section, at the other side an island of parenchyma is enclosed in the xylem tissue, with two protoxylems on each side. At the side where the fused pinna-traces (which have formed a pinna-bar), approach the bundle, a sinus is formed, which has a protoxylem strand in each corner. The pinna-bar comes nearer to this sinus and the ends of the pinna-bar fuse with its margins. Thus an island of parenchymatous tissue is enclosed, surrounded by four protoxylem strands. They fuse two by two. When traced further downwards, the peripheral loop splits up in the middle, the island of softer tissue opening outwards. At a slightly lower level the former structure is restored.

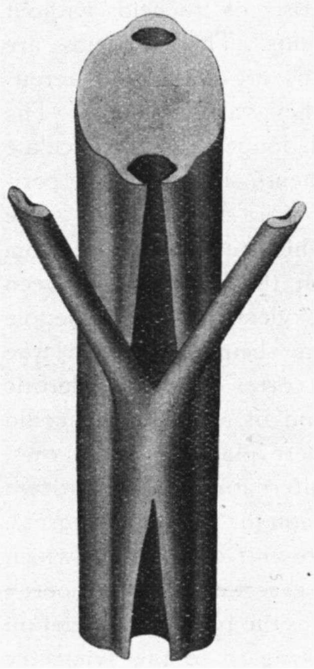

Fig. 7. Dineuron pteroides. Model of the xylemtissue of the petiole, showing the fusion of the pinna-traces and the peripheral loop.

A model of the xylem-tissue of the petiolar bundle is given in fig. 7. In Dineuron ellipticum (R. Kidston, 1908, p. 363, fig. 1—3) the same stages are seen, but the pinnae traces are not known in this plant.

Diplolabis B. Renault. Of this genus only one species is well known, Diplolabis Römeri (Solms) P. Bertrand 1909, p. 133, 211, fig. 5, 96, 97, W. T. Gordon, 1911a). This plant has been found in the Calciferous Sandstone of Culmian age near Pettycur, Fife, in Scotland. Both petioles and stems could be investigated, and the transition of the tissues of the petiole into the stem has been observed. The stelar morphology of this interesting plant is thus well known. The xylem is rather well preserved; the cortex and the phloem have been destroyed by fossilisation. In the petiole these tissues are better preserved, and here the occurrence of an outer sclerotic cortex and an inner one, consisting of softer tissue, could be established. In the stem this distinction could not be drawn.

The stem was a horizontal rhizome, with long internodes. In the rhizome there is a single stele. The xylem is a solid central bundle and consists of tracheids without intermixed parenchymatous elements. The tracheids are unequal in size; in the centre they are wide with a reticulate thickening of the wall, they vary in length. The outer tracheids are wider and longer, with reticulate thickening of the walls. The elements situated at the periphery are narrower. In the outer part of the xylem some groups of protoxylem occur, which are decurrent from the leaf-traces, and end blind at the boundary between the inner and outer parts of the xylem-tissue. The petiole was relatively strong, its diameter being nearly as large as that of the rhizome. In the cortex an outer sclerotic zone and an inner part, consisting of softer tissue, could be distinguished. The pinnae were placed in four rows, radiating from the petiole in alternating pairs, the two pinnae of one pair forming an angle of about 100 degrees. In each pinna a pinna-trace is present, the xylem of which is horse-shoe shaped in transverse section. It is endarch and its concavity is turned towards the petiole, the relation of the pinna to the petiole with regard to the symmetry is analogous to that of a leaf to the stem.

When the two pinna-traces from one pair of pinnae enter the cortex of the petiole, they fuse and form a broad strap of xylem-tissue or the pinna-bar, which has 2 protoxylem strands. The petiolar trace at this level is X shaped, the two sides of the X united by a bar of xylem; each of the 2 arms of the X at this side has a cluster of protoxylem near its apex on each side; then the pinna-bar joins the X shaped petiolar bundle, bridging over the space between the two arms, and enclosing an island of parenchyma. This island, if traced downwards, becomes smaller, and the peripheral loop splits up in the centre, the two halfs gradually merging into the two arms. The two protoxylem strands of the pinna-bar fuse with those of the arms. At a somewhat lower level the two pinna-traces of the following pair enter the cortex and the same formation can be seen. As the pairs of pinna are alternate, in transverse section different levels of these structures are found on the two sides of the petiolar trace.

In the lowermost portion of the petiole, the size of the arms in proportion to the rest diminishes and the included island of parenchyma is relatively small. In one case (W. T. Gordon, 1911a, p. 725, fig. 3) the pinna-bar is seen to bend in towards the inner margin of the island, which thus becomes reniform in transverse section, and the middle part of the xylem bridge fuses with the end of the connecting bar of the X shaped trace, thus cutting the island of parenchyma in two. The protoxylem groups are situated one in each parenchymatous island. Then the xylem on the outer side of this island disappears, the end of the trace now is tridentate. Immediately beyond this stage another bridge appears between the two arms, but does not fuse with the prominence between the two bays. The parenchymatous island thus becomes reniform, and then elliptical by the disappearence of the prominence. The two protoxylem strands of the petiolar strand fuse; so that there are only two protoxylemclusters remaining, situated respectively at the inner and outer side of the parenchymatous island. At a still lower level the parenchyma disappears.

The petiolar strand is now elliptical with two double protoxylem groups, one at each end. They fuse and the petiolar bundle unites with the stem-xylem, without forming any interruption. The protoxylemgroups run downwards into the stem for some distance, on the boundary between outer and inner xylem, but soon they dwindle away. The stems are dichotomously forked; the xylem becomes elliptical in transverse section, then constricted in two parts. No interruptions in the xylem, and no branch-gaps are formed.

It it very probable that the rhizome of this plant was horizontal as in Pteridium aquilinum, and subterranean, as follows from the absence of sclerenchyma in the cortex of the stem. It gives off at large intervals erect petioles with four rows of pinnae. The pinnae were placed with regard to their symmetry like the leaves on the stem; this is shown by the structure of its pinna-traces.

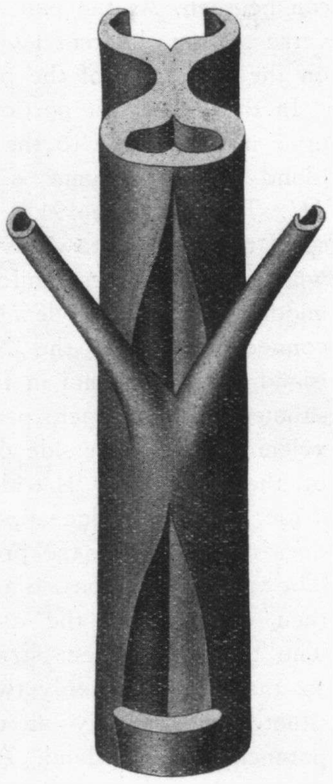

Fig. 8. Diplolabis Römeri (Solms) Bertr. Model of the xylem-tissue of the petiole.

If the vascular system of the petiole, reconstruction of which is given in fig. 8, be considered, it is clearly shown, that above the insertion of the pinna-bar, formed by the fusion of the two pinna-strands, an interruption in the outer part of the xylem of the petiolar bundle is formed. By this interruption the parenchyma, decurrent from the pinna-bar next above and included in the xylem, is brought into free communication with the tissues outside. In this respect it closely resembles Dineuron, and may be derived from it by the constriction of the middle part and the larger development of the pinna-traces. The course of the protoxylem strands is similar.

In this plant thus the occurrence of a zone, situated adaxially to the protoxylem strands, is established, where the development of the xylem tissue is arrested, so that from the procambial cells parenchymatous elements are differentiated. This formation is continuous and decurrent towards the base of the petiole. Those of the successive pairs of pinnae of the same side unite and end blind above the insertion at the xylem of the stem. In the petiole, mentioned by Gordon, the two masses of parenchyma of the two protoxylem strands in the lower part of the petiole attain a certain degree of independence.

The splitting up of the peripheral loop is also caused by this action, the opening formed in this way having the same value as the „gaps" occurring in the branchings of the leaf-trace of Osmunda, By another arrangement of the units in the petiole the peculiar symmetry of this structure can be explained.

Metaclepsydropsis P. Bertrand. This genus contains 2 species: Metaclepsydropsis duplex (Williamson) P. Bertr. and Metaclepsydropsis paradoxa (Unger.) P. Bertrand.

Metaclepsydropsis duplex (Williamson.) P. Bertrand (W. T. Gordon 1911b, P. Bertrand, 1909, p. 121, 205, fig. 90—92). Remains of this plant have been found by W. T. Gordon in association with Diplolabis Römeri in strata of Culmian age near Pettycur in Scotland. The rhizome is horizontal with very long internodes, reaching a length of 55 cM. The outer cortex consists of parenchyma with thick walls, but is most likely not of sclerotic nature; the inner cortex is composed of thin-walled elements, the detailed structure, like that of the phloem, could not be seen owing to the bad preservation of the tissue. The xylem of the solid vascular bundle of the rhizome is solid with a clear distinction between the structure of the outer and central zone. The tracheids of the latter zone are small, intermixed with parenchyma and the thickening of the walls is reticulate or scalariform.

The tracheids of the outer xylem are larger, longer and with more rows of bordered pits. Parenchymatous elements do not occur in this part.

The petiole was relatively strong; its diameter is nearly equal to that of the rhizome. In the cortex in contrast with that of the rhizome an outer slerotic part can be distinguished from the inner parenchymatous tissue, but not in the base of the petiole,

The pinnae were placed in alternating pairs, the petiole thus bore 4 rows of pinnae, placed as in Diplolabis Römeri; their position with regard to the petiole may be compared to that of a leaf on an erect branch. Each pinna branched in a horizontal plane.

The bundles of the tertiary pinnae are, in transverse section, concave at the upper side with incurved ends and with the two protoxylems situated in the corners. They fuse laterally with the bundles of the secundary pinnae, which have the same structure but are of a somewhat larger size. In some cases the margins fuse together or with the abaxial part of the xylem, the bundle thus being closed, including a portion of parenchymatous tissue situated adaxially to the protoxylem strands. The two pinnae bundles of a pair of pinnae enter the cortex of the petiole at the same level. The petiolar bundle is in transverse section constricted in the middle part, there is at each side either an island of enclosed parenchyma or a small sinus. The two pinna-traces fuse, thus forming a broad bundle, which has two pairs of protoxylem strands. Then the margins of this bundle fuse with the xylem of the petiolar trace, and include an island of parenchymatous tissue. In the middle of this part of the petiolar bundle a little bay of parenchyma with two protoxylems is seen.

The mass of parenchyma included by the pinna-bar thus is surrounded by protoxylem strands. This bay gets shallow and disappears and the protoxylems fuse, so that only two are left, placed at each side of the included parenchymatous tissue; this becomes smaller, circular in a transverse section, and does not reach over the whole breadth of the petiolar trace. When at a lower level its peripheral loop is split up in the middle, the next pinna-bar does not fuse with the margins of this sinus, as in Diplolabis, but at some distance on both sides of it. The protoxylem strands of the sinus are not connected with those of the latter pinna-bar, but end blind.

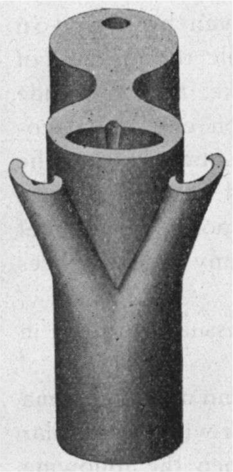

Fig. 9. Metaclepsydropsis duplex (Will.) Bertr. Model of the xylem tissue of the petiole.

In the lower part of the petiole the bundle becomes oval in a transverse section, as in Dineuron. The islands of parenchyma are smaller and do not open outwards; the protoxylems fuse and the parenchymatous tissue ends blind below. On this level the petiolar trace enters the cortex of the stem, its oval xylem bundle with its two mesarch protoxylem strands fuses with the solid mass of xylem in the stem, the protoxylems are decurrent for a short distance in it and end blind.

The stem is dichotomously branched, the xylem is constricted in two parts, no branch gap is formed.

The distance between successive alternating pairs of pinnae is not the same; they thus approach a subopposite po-

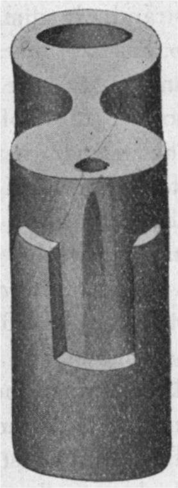

Fig. 10. Metaclepsydropsis duplex (Will.) Bertr. Model of the xylem-tissue of the petiole. Part of the peripheral loop is removed to show the lowest part of the included parenchyma.

sition. This follows from the figures given by Gordon [1911b, textfig. 3 (1 and 4)], where, while the structure of the side with its fusing pinna-bar is alike, the other side shows different forms. In a thin section of the Palaeobotanical collection in the Botanical Laboratory of the Groningen University, the two sides had nearly the same structure. This feature indicates a subopposite position of the pinnae, which is also present in many recent Filices in the lower part of the frond.

Models of the structure of the xylemtissue are given in fig. 9 and 10.

Here too as in the other forms an island of parenchyma is included by the fusion of the pinna-bar with the petiolar strand. It diminishes in size, so that, when the following pinna-bar fuses with the petiolar strand, it is only of a small size; the peripheral loop is split up as in the other forms, the softer tissues then being in connection with the similar tissues outside. Because of its smaller size it does not form a whole with the included parenchyma of the pinna-bar of the pinnae next below, but ends rather independently.

Metaclepsydropsis paradoxa (Unger) P. Bertrand (1911, p. 18-23, pl. I, fig. 7-10, pl. II, fig. 18).

This plant, of which only the petiole is known, was discovered in the Upper Devonian of Salfeld in Thuringia. Its internal structure has been described fully by P. Bertrand. The most striking difference with Metaclepsydropsis duplex is that the constriction in the middle part of the petiolar trace is better developed; in some places even the two halfs are distinct, separated from each other by thin-walled tissue.

This feature is a strong argument against the theory, that the petiolar bundle is to be regarded as a whole. It gives strong supposition that the latter is formed by the bundles of the pinnae, the arrangement of which in the petiole causes the different structures in this organ. Here the elementary bundles of the pinna-traces do not fuse in the median plane.

Etapteris P. Bertrand. This genus has a wide geological range. Of the six species, which have been distinguished, the first member, E. Tubicaulis (Goeppert) P. Bertrand, is found in Lower-Carboniferous, perhaps Upper Devonian, strata of Falkenberg in Silesia; four species, E. diupsilon (Will) P. Bertrand, E. Scotti P. Bertrand, E. shorensis P. Bertrand and E. Bertrandi Scott are known from the upper Carboniferous (Lower Coal-measures) of England and Westphalia. The sixth member of the genus, E. Lacatti (B. Renault) P. Bertr. occurs in the Permian strata of Autun. Only the structure of E. Scotti will be dealt with here in detail.

Etapteris Scotti Bertrand (1909, p. 208, fig. 111, 112). This plant is a common one in the coal-balls of the Lower Coal-measures, both in England and in Westphalia. Only the petiole with the pinnae is known. The pinnae were placed in 4 rows in alternating pairs, the mode of growth and the position of the pinnae to the petiole were similar to the same features in allied forms. The tertiary pinnae, which were placed in one plane with the secundary rachises, have a small C-shaped bundle, each with two protoxylem strands; they fuse with the bundles of the secundary rachises in the usual way. The latter are of a larger size, and on the abaxial side with projecting ridges (these are very well developped in E. Lacatti). The bundle of the petiole is H-shaped in transverse section, the rectangular median band (apolar) is straight, the long lateral arms (antennae) are somewhat reflexed. The protoxylems are external, two at each end, and lie in slight depressions of the xylem at the base of the antennae, facing outwardly.

The two bundles of one pair of pinnae enter the cortex of the petiole. They fuse, forming a broad bundle with two protoxylemstrands, the pinna-bar. This strap of tissue approaches the petiolar bundle, but is meanwhile constricted in its middle part, and divides. The two parts approach the petiolar strand, and lie against it. These bundles are oval in transverse section with a median protoxylem. As only the metaxylem fuses with the arms of the petiolar bundle, the protoxylem borders on a little bay; at first the bundles are quite distinct from the rest because the elements are not of the same size but this difference becomes less, the outer side of the xylem becomes flattened, and the protoxylem is no longer distinguishable, the former structure thus being restored.

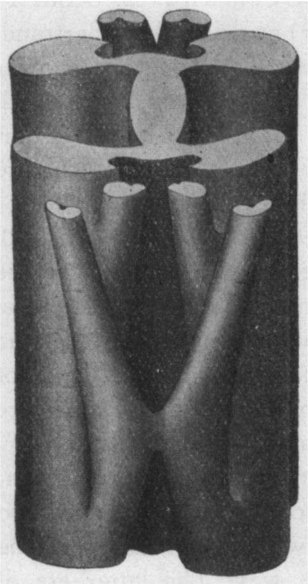

Fig. 11, Etapteris Scotti Bertr. Model of the xylem-tissue of the petiole.

If the reconstruction of this structure, which is given in fig. 11, be considered, it is clear, that the splitting up of the pinna-bar is caused by the larger size of the interruption in the peripheral loop above the fusing pinna-bar. Not only the peripheral loop is interrupted over its whole length, but the interruption reaches higher than the fusion of the pinna-bar with the petiolar strand, so that the former is already divided before the fusion of the petiolar bundle.

In *E. Bertrandi* Scott (O. Posthumus, 1923, p. 850—855, fig. 1—4.) the pinna-traces enter the cortex and fuse in the usual way. The pinna-bar thus formed fuses with the petiolar bundle as a whole, thus enclosing a mass of softer tissue. This parenchymatous island diminishes in size; at a lower level the continuity of the xylem tissue is disturbed at its outer side and so a sinus is formed with a protoxylem at each side. Further below the depression becomes more plain and the protoxylems indistinct (see fig. 12).

This shows that, if the peripheral loops in Etapteris are not closed, this is only dependent on the grade of development of the parenchyma near the protoxylems of the pinna-trace. This parenchyma is not so fully developed in E. Bertrandi. P. Bertrand (1909, p. 206) mentions that in E. Tubicaulis the peripheral loop is as it were temporarily closed, which is to be explained in the same way.

In his memoir on the frond of the Zygopterideae P. Bertrand describes the other forms; the older literature is also therein cited.

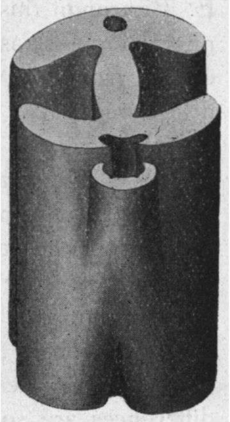

Fig. 12. Etapteris Bertrandi Scott. Model of the xylem-tissue of the petiole.

The family of the Dineuroidaceae contains the genera Dineuron, Metaclepsydropsis and Etapteris. These agree in having 4 rows of pinnae placed in alternating pairs. The pinnae branch in a horizontal plane. They are symmetrical to the plane passing through the pinna and the longitudinal axis of the petiole. The pinna-bundles possess a strand of thin-walled tissue, situated at the upper side of the protoxylem, which is nearly always so large, that they arrest the formation of metaxylem at this side of the xylem bundle. When passing into the petiole, this parenchyma is included in a peripheral loop of tracheids, this is the downward prolongation of the fused pinna-traces, which is interrupted by the similar tissue of the bundles of the pair of pinnae next below.

In Dineuron this interruption is very small, according to the size of the pinna-traces, in Diplolabis and Metaclepsydropsis it is greater, therefore the continuity is shorter. In Etapteris, as a rule, the upper margin of the interruption is higher than the insertion of the pinna bar of the pair of pinnae next higher, so that this latter is split up before the fusion with the petiolar trace. But in E. Bertrandi this interruption is smaller and the peripheral loop is, as it were, temporarily. Metaclepsydropsis differs from the other by the form of its included mass of parenchyma. This diminishes in size, when followed downwards, and the margins of the pinna-bar do not fuse with the margin of the sinus, but do so laterally to it. In such a form the occurrence of two parenchymatous islands on the same side in one and the same transverse section may be expected.

I believe that Sahni's division of the family of the Zygopteridaceae in the Dineurioideae and the Clepsydroideae on these grounds is fully justified. Since the differences are so considerable, not only in the position of the pinnae and the symmetry of the leaf, but also in the different mode of fusion of the petiolar trace with the pinnae bundles, it will therefore perhaps be more in accordance with the real affinity if these two groups be considered as two separate families. The only thing, they have in common, is that they both have the same peculiar mode of arrangement of the elementary bundles in the petiole; for the rest they have a wholly different descent.

CHAPTER IV.

The Stelar Morphology of the Clepsydropsidaceae.

To this family belong the genera Clepsydropsis, Ankyropteris, Asterochlaena and probably Asteropteris.

Clepsydropsis Unger. Of this genus 3 species are known: Clepsydropsis antiqua Unger (P. Bertrand, 1909, p. 127, fig. 94, 95; 1911, p. 15-18, fig. 1-6, 11-17, 20), C. kirgisica Stenzel (1889, p. 20, fig. 38-44), and C. australis Osborn (1915, p. 727), which are much alike and agree in the essential points. Only of the latter species the structure of the stem is known.

C. antiqua has been found in the Upper Devonian of Salfeld in Thuringia, in the same strata as Metaclepsydropsis paradoxa; C. kirgisica is found in Siberia, and is probably of Permian age; B. Sahni (1919) describes a stem of Clepsydropsis from the Upper Devonian of Australia.

The petiole possesses a sclerotic outer cortex; the inner zone consists of thin-walled tissue. The pinnae are placed in two rows, the plane going through the pinnae and their ramifications is about horizontal or inclined towards the petiole. The plane of symmetry of the pinna goes through the petiole. Of the lamina nothing is known.

The vascular bundles of the ultimate ramifications are rounded in transverse section, with a central strand of protoxylem, at the adaxial side of which a number of parenchymatous cells occur. These do not interrupt the metaxylem at the inner side, so that they are wholly included; in transverse section the bundle has an annular form.

The vascular bundles of the pinnae are similar, only the abaxial part of the xylem is better developed and the parenchymatous island broader.

When a tertiary pinna approaches a secundary rachis, the xylem tissue first fuses, and is reduced between the two parenchymatous islands, which fuse later; then the protoxylem strands fuse, so that the annular form of the transverse section is restored.

The petiolar trace is elliptical in transverse section with a constriction of its middle part. In the two ends an included island of parenchymatous tissue is present surrounded by a number of small elements, which may be considered as the protoxylem. When entering the cortex, the pinna-trace approaches the petiolar strand and their xylems fuse; the xylem between the parenchymatous islands of the pinna-trace and of the petiolar bundle is reduced, and disappears; then these islands fuse together and the former structure is restored.

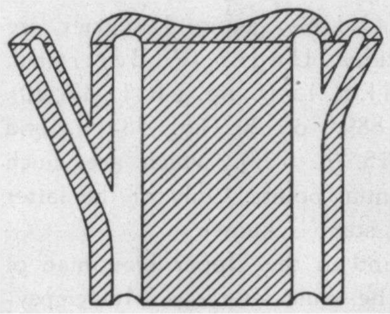

Fig. 13. Clepsydropsis antiqua Unger. Longitudinal section of the model of the xylem-tissue of the petiole.

The stem of C. australis was about 11 cM. thick, its internodes were short, the leafbases crowded. But for this covering of the leafbases, the stem would be very small, only a few cM. in diam. Between the leaf-bases many roots were present.

According to Osborn's (1915, p. 727) description the stele of the stem is shaped like a five-rayed star, with blunt points; the pith, which contains tracheids is also star-shaped. Leaf-traces fuse with the central tissues in the same way as in Ankyropteris Grayi. At their insertion they are of a triangular shape with rounded angles, the apex of the triangle being the point of attachment to the stem. This bundle soon becomes flattened and tangentially elongated, so that, at a short distance above the base of the petiole, it appears as a long band-shaped xylem-mass without curvature, rather constricted in the middle and with a peripheral loop, containing parenchyma and bordered by small tracheids at each end.

As the parenchyma is always included in the xylem, both in the pinna-bundle and in the petiolar bundle, the part of this tissue, situated at the inner or upper side of the parenchyma is never interrupted (See fig. 13). This characteristic separates the Clepsydropsidaceae from the Dineuroidaceae, in which the parenchyma, situated adaxially to the protoxylem strands of the pinna-bundle, reduces the adaxial part of the metaxylem, and on its downward course interrupts the peripheral loop of the petiolar strand.

The pinna-bundle is rounded in transverse section as also the ends of the petiolar bundle. Therefore these two bundles, when fusing, join in the median plane; Ankyropteris shows a modification of this simple mode of fusion.

Ankyropteris Stenzel. To this genus belong 7 species, of which we shall only deal with A. westphaliensis P. Bertrand, from the Upper Carboniferous of England and Westphalia, A. Grayi (Will.) P. Bertr. from the same strata, and A. corrugata (Will) P. Bertr. Of the latter two forms the stem is known. It was a slender rhizome with long internodes, reaching about 22 m.M. in diam. in A. Grayi. It was a creeping, perhaps scrambling, plant among the shrubs. Large petioles were given off from the stems at considerable intervals. The leaves bore two rows of pinnae (of which the plane of symmetry passed through the petiole as in Clepsydropsis). Nevertheless the petiole and rachis show a certain degree of a bilateral symmetry, since the bar of xylem — the apolar — connecting the two arms of the H-shaped strand, is curved, and has the concavity turned to the stem. From the pinnae tertiary rachises were given off; a lamina and reproductive organs are unknown.

Ankyropteris Grayi (Williamson) P. Bertr. (see D. H. Scott 1912). The stem of Ankyropteris Grayi was slender and no doubt attained a considerable length. The stems and petioles of the closely allied A. scandens were found intermixed with the roots of a Psaronius; this leads to the supposition that these plants were scramblers among the tree-ferns of this period.

The diameter of the stem of A. Grayi was about 22 mM. Large petioles, a little smaller than the latter in diam., were given off from the stem at considerable intervals. The phyllotaxis was a spiral one, 2/5 in the cases observed. The rhizome is covered with numerous rudimentary leaf-like organs of a smaller size, which occur on the petiolar base as well as on the stem. They are considered by Dr. Scott as aphlebia. The epidermis bears a great number of multicellular uniseriate hairs, in one specimen in some places a few layers of periderm could be recognized. The outer cortex, especially in the internal layers, has somewhat thicker walls than the parenchymatous inner cortex, yet this difference is not large. The phloem follows the contour of the wood. This has a very characteristic structure; in transverse section it has the outline of an irregular five-rayed star. These rays are of an unequal length, owing to the section level of the outgoing leaf-trace, which is given off from these arms. In the wood a central and a more peripheral region can be distinguished. The latter consists principally of large scalariform tracheids; the central tissue, formerly described as pith, contains a system of small tracheids, distinct from those of the external zone and intermixed with parenchyma. This internal system forms a group or irregular ring round the centre of the stele, and from this central group radial bands of small tracheids extend outwards up to the middle of each arm.

The leaf-trace will be dealt with in connection with that of A. westphaliensis P. Bertr.

In A. corrugata (Williamson) P. Bertrand (1909, p. 110, fig. 87) the stele has a cylindrical form, in a transverse section it is almost circular, except where a leaf-trace is given off, which causes a bilobed projection. The stem was dichotomously branched, not by an axillary bud; it forked into two nearly equal branches without obvious relation to the leaf-insertion.

The petiole of Akyropteris westphaliensis, of which the stem is not known, has an outer sclerotic and an inner parenchymatous cortex. P. Bertrand (1909, p. 76) describes the epidermis as follows: „La surface du petiole est formée par une couche de cellules a parois minces, laissant entre elles des petites lacunes et qui parait jouer la rôle d'un tissu assimilateur. Ce tissu est couvert d'un epiderme, mais on peut se demander si c'est bien l'epiderme qu'on aperçoit sur la figure."

Concerning A. corrugata he says (1909, p. 94): „Extérieurement (du gaine mécanique sclérifié) on trouve comme chez les autres Zygopteridées un tissu assimilateur et un épiderme (visible partiellement sur les figures 83 et 85)". In A. Williamsoni the epidermis was wanting. If we compare his description with the plates, it is not proved with certainty that the structure of the epidermis is, as he stated. The outer cells of the cortex have smaller dimensions than those of the inner layers, also the intercellular spaces are wanting, or at any rate very small. The epidermis itself is not clearly shown in the fig.

In some preparations of the Palaeobotanical Collection of the Botanical Laboratory in Groningen, I could observe some transverse sections of A. westphaliensis and of A.

corrugata in which the epidermis was well preserved. In A. westphaliensis [1]) the epidermal layer consists of isodiametrical cells, with a thick outer and thinner radial and inner walls. The underlying cells of the outer cortex had a narrow lumen and a thick wall; towards the centre the cells became wider, and their walls thinner. Intercellular spaces were absent, at least very scarce. In a petiole of A corrugata, [2]) the cells of the epidermis too had a moderately thick outer wall; the underlying outer cells were much like those in A. westphaliensis, but tertiary layers are arranged on the inner side of their walls, especially towards the periphery, but also against the inner and radial walls; thus the excentric lumen is considerably reduced. This structure has a great resemblance to the alterations of the outer parts of the tissues of the cortex as is described by P. Bäsecke, especially with the structure in Polypodium sinuosum (P. Bäsecke 1908, p. 67, pl. II, fig. 40, 41) but less so with that in Acrostichum axillare (l. c. 1908, p. 67, pl. II fig. 43).

Here the walls of the cells are thickened by the apposition of cutin layers (metacutisation). In some they are all of an equal thickness, covering the wall all over, in other Ferns the metacutis is thicker in its outer part, and the structure shows a close resemblance to that in Ankyropteris corrugata. This metacutisation is found in recent Ferns both in the petiole and in the rhizome but not in this form in the fronds. Therefore it seem to me improbable, that in Ankyropteris assimilating tissue was present in the petiole, situated below the epidermis. Where this tissue occurred is yet uncertain, nothing being known of the lamina of these plants. The tertiary rachis, which is already known in A. westphaliensis, has a vascular

---

[1]) praep. B. 12. (W. Hemingway 343. 4.)
[2]) praep. B. 11. (W. Hemingway 216. 45.)

bundle of which the xylem has one protoxylem strand only, associated with a group of parenchyma at the probable upper side; it does not break the continuity of the metaxylem; in transverse section the bundle has an annular form. They were placed in the pinna in two rows.

The vascular bundle of the pinna was symmetrical, with two enclosed protoxylem strands, each provided with a group of parenchymatous cells which does not break the continuity of the metaxylem at the adpetiolar side. The transverse section of this bundle has an elliptical outline constricted in the middle part. When entering the cortex of the petiole, the bundle becomes less specialised, the contour elliptical and the two parenchyma islands approach and fuse, so that the trace is now annular in transverse section and with two protoxylem strands on each side of the included parenchyma.

The petiolar trace of Ankyropteris has in transverse section the form of the letter H so characteristic for many of these plants. The cross-stroke of the letter is a plate of tracheids without protoxylems and placed tangentially to the stem, but somewhat curved with the concavity directed away from the stem; the two arms of the H are formed by the four antennae. These are four projecting plates of tracheids covered on the outer side by a permanent plate of smaller tracheids, thus enclosing a long narrow island of parenchymatous tissue, with a protoxylem strand at each end. The phloem is situated on the outer side of the xylem. The fusion of the pinna-trace with the petiolar bundle is somewhat different from the same process in Clepsydropsis.

In the latter the xylem of the annular pinna-trace fuses with that of the petiolar strand, and thereafter the two parenchymatous islands fuse in the median plane. In Ankyropteris however the xylem of the elliptical pinna-bundle is incurved when approaching the petiolar trace

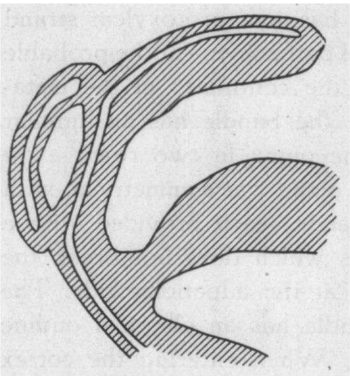

Fig. 14.

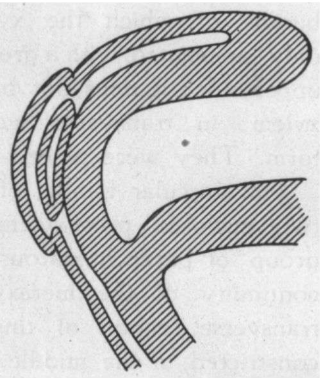

Fig. 15.

so that the fusion does not take place in the middle, but at both ends of the pinna-trace and fusion of the two parenchymatous islands soon follows. By this process a ring of xylem is isolated from the filament; in transverse section (see fig. 14-16) at first one is inclined to look upon this structure as the downward continuation of the pinna-trace, but when studying the successive levels, it becomes evident that the lumen in the centre of this hollow

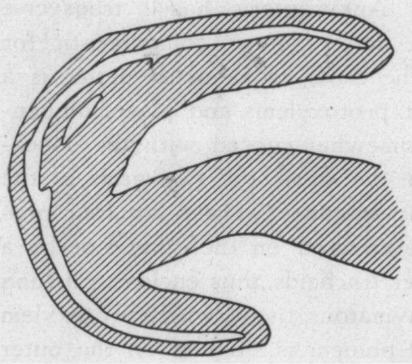

Fig. 16.

Fig. 14. Ankyropteris westphaliensis Bertr. Transverse section of the petiolar trace, showing its union with the pinna-bundle (after Bertrand, modified).

Fig. 15. Ankyropteris westphaliensis Bertr. Transverse section of the petiolar trace, showing a further stage of the fusion of the pinna-bundle (after Bertrand, modified).

Fig. 16. Ankyropteris westphaliensis Bertr. Transverse section of the petiolar trace, showing the fusion of the pinna-bundle, at a still lower level (after Bertrand, modified).

group of tracheids is not continuous with that of the pinna-trace, but with the cortex of the petiole. At a still lower level this annular xylem strand is solid and fuses with the outer side of the antennae. Thus the internal parenchyma of the pinna-trace is continuous with that of the petiolar bundle.

When following the course of the petiolar bundle downwards in the lower part of the rachis and through the cortex, the alterations in A. corrugata are as follows: The relative size of the antennae becomes smaller, the antennae are not so marked off from the apolar, the enclosed parenchymatous islands are of a smaller size. Finally they are composed of but a few parenchymatous elements, the two protoxylems fuse together and at a still lower level they disappear. The strand, which is now elliptical in a transverse section, has two mesarch protoxylems, embedded in the metaxylem; it then fuses with the central xylem strand, the protoxylems loose their individuality and become indistinct.

This simpler structure is to be seen in A. corrugata; in the other form, of which the stem is known, A. Grayi, it is somewhat complicated by the axillary shoot, the stele of which is fused with the leaf trace; the two parenchymatous islands can still be seen below this fusion.

In this genus, like in Clepsydropsis, the parenchymatous tissue, which is associated with the groups of protoxylem, is always included in the metaxylem, in which no interruption is formed. Not only in this respect, but also in the position of the pinnae, they agree and are quite different from the Dineuroidaceae. In both forms the pinnae are alternate in two rows. The main difference between Ankyropteris and Clepsydropsis is the other mode of the growth of the rhizome; in the former it possesses long internodes, it was a scrambler; in the latter the stem is erect with short internodes.

Asterochlaena Corda. The structure in this genus, of which two species are known, A. laxa (P. Bertrand, 1911, p. 129, 217, fig. 81; G. Stenzel, 1889, p. 18, Taf. IV, fig. 33—37; P. Bertrand, 1912, p. 256, 267) and A. ramosa (Cotta) Stenzel (1889, p. 15, pl. IV, fig. 27—32) is in many respects similar to Clepsydropsis. The stem is erect, the internodes, which are covered by the leaf-bases, are short; the leaf-trace bundles pass obliquely through the cortex. Though a little asymmetrical, they show a close resemblance to those of Clepsydropsis; the islands of included parenchymatous tissue can still be seen after the fusion with the stele, and are decurrent into it. The stele is much stellate in transverse section, with longer arms than in Clepsydropsis.

Asteropteris Dawson. The only species of this genus, A. noveboracensis Dawson, (1881, p. 229, pl. XII, fig. 1—9; P. Bertrand, 1912, p. 255, fig. 4) is known from the Devonian of Canada. The stele is much stellate as in Asterochlaena, but the leaf-traces, which pass the cortex very obliquely, are all of one kind in transverse section, as if they were placed in superponed whorls. Another point of difference is the presence of four parenchymatous islands in the xylem of the petiolar trace; it is a pity that the upward continuation of this remarkable structure could not be studied, owing to the destruction of the other parts of the stem.

When comparing the families of the Dineuroidaceae and the Clepsydropsidaceae with the Osmundaceae, the same essentials points in their structure are seen: i.e. the reduction of the central part of the xylem of the stem to a thin-walled tissue and the reduction of the xylem at the adaxial side of the protoxylem strands in the elementary bundles of the leaf. The Dineuroidaceae agree by having a larger development of this structure, so that metaxylem, adaxially to this parenchyma, is hardly ever found. In these forms the reduction extends into other tissues: in the Osmundaceae into the xylem of the stem, in the Dineuroidaceae into the peripheral loop of the petiolar strand above the insertion of the pinna-trace. In the Clepsydropsidaceae the metaxylem at the adaxial side of this parenchyma stops the reduction of the other tissues.

R. Kidston and D. T. Gwynne-Vaughan found in Thamnopteris in the lower part of some leaf-traces a double mesarch protoxylemstrand, so that in transverse section it shows some resemblance to the petiolar bundle of Clepsydropsis. Though the Osmundaceae and the forms, mentioned above, have some points in common, this characteristic is no argument for a close affinity between these two families, their stelar morphology, especially in its symmetry, being so different.

CHAPTER V.

The Stelar morphology of the Polypodiaceae.

To this large family belong more than three quarters of all known Ferns; Christensen in 1906 mentions in his Index Filicum in total 5940 Ferns of which no less than 4527 are Polypodiaceae. New discoveries have not materially affected this relation.

The Polypodiaceae seem to be a relatively young group of plants; when excluding a somewhat aberrant form as Dipteris, which has been placed by some authors in a separate group, fossil remains are only known in the Cretaceous and Tertiary deposits. Their affinity with the Ferns of the Palaeozoic age is rather distant. Some of these fossils are more closely related to the recent Osmundaceae, others to the Marattiaceae, which also have been found in older strata than the Polypodiaceae.

The greater wealth of forms is in agreement with this fact, not only as regards the morphological features of the leaves and the reproductive organs, but also in their anatomical characteristics. The study of the internal structures in this family will no doubt have important results, if enough data are available, for, by the larger variation, the comparison of the structures and the correlation of these characters with the habit and the mode of growth, will give more possibilities than in other groups of Ferns.

In the following chapter I intend to demonstrate that the different structures are without, or at any rate almost without exception, variations of one prototype. The great variation is a consequence of the varying relationship between the determining factors in stelar structure. From a stelar morphological standpoint all structures may be explained as being derived from an originally solid stem bundle with mesarch leaf-traces, where by reduction the differentiation of the xylem, situated adaxially to the protoxylem, is arrested. Thus funnels of parenchyma descend in the leaf-trace and penetrate into the stem-xylem, In a later stage these funnels of the successive leaves unite, hollowing the originally solid cylinder of xylem. No reduction of the internal part of the stem xylem to a pith can be demonstrated. In this funnel phloem is differentiated; when the specialisation has gone further endodermal cells are developed in it and the central tissues are continuous with the cortex and of the same structure.

The simplest form of stele occurs in those plants where the internodes are long, so that in one internode only the influence of one leaf-trace is found, especially when the leaf-trace is simple and the leaf-gap rather short.

The most complex structure is seen in those plants, where the leaf-trace is compound and where the internodes are short, so that the gaps overlap; a further complication occurs when interruptions in the stele are formed, other than those which are in relation to the leaf-gap.

If the conclusions, drawn from the study of the anatomy of the Osmundaceae, the Gleicheniaceae, Clepsydropsidaceae and Dineuroidaceae, be accepted, we may expect a form in which the vascular system of the stem has a solid xylem-bundle, in which the leaf-trace is endarch and crescent in its upper part and mesarch in its lower part, and in which the parenchyma situated adaxially to the protoxylemstrands ends blind in the xylem of the leaf-trace after having gradually diminished in size.

Such a form is known to us from Bower's investigations: it is *Cheiropleuria bicuspis* (Bl.) Presl (F. O. Bower, 1915, p. 502, 507, fig. 7-15). This fern occurs in the Malayan Regions, in the Philippines, Formosa, and New-Guinea, living in open planes and at the edge of the woods. The rhizome is creeping, probably underground, densely beset with yellow silky hairs and brown roots; the internodes are distinct and of different length. Branching by dichotomy has not been found, lateral branches occur and are situated on the abaxial face of some leaf-bases. The leaves are petiolate, simple and bilobed, the venation is complex with a close network with free veinlets in the meshes. A good figure of the habit has been given by H. Christ (1910, fig. 7, p. 18).

The outer layers of the cortex are sclerotic, the inner layers consist of parenchymatous tissue. The leaf-trace in the base of the petiole is formed by two bundles, each provided with one protoxylem strand situated on the inner surface. Lower down they fuse. In a transverse section the bundle resulting from this fusion is crescent, the ends of the xylem being curved inwards. At a lower level, where the endodermis has meanwhile retreated from the concavity of the leaf-trace, these two sides of the xylem approach each other and fuse. The xylem is now annular, with two protoxylem bundles on the inner surface at the adaxial side. Still lower it is more oval; the endodermis of the leaf-trace fuses with that of the central vascular bundle. The xylem of the latter is a solid cylinder consisting of tracheids intermixed with parenchymatous cells, and without any protoxylem strands. It fuses with the annular leaf-trace and at a slightly lower level the two protoxylem strands fuse, the parenchyma adaxially to the protoxylem is, when traced further downwards, reduced in size, and ends blind; at a still lower level the protoxylem disappears also. In the rest of the internode the xylem consists of metaxylem only. The leaf-trace is relatively large; the diameter of the xylem of the rhizome is only twice that of the petiolar-trace. The phloem is situated round the xylem, the protophloem is found on the outer side.

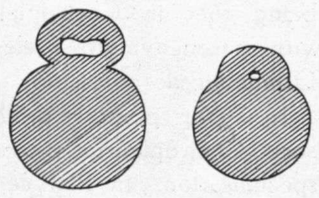

Fig. 17. Cheiropleuria bicuspis (Bl.) Presl. Transverse sections of the lowest part of the petiolar trace, when fusing with the stem-xylem (after Bower, modified).

The vascular bundle of the lateral branch is in close relation to the leaf-trace. When there is a lateral branch, the outer part of the xylem of the latter is thicker than usual and nearer the periphery this larger bundle gives off two branches, each with a protoxylem strand; these two bundles are equivalent to the divided leaf-trace in the normal leaf-base. The rest of the leaf-bundle moves outwards into the lateral branch.

It is evident that this structure may be explained in the same way as in Thamnopteris; the funnel which ends there before the fusion of the leaf-trace with the stele is here found at a lower level, after the leaf-trace has fused with the xylem of the stem. Yet the inner margin of the funnel is situated at a higher level than the insertion of the leaf-trace in the stem xylem. The xylem therefore is not interrupted above the insertion of the leaf-trace. In the upper part of the funnel two protoxylem strands are to be found, the fusion of which takes place at about the same level as the insertion of the leaf-trace into the stem bundle.

Thus the structure of the lower part of the leaf-trace in Cheiropleuria is in many respects intermediate between the structure in Thamnopteris Schlechtendali and Osmundites Dunlopi. This resemblance is most likely caused by a relatively small change from the prototype with a solid stele and mesarch leaf-traces. The differences are due to the different habit, the rhizome not being erect, but horizontal, with relatively long internodes, and of a small size in relation to the leaf-trace. Further the histological facts are quite different in these plants; the chief difference being that in Cheiropleuria the tracheids are intermixed with parenchymatous elements, while the wood in the Osmundaceae consist of tracheids only.

In other points e.g. the venation, the structure of the sori, Cheiropleuria proves to possess a high degree of specialisation. In Platycerium, which has been considered as its nearest ally, there is a highly perforated dictyostele; in some species there is even a complex medullary system.

In a more elaborate form we may expect the phloem to be decurrent into the funnel. The factors, which would cause the meristematic cells to be differentiated as xylem-tissue, having been suppressed, the possibility occurs that this tissue remains parenchymatous or that some elements in it are differentiated as phloem, endodermal cells or sclerenchyma.

There is no form known among the Ferns in which the successive funnels do not unite in the mature stem, neither is there any in which the funnels are continuous, so that the xylem would have the form of a tube without phloem elements in it. But other structures are known, which may be explained as further stages in the series, resulting from the elaboration of the more primitive type.

In most species of the genus Lindsaya, which possesses a creeping rhizome with the leaves arranged im 2 rows on the upper side, the leaf-trace is simple, and its xylem shows in transverse section but little incurving of the margins. The vascular system of the stem consists of a tube of xylem tissue, on the outer side surrounded by the phloem and endodermis; the inner part of the xylem tube is filled up with phloem. Protophloem is only present on the outer side. The ventral portion of the xylem is much better developed than the upper side, in some species it is about 10 times as thick as the upper part. Where the leaf-trace approaches the stem bundle, the endodermis of both fuses, the xylem of the leaf-trace approaches the xylem of the stem, in which an interruption is formed; the ends of the leaf-trace fuse with the margins of this gap and the structure of the internode is regained. The protoxylem of the leaf-trace dies away towards the insertion of the leaf-trace into the vascular system of the stem or a little distance below it. Protophloem is only present on the outer side.

A further step towards a more elaborate structure is present, when other elements than phloem cells are differentiated in the continuous pith, formed by the fusion of the successive funnels. In Lindsaya the endodermis of the leaf-trace fuses with that of the stem bundle but never enters it. In Tapaenidium, however, a closely allied plant, the conditions were present, essential for the differentation of endodermal cells deeper in the vascular tissue of the stem; thus the endodermis is decurrent through the leaf-gap into it, but only for a short distance. In a transverse section just below the insertion of the leaf-trace we find a ring of xylem-elements, lined on the inner and outer surface by phloem and endodermis. In the centre the tissue is similar to that in the cortex and continuous with it through the leaf-gap. At a somewhat lower level the endodermis disappears, and only phloem is present in the centre, the structure then being similar to the Lindsaya-stele. When these endodermal pockets of the successive internodes are continuous, the vascular system consists of a hollow xylem tube lined on the inner and outer side with phloem, limited by an endodermis with interruptions above the insertions of the leaf-traces. This structure is well known as the solenostele.

The interruptions above the insertions of the leaf-trace vary in size, in proportion to the length of the internode; if the internodes are long and the interruptions short, the greater part of the internode is of an annular form in transverse section. There is a crescent bundle for only a short distance. If the gaps are longer, especially when the internodes are short, their length may be equal to or greater than the internode. In this case an interruption is always present in transverse section. The length may even be that of several internodes, so that the tubular bundle of the stem in transverse section appears to be split up in many bundles.

The arrangement of these bundles is dependent on the phyllotaxis and the length of the gaps. If the leaf-gap is so long, that it nearly reaches the leaf next above, the number of bundles seen in transverse section is that of the orthostichies; the gaps are equally distributed and the bundles are all nearly of the same size. If the gaps are shorter, the interruptions will not be present at all levels; in a transverse section they are not regularly arranged and the bundles are not of the same size. When the arrangment of the leaves and in consequence of the gaps is taken into account, it is not difficult to construct a stereometric model from one transverse section or from a very small number of transverse sections.

The symmetry of the different parts of the stele may be very different; sometimes there is a correlation between the mode of growth and the habit of the rootstock. When this is erect and the leaves are radially arranged, the stele too has a radial symmetry. In these rhizomes the internodes are mostly short. If the rhizome is horizontal, there are two possibilities: — either the rhizome may have its leaves radially arranged and thus the structure has its symmetry in accordance there with, or the leaves may be placed in two rows. These rows may be situated laterally and the gaps in the xylem are placed on both sides of the xylem-tube. In many cases however the leaves are arranged in 2 rows on the upper surface. The gaps then also lie on the upper surface and the part of the xylem-tube lying between them on the upper side is smaller than the lower part. When the transverse sections are considered, the two interruptions lie close together; if the successive sections be studied, the smaller strand seems to move across from one margin of the larger strand to the other, When reconstructed, the lower part of the stele consists of a large gutter shaped strand, on the margins of which the leaf-traces are inserted, while the upper part runs obliquely across between these insertions. In the lower part, which consists almost entirely of stem-xylem, the differentiation of the elements may be arrested in some parts, the xylem is not continuous and perforations may be formed in this part of the stele. In one case only, in Hypoderris Brownii, perforations also occur in the upper part of the rhizome.

In Polypodium and other genera the lower part is wholly split up into a number of bundles, forming an irregular network.

The position of the leaf-trace towards the stele in the erect rhizomes is always a regular one, its plane of symmetry passing through the axis of the stem. This is not always the case, however, in the creeping rhizomes. In many of them the leaf-trace faces the apex, the structure thus being symmetrical, but in some forms the leaf-trace faces the medial plane, so that it is obliquely inserted. In these cases the symmetry of the leaf-gap corresponds with that of the leaf-trace. The leaf-trace varies greatly; in its simplest form it consists of a simple strand, the xylem of which is horse-shoe shaped in transverse section, the number of protoxylem strands is one in the lowest part. In more specialised forms the bundle is divided in the upper part; the number of protoxylem strands may be larger; the bundles of the leaf-trace may even remain distinct till their insertion into the xylem of the stem. Then they have their insertion at the sides of the gap, the median bundle, if present, at the bottom of the gap.

A great variation may be found in the arrangement of the elementary bundles in the petiole. From the simplest form of arrangement, that of the horse-shoe, two main types arise: I, where the bundles in the flancs move inwards, so that the transverse section shows a lateral fold, or II, that those situated at the ends of the arc bend inwards, so that in a transverse section the ends of the horse-shoe are much incurved. The relative independence of these parts is shown by the different ways in which the pinna-bundles fuse with the petiolar trace. These different features will not be discussed here; the reader is referred to the litterature.

In the dictyostele the increase of the number of vascular bundles is reached by the larger development of the gaps; the vascular system then having the form of a much perforated cylinder, a network of anastomosing strands around the medullary tissues. The perforated stele in Polypodium and allied forms is also derived from a solenostele or from a dictyostele, which is but little different from it, by formation of accessory gaps. Another way in which a complex structure may come about — the increase of the number of bundles, situated in and round a parenchymatous tissue — is the formation of an internal system. This is formed in three different ways, if the Cyatheaceae are also taken into account. In Dennstaedtia in many species there is a normal solenostele, but in some species the anterior margin of the leaf-gap is thickened; this thickening runs as a ridge on the inner surface of the solenostele to the following gap. Next, this strand of tissue becomes separate, but fuses again with the outer tube at the margin of the gaps. The bundles move further towards the centre, so that the structure may also be described as if a central strand were present, which recieves vascular bundles from the upper margins of the leaf-gaps. In a later stage this central bundle, which originally is solid, becomes hollow above the insertion of the bundle which springs from the upper margin of the leaf-gap; the funnels thus formed in the internal strands are continuous, and in the solenostele a second tubular bundle is formed. Sometimes the same process is repeated in the latter bundle. This structure occurs in the genus Dennstaedtia, in some species of Pteris, e. g. Pteris Kunzeana; and in some of the Dicksonieae and in Thyrsopteris. If the successive transverse sections be studied, the leaf-trace seems to approach the stele. As the leaf-trace approaches, the tissue opposite to the leaf-trace bends inwards, so that, when the margins of the leaf-trace fuse with the tissue of the stele, a certain amount of tissue is included between the leaf-trace and the stele. At a somewhat lower level, part of the stele, opposite to the leaf-trace, becomes free at both sides and moves inwards towards the central system. It seems therefore as if the continuity of the stele was not interrupted at all, but really it is the tissue situated at the upper margin of the leaf-trace which moves inwards. This structure is well shown e. g. in the runners of Thyrsopteris, in the lower parts of which there is only a solenostele. At a slightly higher level a single strand is given off from the upper margin of the leaf-gap, but long before the leaf-trace has fused with it.

Another mode of formation of the inner system is present in Histiopteris incisa Th. var. integrifolia Bedd. (Tansley and Lulham, 1903). Here the elementary bundles of the leaf-trace are so arranged that there are two lateral folds. At a lower level these folds are not reduced as in other Ferns, but are continued into the stem, where some of the bundles become separate and placed in the middle of the stem.

The third mode is found in the Cyatheaceae-Cyatheae. Here the leaf-trace shows in transverse section two large lateral folds, the elementary bundles are quite free, or only a few of them are united. Lower down this arrangement is still present, the bundles which lie in the inner part of the folds do not reach the margins of the gap, but come just before the opening of the gap, and pass through it, their lower part being decurrent into the pith. Here they may anastomose or end blind.

A structure differing in some respects from the other Ferns is present in some species of the genera Vittaria and Anthrophyum. These closely allied genera are characterised by simple leaves, which are oblong, lanceolate to linear, nearly sessile and placed close together on a creeping or erect rhizome. They are epiphyts, and are xerophytic, which in many cases is correlated with reduction. In Anthrophyum semicostatum Blume the leaf-trace is double, the vascular system is a solenostele with well developed leaf-gaps; the outer phloem curves in around the margins of the leaf-gap, but does not extend all over the inner surface of the xylem; an inner endodermis is present. This type of structure also occurs in other species of Anthrophyum.

In A. plantagineum (Cav.) Kaulfuss there is a well marked outer endodermis; the phloem is almost continuous on the outer side of the xylem. The endodermis however does not curve around the margins of the leaf-gap, so that there is no internal endodermis. The hollow xylem-tube is filled up by parenchyma, which is here thus "intrastelar", if we consider the endodermis as being the boundary of the stele. It is not continuous with the cortex as in the other species. In the pith some sieve-elements occur, but the phloem as a whole does not run through the leaf-gap.

In A. reticulatum (Forst.) Kaulfuss nearly the same structure is found; the phloem occurs only at the inner side of the xylem-tube at the margins of the gap and the endodermis is not decurrent through the latter. This structure is not constant however, as has been shown by Gwynne-Vaughan, who found a typical dictyostele but without internal phloem.

The anatomical features of the genus Vittaria are known in V. stipitata and V. elongata. The former has a dorsiventral rhizome, the leaves are placed in two rows on its dorsal surface; the stele is very small, the xylem-ring is only two or three cells thick. The leaf is supplied with two separate traces, one of which runs to each side of the leaf-gap. The ground-tissue is decurrent through the leaf-gaps into the centre of the vascular system of the stem. If we consider the stele itself — as being limited by the endodermis — the leaf-gaps are closed before the one next above has been formed, but the gaps in the xylem remain open long enough to overlap, so that the xylem itself is shaped like a dictyostele, it is therefore called dictyoxylic. At the level of the gap the internal ground-tissue is fairly voluminous, but it rapidly diminishes as it passes down the internode, until only a small strand remains, which lies near the dorsal side on the stele. In some specimens however, D. T. Gwynne-Vaughan found the ground-tissue not to be continuous with that of the lower internode; this resembles the analogous condition in Tapaenidium pinnata, but in the latter the ground-tissue is not replaced by pericyclic parenchyma but by phloem, while the xylem-tissue too is better developed.

In Vittaria elongata the structure seems to be liable to variation. Poirault notes the absence, not only of the inner phloem, but of also the inner endodermis. E. C. Jeffrey notes the occurrence of an inner endodermis in some of his specimens, while Gwynne—Vaughan found a certain amount of internal phloem in the specimens he examined, though it was replaced by parenchyma on the ventral side. The endodermis was sometimes decurrent through the gap, or did not pass in through the leaf-gap at all.

These characteristics, which in many points resemble those in Tapaenidium, fit well in our scheme. The peculiarities however, are best explained as being caused by reduction, which often occurs in plants of a xerophytic habit as Anthrophyum and Vittaria. In agreement with this supposition is the fact, that, while the form of the xylem is alike, the relation between the inner phloem and endodermis varies greatly; this indicates an inconstant value for the factors which influence the differentation of these tissues and are near the "threshold" value. This is hardly to be expected in a progressive process.

The protoxylem strands of the leaf-trace are mostly decurrent for only a short distance into the stem; in the rest of the xylem the first formed elements may have a different position. In many plants [Loxsoma, Dennstaedtia, Microlepia, (D. T. Gwynne—Vaughan 1903, p. 727)] they are situated on the outer side. Sometimes (Dipteris) they are centrally placed in the metaxylem, while in other plants they are situated on the inner surface of the xylem tube. In this case they may sometimes be decurrent from the leaf-traces, but this is not so in the other mode of development. This argues for the independence of the stem xylem and the tissue which is differentiated in relation to that of the leaf-trace.

Only a few points of the ontogeny of the Polypodiaceae need be mentioned here [1]. In the lowest part of the stem the xylem-cylinder is wholly solid. When traced upwards some

---

[1] See Chandler, 1905; Jeffrey, 1903; Leclerc du Sablon, 1890; J. M'Lean Thompson 1920.

parenchyma is formed in the centre of the stem, it often contains some sieve-tubes. This mass of softer tissue appears to be decurrent from the axil of the leaf-trace into the stem. In the following internode a similar pocket is present, those of successive internodes unite and form a continuous rod of softer tissue within the xylem of the stem. Then the endodermis is decurrent into it, and the structure, which was up till now a Lindsaya stele, now becomes a normal solenostele. In many ferns the length of the gaps increases, they overlap, and a dictyostele is formed. In the meantime the petiolar trace, which is always simple in the young plant, increases in size, and often splits up into a number of bundles, thus attaining the structure characteristic for the mature plant.

The transitional region of the haplostele into the definite structure is different in length, the conditions for the length of the gaps and the degree to which the endodermis is decurrent being rather independent of each other. The transition from the solenostele to the dictyostele is independent of the transition of the Lindsaya stele to the amphiphloic tubostele; in most Ferns the Lindsaya stele first becomes a solenostele, then a dictyostele, but in Blechnum Spicant the gaps in the „Lindsaya" stadium overlap, so that a typical dictyostele as regards to the shape of the xylem is formed, the interior of which is filled up with phloem. The various details on this subject are to be found in the literature, which is given in the following list. Besides this, the same conclusions may be drawn from the study of ontogeny in the Cyatheaceae.

If we recapitulate the stelar morphological characteristics of the Polypodiaceae, which are also present in the Cyatheaceae, it must be noted, that here, as in the former groups, a stem-xylem and a leaf-trace xylem is distinguishable; that the leaf-trace is composed of elementary bundles in which metaxylem situated adaxially to the protoxylem strands is reduced. In Cheiropleuria this reduction does not reach the stem xylem, but the lower end of the funnel is at a lower level than the insertion of the leaf-trace into the stem-xylem.

The other structures may be explained by the assumption that the funnels of the successive leaf-traces are decurrent into the stem and unite, so reducing the stem xylem in the centre, forming a hollow tube. The different structural types are brought about by the relative size of the gaps to the length of the internodes, and by the structure and symmetry of the leaf-trace. It is important to note that in none of the Polypodiaceae pith is formed by reduction of the central tissue alone, as is the case in the Osmundaceae and the Gleicheniaceae.

In no Fern of this group is there a separate lower part of the funnel, separated from the tissue of the pith by a flange of tracheids, neither could this structure be distinguished in the young plant. It is therefore very probable, that the affinity of the Gleicheniaceae or the Osmundaceae with the Polypodiaceae and the Cyatheaceae is a very remote one.

In the following list the data concerning the anatomy of the Polypodiaceae are collected for so far as I could find them. The nomenclature is that of C. Christensen's Index Filicum; the name under which the structure has been described is placed after the name of the author. Only the principal characteristics have been mentioned; for further details the reader is referred to the literature cited.

I. WOODSIEAE.

1. WOODSIINAE.

1. **Diacalpe** Blume.
   D. aspidioides Blume.
   R. C. Davie, 1912, p. 257: rhizome erect, with short internodes, with an advanced dictyostele; leaf-trace double.
2. **Peranema** Don.
   P. cyatheoides Don.
   R. C. Davie, 1912, p. 257: rhizome erect, with short internodes, with an advanced radial dictyostele; leaf-trace double.
3. **Woodsia** R. Brown.
   W. ilvensis (L) R. Brown.
   O. Schlumberger, 1911, p. 409, fig. 14/1: rhizome short, erect, with a radial dictyostele; leaf-trace double, inserted near the lowest part of the leaf-gap, simple in the young plant.

   W. obtusa (Spr.) Torrey.
   O. Schlumberger, 1911, p. 409, fig. 14/2: rhizome short, erect, with a radial dictyostele; leaf-trace double.

   W. polystichioides Eaton.
   F. O. Bower, 1912, p. 309; rhizome erect, with short internodes, with a dictyostele; leaf-trace double.
4. **Hypoderris** R. Brown.
   H. Brownii J. Smith.
   O. Schlumberger, 1911, p. 409, fig. 14/5: rhizome creeping with distinct internodes, with a dorsiventral dictyostele, the upper and lower part of which both with perforations; leaf-trace bundles four in number.
   F. O. Bower, 1912, p. 309: dictyostele, the leaf-trace with 4 bundles.

5. **Cystopteris** Bernhardi.
C. fragilis (L.) Bernhardi.
P. Lachmann, 1889, p. 59, pl. II, fig. 25, 26 (the latter as Cystopteris alpina): rhizome short, erect, with a radial dictyostele; leaf-trace double.
D. T. Gwynne—Vaughan, 1905, p. 215, fig. 44: a radial dictyostele with epidermal pockets reaching into the pith; 2—3 of them visible in one and the same transverse section.
O. Schlumberger, 1911, p. 410, fig. 14/4; rhizome with dictyostele; leaf-trace simple in the young plant.

6. **Acrophorus** Presl.
A. stipellatus (Wall.) Moore.
F. O. Bower, 1918, p. 56 (Acrophorus nodosus): rhizome with a radial dictyostele: leaf-trace bundles numerous.

2. ONOCLEINEAE.

7. **Matteuccia** Todaro.
M. intermedia C. Christensen.
F. O. Bower. 1914, p. 367, fig. 2: rhizome with a radial dictyostele, with a relatively large pith; leaf-trace double.

M. orientalis (Hook.) Trev.
F. O. Bower. 1912, p. 300 (Struthiopteris orientalis): rhizome with a radial dictyostele; leaf-trace double.
Y. Ogura, 1921, p. 131: idem.

M. struthiopteris (L.) Todaro.
K. G. Stenzel, 1861, p. 21, pl. 2, fig. 2, 3 (Struthiopteris germanica): rhizome erect, with a radial dictyostele; leaf-trace double.
P. Terletzki, 1884, p. 453 (Struthiopteris germanica): gives histological details.
D. H. Campbell, 1887, p. 41 (Onoclea struthiopteris): rhizome with a radial dictyostele; leaf-trace double.
R. Kühn, 1889, p. 497 (Struthiopteris germanica): a radial dictyostele with a double leaf-trace, inserted into the lower part of the gap.
D. T. Gwynne—Vaughan, 1905, p. 213, fig. 41—42 (Onoclea germanica): rhizome erect, with short inter-

nodes, with a radial dictyostele and epidermal pockets reaching into the pith; till 6 of these pockets are seen in one and the same transverse section; these pockets are not present in the stolons.
H. Lüthje, 1914, p. 22, pl. 1—6 (Struthiopteris germanica): rhizome with a radial dictyostele with a double leaf-trace.

8. **Onoclea** Linnaeus.

O. sensibilis Linn.
P. Lachmann, 1889, p. 44, pl. II. fig. 2: rhizome creeping, with a radial dictyostele; leaf-trace double.
D. T. Gwynne—Vaughan, 1905, p. 215: rhizome erect, with short internodes, with a radial dictyostele; epidermal pockets are intruding into the pith, only one is seen in one and the same transverse section.
Y. Ogura, 1921, p. 121: rhizome with a dictyostele.

II. ASPIDIEAE.

1. ASPIDIINAE.

9. **Dryopteris** Adanson.

§ 1. Eudryopteris.

D. cristata (L.) Gray.
K. G. Stenzel, 1861, p. 6, pl. 2, fig. 6—8 (Aspidium cristatum): rhizome with short internodes with a radial dictyostele; leaf-trace bundles 3—5 in number.
P. Lachman, 1889, p. 71 (Aspidium cristatum): structure as in Dryopteris Filix mas.

D. decomposita (R. Brown) O. Kuntze.
A. Trécul, 1869*a*, p. 239; A. Trécul, 1869*b*, p. 366 (Aspidium quinquangulare): rhizome creeping, with a dictyostele.

D. decursive-pinnata (van Hall) O. Kuntze.
A. Trécul, 1885*a*, p. 917, (Aspidium decursive-pinnatum): rhizome short, no spiral or annular tracheids are present in the stem.

Y. Ogura, 1921, p. 118: rhizome with short internodes, with a radial dictyostele; leaf-trace double.

D. filix Mas (L.) Schott.
G. Ogilvie, 1859, fig. 11, 12 (Lastrea Filix Mas): rhizome with a dictyostele.
K. G. Stenzel, 1861, p. 25, pl. 4, fig. 5—12 (Aspidium Filix-Mas): rhizome with short internodes, mostly inclined, with a radial dictyostele; leaf-trace double in the lower parts or with numerous bundles.
A. de Bary, 1877, p. 296, fig. 132, 133 (Aspidium Filix Mas): a radial dictyostele with numerous leaf-trace bundles.
P. Lachmann, 1889, p. 64, fig. 2, p. 68, pl. II fig. 2—6 (Aspidium Filix Mas): a radial dictyostele, leaf-trace bundles numerous.

D. gracilescens (Blume) O. Kuntze, (var. abbreviatum).
Y. Ogura, 1921, p. 120: rhizome with a radial dictyostele; leaf-trace double.

D. hirtipes (Blume) O. Kuntze.
S. E. Chandler, 1905, p. 393 (Nephrodium hirtipes): rhizome short, with dictyostele.

D. japonica (Baker) C. Christensen.
Y. Ogura, 1921, p. 120: rhizome creeping, with a radial dictyostele; leaf-trace double.

D. Oreopterus (Ehrh.) Maxon.
K. C. Stenzel, 1861, p. 15 (Aspidium oreopteris): rhizome strong, erect, with a radial dictyostele.

D. orientalis (Gmel.) C. Christ., see Arthropteris orientalis.

D. setigera (Bl.) O. Kuntze.
Y. Ogura, 1921, p, 121: rhizome inclined, with a radial dictyostele; leaf-trace double.

D. spinulosa (Müll.) O. Kuntze.
K. C. Stenzel, 1861, p. 6, pl. 4, fig. 1, 2 (Aspidium spinulosum): rhizome short, inclined, with a radial dictyostele; leaf-trace with 3—5 bundles; lateral branches with a haplostele below, then solenostelic, at last with a dictyostele.
P. Lachmann, 1889, p. 64, 71 (Aspidium spinulosum): rhizome with a radial dictyostele.

S. E. Chandler, 1905, p. 369 (Nephrodium spinulosum): stem with a dictyostele.

D. thelypteris (L.) A. Gray.
K. G. Stenzel, 1861, p. 36, pl. 5, fig. 18 (Aspidium thelypteris): rhizome creeping, thin, with long internodes; a radial dictyostele with long, narrow gaps; leaf-trace double.
A. de Bary, 1877, p. 296 (Aspidium thelypteris): rhizome with a radial dictyostele.
A. Trécul, 1885a, p. 918 (Aspidium thelypteris): rhizome with a dictyostele.

§ 2. Phegopteris.

D. Linneana C. Christensen.
K. G. Stenzel, 1861, p. 36 (Polypodium Dryopteris): rhizome thin, creeping, with long internodes; with a radial dictyostele; gaps long and narrow, leaf-trace double.

D. phegopteris (Linn.) C. Christensen.
K. G. Stenzel, 1861, p. 36 (Polypodium phegopteris): rhizome creeping, thin, with long internodes; with a radial dictyostele; gaps long and narrow; leaf-trace double.

D. Robertiana (Hoffm.) C. Christensen.
P. Lachmann, 1889, p. 51 (Phegopteris calcarea); rhizome creeping, thin, with long internodes; a radial dictyostele with long and narrow gaps; leaf-trace double.

§ 3. Leptogramme.

D. africana (Desv.) C. Christensen.
Y. Ogura, 1921, p. 119: rhizome creeping, with a radial dictyostele; leaf-trace double.

§ 4. Cyclosorus.

D. gongylodes (Schkuhr) O. Kuntze.
P. Lachmann, 1889, p. 48 (Aspidium Serra): rhizome creeping, with distinct internodes, with a radial dictyostele; leaf-trace double.

D. sophoroides (Thunb.) O. Kuntze.
Y. Ogura, 1921, p. 120: rhizome creeping, with very long internodes with a radial dictyostele; leaf-trace double.

§ 7. Meniscium.

D. triphylla (Sw.) C. Christensen.
P. Lachmann, 1889, p. 52, pl. II, fig. 11 (Phegopteris triphylla): rhizome creeping with a radial dictyosstele; leaf-trace double.

13. **Didymochlaena** Desvaux.
D. truncatula (Sw.) J. Smith.
A. Trécul, 1885a, p. 917 (Didymochlaena sinuosa): no annular or spiral tracheids are present in the stem.
P. Lachmann, 1889, p. 75, pl. III, fig. 7, 8: stem with a radial dictyostele, leaf-trace bundles about 4 in number.

16. **Neocheiropteris** Christ.
N. palmatopedata (Baker) Christ.
F. O. Bower, 1913, p. 473, fig. B. rhizome creeping, with a perforated solenostele; leaf-trace bundles numerous.

17. **Polystichum** Roth.
P. aculeatum (L.) Schott.
P. Lachmann, 1889, p. 63 (Aspidium aculeatum): rhizome strong, erect, with a radial dictyostele.
Y. Ogura, 1921, p. 119, (var. japonicum): rhizome with dictyostele; leaf-trace composed of three bundles.

P. adiantiforme (Forst). J. Smith.
G. G. Mettenius, 1864, p. 547, pl. VIII, fig. IX (Aspidium coriaceum): rhizome wide-creeping, with a dorsiventral dictyostele; leaf-trace bundles numerous.
A. de Bary, 1877, p. 298, fig. 135, cites Mettenius.
A. Trécul, 1885a, p. 917 (Aspidium coriaceum): rhizome with a dorsiventral dictyostele; leaf-gaps 2—3 internodes long.
P. Lachmann, 1889, p. 33 (Aspidium coriaceum): rhizome with a dorsiventral dictyostele.

P. aristatum (Forst.) Presl.
Rhizome creeping, with a dictyostele; leaf-trace bundles numerous.

P. foeniculaceum (Hook.) J. Smith.
P. Lachmann, 1889, p. 57 (Aspidium foeniculaceum): rhizome short, thick, inclined, with a dorsiventral dictyostele.

P. lepidocaulon (Hook.) J. Smith.
Y. Ogura 1921, p. 119: rhizome creeping, with a radial dictyostele; leaf-trace bundles three in number.

P. lobatum (Huds.) Presl.
S. E. Chandler, 1905, p. 376, fig. 152—164 (Aspidium Tsus-Shimense): rhizome with dictyostele; leaf-trace double in the young stem.

P. lonchitis (L.) Roth.
P. Lachmann, 1889, p. 59 (Aspidium lonchitis): rhizome strong, erect, with a radial dictyostele; leaf-trace bundles two or more.

P. Standishii (Moore) C. Christensen.
Y. Ogura, 1921, p. 122; rhizome erect, with a radial dictyostele and a double leaf-trace.

P. varium (Linn.) Presl.
Y. Ogura, 1921, p. 122: rhizome erect, with a radial dictyostele; leaf-trace double.

17a. **Cyrtomium** Presl.

C. falcatum Presl.
P. Lachmann, 1889, p. 65, pl. II, fig. 29, 30: rhizome erect, with a radial dictyostele and a double leaf-trace.
S. E. Chandler, 1905, p. 647 (Aspidium falcatum): rhizome with a dictyostele.
Y. Ogura, 1921, p. 121 (var. Fortunei): rhizome oblique, with the leaves spirally arranged; with a dictyostele; leaf-trace bundles three in number.

21. **Polybotrya** H. B. Willdenow.

§ 5. Olfersia..

P. cervina (L.) Kaulfuss.
P. Lachmann, 1889. p. 42, pl. I. fig. 27, 28 (Olfersia cervina): rhizome thick, creeping, with the leaves spirally arranged; a radial dictyostele; leaf-trace bundles numerous, anastomosing in their lower part.

§ 6. Soromanes.

P. serratifolia (Fée) Klotzsch.
H. Karsten, 1847, p. 196: rhizome with a radial solenostele; leaf-trace simple or divided.

22. **Stenosemia** Presl.

S. aurita (Sw.) Presl.

E. Schumann, 1915, p. 228: rhizome short, erect, with a dictyostele; leaf-trace bundles 5 in number.

23. **Leptochilus** Kaulfuss.

§ 1. **Euleptochilus.**

L. axillaris (Cav.) Kaulfuss.

G. G. Mettenius, 1864, p. 554, pl. IX, fig. III (Acrostichum axillare): rhizome scandent with long internodes, with a dorsiventral dictyostele, the lower part of which with profuse perforations; leaf-trace double.

L. tricuspis (Hook.) C. Christensen.

F. O. Bower, 1917, p. 4, fig. 1.: rhizome creeping, dorsiventral; solenostele with profuse perforations; leaf-trace bundles numerous.

L. zeylanicus (Houtt.) C. Christensen.

E. N. Thomas, 1905, p. 185 (Acrostichum quercifolium): rhizome creeping, with a dictyostele with leaf-gaps little longer than one internode; leaf-trace double.

E. Schumann, 1915, p. 226: dictyostele with long leaf-gaps.

§ 2. **Anapausia.**

L. alienus (Sw.) C. Christensen.

F. O. Bower, 1917, p. 30: rhizome short, creeping, structure as in L. nicotianifolius.

L. decurrens Blume.

E. Schumann, 1915, p. 225: rhizome creeping with leaves in 2 rows, with a dorsiventral dictyostele; leaf-trace bundles numerous.

L. nicotianifolius (Sw.) C. Christensen.

F. O. Bower, 1917, p. 19, fig. 19: rhizome creeping with a dorsiventral dictyostele; leaf-gaps not reaching two internodes in length; the lower part of the stele as a large gutter-shaped strand; leaf-trace bundles numerous.

§ 3. Bolbitis.

L. cuspidatus (Presl) C. Christensen.
E. Schumann, 1915, p. 224: rhizome creeping, with a dorsiventral dictyostele; leaf-trace bundles about 7 in number.
F. O. Bower, 1917, p. 22, fig. 10; rhizome with a dorsiventral dictyostele with leaf-gaps about 2 internodes long; the lower part as a gutter shaped strand with profuse perforations; leaf-trace bundles numerous.

L. guianensis (Aublet) C. Christensen.
E. Schumann, 1915, p. 225: rhizome creeping, with the leaves placed in 2 rows; with a dorsiventral dictyostele; leaf-trace bundles numerous.

L. heteroclitus (Presl) C. Christensen.
E. Schumann, 1915, p. 222; F. O. Bower, 1917, p. 22; structure as in L. nicotianifolius.

2. DIPTERIDINAE.

24. Dipteris Reinwardt.

D. conjugata Reinwardt.
A. C. Seward and S. Dale, 1901, p. 402, pl. 47, 49: rhizome creeping, with distinct internodes; solenostele with a simple leaf-trace.
H. de Bruyn, 1911, p. 761, fig. 1, 13, 14: In the young plant at first a Lindsaya-stele (the ventral part of the xylem being much thicker), in younger parts a solenostele with a medullary system is found. Leaf-trace simple.

D. Lobbiana (Hook.) Moore.
H. de Bruyn, 1911, p. 768, fig. 4, 7, 15, 16, 17: In the young plant successively a protostele, a Lindsaya-stele, and a solenostele with a double leaf-trace is found.
F. O. Bower, 1915, p. 504, fig. 6: rhizome with a solenostele; leaf-trace double below, very soon divided into four strands.

D. Wallichii (R. Brown) Moore.
G. Mettenius, 1864, p. 546, pl. VII, fig. IV (Polypodium Wallichii): rhizome creeping, with distinct internodes; solenostele with a double leaf-trace.

IV. DAVALLIEAE.

26. **Arthropteris** J. Smith.

A. altescandens (Colla) J. Smith.
G. Mettenius, 1864, p. 548 (Polypodium altescandens): structure as in Arthropteris orientalis.

A. obliterata (R. Brown) J. Smith.
G. Mettenius, 1864. p. 546 (Nephrolepis ramosa): structure as in Arthropteris orientalis.

A. orientalis (Gmel.) nov. comb.
G. Mettenius, 1864, p. 546, pl. VII, fig. III (Aspidium albopunctatum): rhizome epiphytic, far-creeping, with the leaves arranged in 2 rows; a dorsiventral dictyostele with a double leaf-trace.
P. Lachmann, 1889, p. 33 (Aspidium albo-punctatum): stem with a dorsiventral dictyostele.

A. tenella (Forst.) J. Smith.
G. Mettenius, 1864, p. 546 (Polypodium tenellum): structure as in Arthropteris orientalis.

27. **Nephrolepis.** Schott.

§ 1. Lindsayoideae.

N. acutifolia (Desv.) C. Christensen.
F. O. Bower, 1918, p. 14: rhizome with a dictyostele with leaf-gaps right and left; leaf-trace much divided.

§ 2. Aspidioideae.

N. cordifolia (Linn.) Brown.
S. E. Chandler, 1905, p. 369: rhizome short, with a dictyostele.

28. **Humata** Cavanilles.

H. heterophylla (Smith) Desvaux.
G. Mettenius, 1864, p. 547, pl. VIII, fig. II (Davallia heterophylla): rhizome long-creeping, with a dorsiventral dictyostele; leaf-trace bundles numerous, anastomosing below.

H. repens (Linn. fils) Diels.
A. de Bary, 1877, p. 298 (Davallia pedata): rhizome creeping, with a dorsiventral dictyostele; leaf-trace much divided.

29. Saccoloma Kaulfuss.

§ 1. Eusaccoloma.

S. elegans Kaulfuss.
F. O. Bower, 1918, p. 18, fig. 16, 17: stem with a solenostele, which possesses an internal system, comparable to Pteris Kunzeana.

§ 2. Parasaccoloma.

S. domingense (Sprengel) Prantl.
H. Karsten, 1847, p. 194, pl. IX, fig. 5, 6 (Dicksonia Lindeni): rhizome creeping, with a radial solenostele which possesses an internal strand, which is solid below, tubular at a higher level; leaf-trace simple.
G. Mettenius, 1864, p. 531, pl. VI, fig. 1—11 (Saccoloma adiantoides): solenostele with a tubular internal strand, often containing an internal strand also.
F. O. Bower, 1913, p. 457: A reparatory strand is given off from the upper margin of the leaf-gap and goes inwards; it fuses with the inner tubular cylinder with a gap above its insertion; from the upper margin of this gap a bundle is going to the innermost strand in the same way.

S. inaequale (Kunze) Mettenius.
G. Mettenius, 1864, p. 535: rhizome creeping; structure as in Saccoloma domingense; usually only one internal strand is present.

31. Leptolepia Mettenius.

L. Novae-Zelandiae (Col.) Kuhn.
A. Trécul, 1885a, p. 918 (Davallia Novae-Zelandiae): solenostele.
P. Lachmann, 1889, p. 30 (Microlepia Novae-Zelandiae): rhizome with a solenostele.
D. T. Gwynne-Vaughan. 1903, p. 691 (Microlepia Novae-Zelandiae): rhizome creeping, with leaves in 2 rows; a dorsiventral solenostele with a simple leaf-trace.

32. Davallia Smith.

§ 1. Prosaptia.

D. alata Blume.
D. T. Gwynne-Vaughan, 1903, p. 735 (Davallia

Emersoni): rhizome erect, with short internodes, with a radial dictyostele.

D. contigua (Forst.) Sprengel.
D. T. Gwynne-Vaughan, 1903, p. 731: rhizome erect, with short internodes, with a radial dictyostele.

§ 2. Scyphularia.

D. pentaphylla Blume.
A. Trécul, 1885a, p. 1457; rhizome creeping, with long internodes, with a dictyostele.

§ 3. Eudavallia.

D. bullata Wallich.
G. Mettenius, 1864, p. 548, pl. VIII. fig. III: rhizome creeping with the leaves placed in 2 rows; a dorsiventral dictyostele with a double leaf-trace.

D. canariensis (L.) Smith.
G. Mettenius, 1864, p. 549: rhizome creeping, the leaves placed in 2 rows; a dorsiventral dictyostele with a divided leaf-trace.
A. Trécul, 1885b, p. 1456: stem with a dictyostele.
P. Lachmann, 1889, p. 33, pl. I. fig. 18, 19: stem with a dictyostele; leaf-trace bundles numerous.

D. dissecta J. Smith.
G. Mettenius, 1864, p. 148, pl. VIII, fig. V: rhizome creeping, the leaves arranged in 2 rows; a dorsiventral dictyostele, leaf-trace double with some smaller anastomosing strands.

D. divaricata Blume.
G. Mettenius, 1864, p. 549, pl. VIII, fig. VII: rhizome creeping, the leaves arranged in 2 rows, with a dorsiventral dictyostele; leaf-trace bundles numerous.

D. Mariesi Moore.
P. Lachmann, 1889, p. 33, pl. I. fig. 20, 31: stem with a dictyostele.

D. pallida Mettenius.
P. Lachmann, 1886a, p. 1-3; 1889, p. 39, pl. I. fig. 22—24 (Davallia Mooreana): rhizome creeping, with a dorsiventral dictyostele.

D. pyxidata Cavanilles.
G. Mettenius, 1864, p. 549: rhizome creeping, structure as in Davallia dissecta.

§ 4. Leucostegia.

D. immersa Wallich.
A. Trécul, 1885a, p. 918, 1885b, p. 1456: rhizome creeping, with a solenostele; leaf-trace simple.
P. Lachmann, 1889, p. 30 (Leucostegia immersa): rhizome with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 715; rhizome with a solenostele and cortical strands (leaf-traces passing through the cortex?).

D. parvula Wallich.
A. de Bary, 1877, p. 298: rhizome creeping, with a dorsiventral dictyostele; leaf-trace divided.

D. pulchra Don.
G. Mettenius, 1864, p. 5, pl. VIII, fig. VI (Davallia chaerophylla): rhizome creeping, with a dorsiventral dictyostele; leaf-trace divided; the upper boundary of the leaf-gap indistinct.

incertae sedis.

D. stenocarpa Klotzsch (Hort.)
G. Mettenius, 1864, p. 549, pl. VIII, fig. IV: rhizome creeping with a dorsiventral dictyostele; leaf-trace bundles numerous.

? D. stricta.
E. C. Jeffrey, 1903, p. 133: solenostele without internal phloem and endodermis.

33. Microlepia Presl.

M. marginata (Houtt.) C. Christensen.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia marginalis): rhizome creeping, with a dorsiventral solenostele; leaf trace simple, facing the medial plane.
Y. Ogura, 1921, p. 117: the same result.

M. hirta (Kaulf.) Presl.
P. Lachmann, 1889, p. 30, pl. I. fig. 11: stem with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia hirta): rhizome creeping, the leaves arranged in 2 rows; a dorsiventral solenostele with a simple leaf-trace.

M. pilosella (Hook.) Moore.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia hirsuta): rhizome creeping, with a dorsiventral solenostele; leaf-trace simple, facing the medial plane.
Y. Ogura, 1921, p. 117; the same result.

M. platyphylla (Don) J. Smith.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia platyphylla Don): rhizome creeping, with a dorsiventral solenostele; leaf-trace simple.

M. speluncae (Linn.) Moore.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia Speluncae): rhizome creeping, the leaves in 2 rows; a dorsiventral solenostele with a simple leaf-trace.

M. strigosa (Thunbg) Presl.
A. Trécul, 1885a, p. 918, 1885b, p. 1456 (Davallia strigosa): rhizome creeping, with a dorsiventral solenostele with a simple leaf-trace; no protoxylem in the stem.
D. T. Gwynne-Vaughan, 1903, p. 691 (Davallia strigosa): rhizome creeping, with a dorsiventral solenostele with a simple leaf-trace.

M. trichosticha J. Smith.
A. Trécul, 1885a, p. 918, 1885 p. 1456 (Davallia trichosticha): rhizome creeping with distinct internodes; with a dorsiventral solenostele; leaf-trace simple; no protoxylem in the stem.

M. Wilfordii Moore.
Y. Ogura, 1921, p. 117: structure as in M. pilosella.

Solenostelopteris japonica Kershaw.
E. M. Kershaw, 1910, p. 684, pl. 48: a fossil fern-rhizome with a solenostele, much resembling that in the genus Microlepia, especially M. hirta.
Cretaceous, Japonia.

34. Odontosoria (Presl) Fée emend.

§ 1. Euodontosoria.

O. chinensis (Linn.) J. Smith.
D. T. Gwynne-Vaughan, 1904, p. 716, fig. 35 (Davallia tenuifolia): rhizome creeping, with short internodes with a Lindsaya stele.

O. clavata (Linn.) J. Smith.
D. T. Gwynne-Vaughan, 1903, p. 716 (Davallia clavata): rhizome strong, creeping, with a Lindsaya stele. F. O. Bower, 1908, p. 13 (Lindsaya clavata): stem with a Lindsaya-stele.

O. retusa (Cavan.) J. Smith.
A. G. Tansley and R. G. Lulham, 1905, p. 158: rhizome with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 691 (Lindsaya retusa): rhizome creeping, with leaves in 2 rows; with a dorsiventral solenostele; leaf-trace simple.

§ 2. Stenoloma.

O. aculeata (Linn.) J. Smith.
D. T. Gwynne-Vaughan, 1903, p. 712, fig. 19—20 (Davallia aculeata): rhizome creeping, with solenostele; the ventral part of the xylem twice as thick as the dorsal part; no internal protophloem; leaf-gaps very small, leaf-trace simple.

O. fumarioides (Sw.) J. Smith.
D. T. Gwynne-Vaughan, 1916, p. 500 (Davallia fumarioides): rhizome creeping, with a solenostele; leaf-trace simple, facing the medial plane.

35. **Tapeinidium** (Presl.) C. Christensen.
T. pinnatum (Cavan.) C. Christensen.
D. T. Gwynne-Vaughan, 1903, p. 713, fig. 21, 23 (Davallia pinnata): rhizome creeping, with the leaves arranged on the upper surface in 2 rows; the xylem of the vascular bundle has the shape of that of a solenostele; the sclerotic tissue of the cortex is decurrent for some distance through the small leaf-gaps, but ends blind, as the endodermis; in the lowest part of the internode inner phloem is present only; leaf-trace simple.
F. O. Bower, 1923b. p. 74, fig. 68, II, IV: the same result.

36. **Dennstaedtia** Bernhardi.
D. adiantioides (H. B. Willd.) Moore.
A. Trécul, 1885a, p. 918 (Dicksonia adiantioides) rhizome creeping, with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 691, fig. 2, 28, 29,

(Dicksonia apiifolia): stem with a dorsiventral solenostele; leaf-trace obliquely inserted.

D. consanguinea (Kl.) Moore.
H. W. Reichardt, 1859, p. 40, pl. II, fig. 37-41: rhizome creeping, with a solenostele.

D. cornuta (Kaulfuss) Mettenius.
G. Mettenius, 1864, p. 543: structure as in D. rubiginosa, but with a tubular internal system.

D. davallioides (R. Brown) Moore.
A. Trécul, 1885a, p. 918 (Dicksonia nitidula): rhizome creeping, with a solenostele; protoxylem strands of the leaf-trace not continued into the stem.
D. T. Gwynne-Vaughan, 1903, p. 691 (Dicksonia davallioides): stem with a dorsiventral solenostele; leaf-trace simple.

D. ordinata (Kaulf.) Moore.
D. T. Gwynne-Vaughan, 1903, p. 691 (Dicksonia cicutaria): rhizome creeping, the leaves in 2 rows; a dorsiventral solenostele with a simple leaf-trace.

D. punctilobula (Mich.) Moore.
D. E. Eaton, 1879, p. 341: rhizome creeping, with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 691, fig. 11 (Dicksonia punctilobula): rhizome with a dorsiventral solenostele; leaf-trace simple, obliquely inserted.
E. S. Conard, 1908, p. 16 fig. 63—89: a dorsiventral solenostele with a simple leaf-trace.

D. rubiginosa (Kaulf) Moore.
H. Karsten, 1847, p. 193 (Dicksonia rubiginosa): rhizome creeping, the leaves placed in 2 rows; a solenostele with an internal tubular system, connected by a little strand with the outer tube; leaf-trace simple.
D. T. Gwynne-Vaughan, 1903, p. 700, fig. 13 (Dicksonia rubiginosa): rhizome with a dorsiventral solenostele with some perforations, with internal vascular strands, which fuse with the outer tube at the free margins of the leaf-gap.

D. rufescens Moore.
G. Mettenius, 1864, p. 540, pl. VII, fig. I: rhizome creeping, stele with internal strands.

D. scabra (Wall.) Moore.
D. T. Gwynne-Vaughan, 1903, p. 691 (Dicksonia scabra): rhizome creeping, with a dorsiventral solenostele; leaf-trace simple.
Allied genera are:

Loxsoma R. Brown.
L. Cunninghami R. Brown.
D. T. Gwynne-Vaughan, 1901, p. 71—98, pl. III: rhizome creeping, with a typical solenostele; leaf-trace simple, facing the apex.
K. Goebel, 1912, p. 44: quotes Gwynne-Vaughan.

Loxsomopsis Christ.
L. notabilis Slosson.
F. O. Bower, 1923a, p. 350: a typical solenostele with a simple leaf-trace.

37. **Monachosorum** Kunze.
M. subdigitatum (Blume) Kuhn.
G. Mettenius, 1864, p. 540, pl. VII, fig. 1: rhizome creeping, with a solenostele; an internal strand is present, fusing with the margins of the leaf-gap.
H. Christ, 1897, p. 76: rhizome thin, creeping, with a solenostele.
F. O. Bower, 1918, p. 57, fig. 42: rhizome with short internodes, with a radial dictyostele; leaf-gaps about 2 internodes long; leaf-trace double.

38. **Lindsaya** Dryander.

§ 1. Eulindsaya.

L. cultrata (Willd.) Swartz.
D. T. Gwynne-Vaughan, 1903, p. 717: rhizome short, creeping, with a small, thin solenostele; leaf-trace consisting of 2 separate strands.
F. O. Bower 1918, p. 13: rhizome with a Lindsaya-stele; the determination of the material of Gwynne-Vaughan is incorrect.

L. guianensis (Aublet) Dryander.
A. G. Tansley and R. B. Lulham, 1902, p. 156: rhizome creeping, with a Lindsaya-stele.

L. lancea (Linn.) Beddome.
A. G. Tansley and R. B. Lulham, 1902, p. 156:

rhizome creeping, with a Lindsaya-stele; F. O. Bower, 1918: the same result.

L. linearis Swartz.
F. O. Bower, 1918, p. 131: rhizome creeping, with a Lindsaya-stele.

L. orbiculatea (Lam.) Mettenius.
A. G. Tansley and R. B. Lulham, 1902, p. 156: rhizome creeping, with a Lindsaya-stele.

L. reniformis Dryander.
F. O. Bower, 1923b, p. 74, fig. 68 IV: rhizome creeping, with a Lindsaya-stele.

L. rigida J. Smith.
A. G. Tansley and R. B. Lulham, 1902, p. 156: rhizome creeping, with a Lindsaya-stele.

L. scandens Hooker.
A. G. Tansley and R. B. Lulham, 1902, p. 156: rhizome creeping, with a Lindsaya-stele.

§ 2. Hymenotomia.

L. cuneata (Forst.) C. Christensen.
F. O. Bower, 1918, p. 13: rhizome creeping, with a Lindsaya-stele.

L. microphylla Swartz.
F. O. Bower, 1918, p. 13: rhizome creeping, with a Lindsaya-stele.

§ 3. Odontoloma.

L. Blumeana (Hook.) Kuhn.
P. Lachmann, 1889, p. 29, pl. I, fig. 9, 10 (Odontoloma tenuifolium): rhizome creeping, with distinct internodes; structure as in L. repens.

L. hymenophylloides Blume.
D. T. Gwynne-Vaughan, 1903, p. 716 (Davallia hymenophylloides) rhizome creeping, with a Lindsaya-stele.

L. Parkeri (Hook.) Kuhn.
D. T. Gwynne-Vaughan, 1903, p. 716 (Davallia Parkeri): rhizome slender, with a Lindsaya-stele.

L. repens (Bory) Beddome.
A. Trécul, 1885b, p. 1456 (Davallia repens): see D. T. Gwynne-Vaughan, 1903, p. 715.

D. T. Gwynne-Vaughan, 1903, p. 715: rhizome scandent, the leaves placed in 2 rows; with a Lindsaya-stele. F. O. Bower, 1918, p. 14: structure as has been described by Gwynne-Vaughan in L. cultrata: a solenostele with a double leaf-trace.

§ 4. Synaphlebium.

L. davallioides Blume.

A. G. Tansley and R. B. Lulham, 1902, p. 156: rhizome creeping, with a Lindsaya-stele.

L. decomposita Willdenow.

A. G. Transley and R. B. Lulham, 1902, p. 156 (Lindsaya lobata) rhizome creeping, with a Lindsaya-stele.

V. ASPLENIEAE.

1. ASPLENIINAE.

41. **Athyrium** Roth.

A. alpestre (Hoppe) Rylands.

P. Lachmann, 1889, p. 54; structrure as in A. Filix Femina.

A. filix femina (Linn.) Roth.

A. Trécul, 1885a, p. 917: rhizome strong, erect; no spiral or annular tracheids are found in the stem. P. Lachmann, 1889, p. 53, pl. II, fig. 12—16; stem with a radial dictyostele with a simple leaf-trace.

A. yokoscense (Fr. et Sav.) Christ.

Y. Ogura, 1921, p. 118: rhizome oblique with short internodes with a radial dictyostele; leaf-trace simple, but soon divided in the cortex.

A. niponicum (Mettenius) Hance.

Y. Ogura 1921, p. 118, fig. 1: rhizome creeping, with rather short internodes, with a radial dictyostele; leaf-trace simple.

42. **Diplazium** Swartz.

§ 1. Eudiplazium.

D. celtidifolium Kunze.

P. Lachmann, 1889, p. 775, pl. III, fig. 11—13: stem with a radial dictyostele; leaf-trace double.

D. japonicum (Thunberg) Beddome.
Y. Ogura, 1921: p. 120: rhizome creeping, with a radial dictyostele; leaf-trace double.
Y. Ogura, 1921, p. 121 (Diplazium Conelli): idem.

D. striatum (Linn.) Presl.
P. Lachmann, 1889, p. 56 (Asplenium striatum): stem large, erect, with a radial dictyostele.

D. Wichurae (Mettenius) Diels.
Y. Ogura, 1921, p. 119: rhizome creeping, with a radial dictyostele; leaf-trace double.

§ 2. Anisogonium.

D. esculentum (Retz.) Swartz.
P. Lachmann, 1889, p. 13; 1889, p. 78, pl. III, fig. 14 (Anisogonium seramporense): stem strong, erect, with a radial dictyostele; leaf-trace double.

D. proliferum (Lam.) Thouars.
P. Lachmann, 1889, p. 77: rhizome creeping, with a radial dictyostele; leaf-trace double.

§ 3. Hemidictyum.

D. marginatum (Linn.) Diels.
K. G. Stenzel, 1861, p. 23 (Diplazium giganteum): dictyostele with internal strands; the determination of the material is probably erronous; cf. Mettenius, 1864, p. 549.

46. **Phyllitis** Ludwig.

P. scolopendrium (Linn.) Newman.
P. Lachmann, 1889, p. 103, pl. IV. fig. 15—16 (Scolopendrium officinale): rhizome strong, erect, with a radial dictyostele; leaf-trace double.
F. O. Bower, 1914, p. 411, fig. 18 (Scolopendrium officinale): stem with a radial dictyostele; leaf-trace double.

48. **Asplenium** Linnaeus.

§ 1. Thamnopteris.

A. nidus Linnaeus.
P. Lachmann, 1889, p. 99, pl. III, fig. 15: rhizome short, erect, with a radial dictyostele; leaf-trace double.
S. E. Chandler, 1905, p. 396: stem with a dictyostele.

§ 3. Acropteris.

A. germanicum Weiss.
P. Lachmann, 1889, p. 55; rhizome short, with a radial dictyostele; leaf-trace simple.

A. ruta muraria Linn.
P. Lachmann, 1889, p. 55: rhizome short, with a radial dictyostele; leaf-trace simple.

§ 4. Euasplenium.

A. adiantum nigrum Linn.
P. Lachmann, 1889, p. 56, pl. II, fig. 20: rhizome short, with a radial dictyostele; leaf-trace double.

A. alatum H. B. Willd.
F. O. Bower, 1914, fig. 19*b*: rhizome short, with a radial dictyostele; leaf-trace double.

A. bulbiferum Forst.
S. E. Chandler, 1905, p. 376, fig. 152—164: rhizome short, with a radial dictyostele; leaf-trace divided.

A. incisum Thunberg.
Y. Ogura, 1921, p. 121: rhizome with a radial dicdyostele; leaf-trace double.

A. fontanum (Linn.) Bernhardi.
P. Lachmann, 1889, p. 55 (Asplenium Halleri): rhizome short, with a radial dictyostele; leaf-trace double.

A. obtusatum Forst.
F. O. Bower, 1914, fig. 14*a*. rhizome short, with a radial dictyostele and a large pith; leaf-trace-double.

A. obtusifolium Linn.
G. Mettenius, 1864, p. 546, pl. VII, fig. V: rhizome short, creeping, with a dorsiventral dictyostele which is transitional to a solenostele; leaf-trace bundles numerous;
K. Giesenhagen, 1892, p. 164:... „ein centraler Gefäszbündelstrang"...; protostele?

A. trichomanes Linn.
P. Lachmann, 1889, p. 55, pl. II, fig. 18: rhizome short, erect, with a radial dictyostele; leaf-trace double.

A. unilaterale Lamark.
G. Mettenius, 1864, p. 546, pl. VII, fig. IV (As-

plenium resectum): rhizome creeping, with distinct internodes; with a dorsiventral dictyostele transitional to a solenostele; leaf-trace bundles numerous.

A. viride Hudson.

P. Lachmann, 1889, p. 55: rhizome short, with a radial dictyostele; leaf-trace simple.

§ 5. Caenopteris.

A. fragrans Swartz.

P. Lachman, 1889, p. 57, pl. II, fig. 22—23 (Caenopteris foeniculacea): stem with a radial dictyostele; leaf-trace double.

A. scandens J. Smith.

D. T. Gwynne—Vaughan, 1903, p. 696: rhizome creeping with long internodes; leaf-gaps little more than one internode long; upper and lower strand of the dictyostele about equal in size.

A. tenerum Forst.

P. Lachmann, 1889, p. 56, pl. II, fig. 19 (Asplenium Belangeri): stem with a radial dictyostele; leaf-trace double.

49. **Ceterach** Adanson.

C. officinarum DC.

P. Lachmann, 1889, p. 55. pl. II, fig, 17: rhizome short, with a radial dictyostele; leaf-trace double, the two halves nearly fused.

2. BLECHNINAE.

51. **Blechnum** Linnaeus.

§ 1. Eublechnum.

B. brasiliense Desvaux.

P. Lachmann, 1889, p. 103, pl. IV, fig. 13, 14: stem strong, erect, with a radial dictyostele; leaf-trace bundles four in number.

S. E. Chandler, 1905, p. 376: stem with a radial dictyostele.

§ 3. Lomaria.

B. attenuatum (Sw.) Mettenius.

F. O. Bower, 1914, p. 377, fig. 4: stem creeping, with a radial dictyostele with numerous narrow gaps; leaf-trace divided.

B. capense (Linn.) Schlecht.
F. O. Bower, 1914, p. 381: stem strong, subarborescent with a radial dictyostele; leaf-trace bundles numerous.

B. discolor (Forst.) Keys.
F. O. Bower, 1914, p. 371: stem subarborescent with a radial dictyostele; leaf-trace double.

B. filiforme (Cumm.) Ettinghausen.
F. O. Bower, 1914, p. 390, fig. 10: rhizome long-creeping with a radial dictyostele; leaf-trace double.

B. Patersoni (R. Brown) Mettenius.
F. O. Bower, 1914. p. 387, fig. 7: rhizome strong, inclined, with a radial dictyostele; leaf-trace double.

B. penna marina (Poiret) Kuhn.
F. O. Bower, 1914, p. 389. fig, 9: rhizome creeping, thin, with a radial dictyostele, leaf-trace double.

B. punctulatum Swartz, var. Krebsi Kunze.
F. O. Bower, 1914. p. 407, fig. 17: rhizome short, with a radial dictyostele with numerous narrow leaf-gaps; leaf-trace double; the structure much resembling that of B. attenuatum.

B. spicant (Linn.) Wither.
K. G. Stenzel, 1861, p. 11, pl. II, fig. 4—5: rhizome short, erect, with a radial dictyostele; leaf-trace double.
P. Lachmann, 1889, p. 56, pl. II, fig. 21: stem with a radial dictyostele.
S. E. Chandler, 1905, p. 376 (Lomaria Spicant): stem with a dictyostele.
F. O. Bower, 1918, p. 380, fig. 5: stem with a radial dictyostele; leaf-trace double.

B. tabulare (Thunberg) Kuhn.
F. O. Bower, 1914, p. 373, fig. 3: a dwarf tree-fern with a radial dictyostele with a large pith; leaf-trace bundles 5 in number.

53. **Brainea** J. Smith.

B. insignis (Hook.) J. Smith.
F. O. Bower 1914, p. 396: a small tree-fern with a radial dictyostele; leaf-trace bundles 2 or more.

54. **Stenochlaena** J. Smith.

§ 1. Eustenochlaena.

S. sorbifolia (Linn.) J. Smith.
F. O. Bower, 1914, p. 39, fig. 11: rhizome climbing, with long internodes, with a radial dictyostele; leaf-trace bundles numerous, mostly 4—6.

§ 2. Cafraria.

S. tenuifolia (Desvaux) Moore.
G. Mettenius, 1864, p. 559, pl. VII, fig. II (Polybotrya Meyeriana): rhizome climbing, with long internodes; leaves in 2 rows; a dorsiventral perforated dictyostele with accessory cortical bundles.
P. Lachmann, p. 40 (Polybotrya Meyeriana): dictyostele with cortical strands.
E. Schumann, 1915, p. 221: dictyostele with cortical bundles.

55. **Woodwardia** Smith.
W. radicans (Linn.) Smith.
P. Lachmann, 1889, p. 373, pl. III, fig. 9: stem with a radial dictyostele; leaf-trace bundles numerous.
F. O. Bower, 1914, p. 403, fig. 16: rhizome erect, with short internodes, with a radial dictyostele; leaf-trace bundles numerous.
Y. Ogura, 1921, p. 121: rhizome erect, with a radial dictyostele; leaf-trace double.

56. **Doodia** R. Brown.
D. aspera R. Brown.
S. E. Chandler, 1905, p. 368, fig. 1—12: rhizome erect with short internodes, with a radial dictyostele; leaf-trace double.

D. maxima J. Smith.
F. O. Bower, 1914, p. 402, fig. 15; rhizome erect with short internodes, with a radial dictyostele; leaf-trace double.

VI. PTERIDEAE.

1. GYMNOGRAMMINAE.

61. **Jamesonia** Hook et Grev.

J. imbricata (Cavan.) Hk. et Grev.

D. T. Gwynne-Vaughan, 1903, p. 691: rhizome creeping; leaves in 2 rows; solenostele with a simple leaf-trace.

J. scalaris Kunze.

J. M. Lean Thompson, 1918, p. 364, pl. I. fig. 4: rhizome creeping, with the leaves arranged in 2 rows; a solenostele with long and narrow gaps; leaf-trace simple.

62. **Coniogramme** Fée.

C. fraxinea (Don) Diels.

Y. Ogura, 1921, p. 119: rhizome creeping, with long internodes with a radial dictyostele; leaf-trace double.

C. japonica (Thunberg) Diels.

J. M. Lean Thompson, 1918, p. 382, fig. 23, pl. VII, fig. 56: rhizome creeping, with distinct internodes; dictyostele with perforations; leaf-trace double.

63. **Hemionitis** Linnaeus.

H. palmata Linn.

D. T. Gwynne—Vaughan, 1903, p. 698; rhizome erect with short internodes, with a radial dictyostele; leaf-gaps little longer than one internode.

64. **Gymnopteris** Bernhardi.

G. vestita (Wall.) Underwood.

D. T. Gwynne—Vaughan, 1903, p. 695 (Gymnogramme vestita): rhizome short, dorsiventral with the leaves arranged in 2 rows; dictyostele with leaf-gaps little longer than one internode, consisting of a larger ventral gutter-shaped strand and a smaller dorsal one, running across between the insertion of the simple leaf-traces.

65. **Ceropteris** Link.

C. calomelanos (Linn.) Underwood.

P. Lachmann, 1889, p. 82, pl. III, fig. 22, 23 (Gymnogramme hybrida and G. chrysophyllum): rhizome short, inclined with a radial solenostele; leaf-trace double or simple.

D. T. Gwynne—Vaughan, 1903, p. 698, fig. 9 (Gymnogramme calomelanos): stem with a radial dictyostele; leaf-gaps but little longer than one internode; leaf-trace double.

66. **Trismeria Fée.**

T. trifoliata (L.) Diels.

J. M. Lean Thompson, 1918, p. 379, fig. 16, pl. IV, fig. 45: rhizome short, erect, with a solenostele; leaf-gaps wide; leaf-trace double.

2. CHEILANTHINAE.

67. **Pellaea Link.**

§ 1. **Platyloma.**

P. falcata (R. Brown) Fée.

D. T. Gwynne—Vaughan, 1903, p. 691: rhizome creeping, the leaves in 2 rows; a dorsiventral solenostele with a simple leaf-trace.

A. S. Marsh, 1914, p. 676: stem with a solenostele.

F. O. Bower, 1923*b*. p. 74, fig. 681: stem with a solenostele with a simple leaf-trace.

P. rotundifolia (Forst.) Hooker.

D. T. Gwynne—Vaughan, 1903, p. 695, fig. 8: rhizome creeping, with a dorsiventral dictyostele, the leaf-gaps but few internodes long; leaf-trace simple.

§ 2. **Eupellaea.**

P. andromedifolia (Klf.) Fée.

D. T. Gwynne—Vaughan, 1903, p. 695: rhizome creeping, with a dorsiventral dictyostele; leaf-gaps few internodes long; leaf-trace simple.

A. S. Marsh, 1914, p. 676, fig. 6: stem with a dorsiventral dictyostele with a simple leaf-trace.

P. atropurpurea (Linn.) Link.

D. T. Gwynne—Vaughan, 1903, p. 691: rhizome horizontal with a dorsiventral dictyostele; leaf-trace simple.

P. cordata (Cavan.) J. Smith.
D. T. Gwynne—Vaughan, 1903, p. 698: rhizome creeping, with a dorsiventral dictyostele; leaf-trace simple.

68. **Doryopteris** J. Smith.
D. ludens (Wall.) J. Smith.
D. T. Gwynne—Vaughan, 1903, p. 691 (Pteris ludens): rhizome short, dorsiventral, with a solenostele; leaf-trace simple.

71. **Notholaena** Brown.
N. ferruginea Hook.
D. T. Gwynne—Vaughan, 1903, p. 695: rhizome creeping, with short internodes, with a dorsiventral dictyostele; leaf-gaps not quite 2 internodes long; leaf-trace simple.

N. Marantae (Linn.) R. Brown.
D. T. Gwynne—Vaughan, 1903, p. 695, fig. 7: structure as in N. ferruginea.

N. sinuata (Lagasca) Kaulfuss.
S. E. Chandler, 1905, p. 385, fig. 172—196: rhizome creeping, with a solenostele.

N. trichomanoides (Linn.) R. Brown.
D. T. Gwynne—Vaughan, 1903, p. 695; structure as in N. ferruginea.

72. **Cheilanthes** Swartz.

§ 1. Eucheilanthes.

C. microphylla Swartz.
D. T. Gwynne—Vaughan, 1903, p. 696: rhizome creeping, with a dorsiventral solenostele (the gaps in the xylem are but little longer than one internode); leaf-trace simple.

§ 3. Physapteris.

C. Feei Moore.
A. S. Marsh, 1914, p. 673, fig. 4 (Cheilanthes lanuginosa): rhizome with a dorsiventral dictyostele with short gaps; leaf-trace simple.

C. Fendleri Hooker.
A. S. Marsh, 1914, p. 673: rhizome creeping, with a dorsiventral solenostele; leaf-trace simple.

C. gracillima Eaton.
A. S. Marsh, 1914, p. 673, fig. 1: rhizome creeping with a dictyostele which is transitional to a solenostele; leaf-trace simple.

C. lendigera (Cavan.) Swartz.
D. T. Gwynne—Vaughan, 1903, p. 696: rhizome creeping; structure as in C. microphylla.

C. persica (Bory) Mettenius.
A. S. Marsh, 1914, p. 673, fig. 5: rhizome radially built, with short internodes, with a radial dictyostele; leaf-trace simple.

73. Hypolepis Bernhardi.

H. Bergiana (Schlechtend.) Hooker.
P. Lachmann, 1889, p. 81 (Cheilanthes Bergiana): rhizome with short internodes, with a dictyostele; leaf-trace double.

H. distans (Col.) Hooker.
D. T. Gwynne—Vaughan, 1903, p. 693; rhizome creeping, with a dorsiventral solenostele; leaf-gaps rather long; leaf-trace simple.

H. millefolium Hooker.
D. T. Gwynne—Vaughan, 1903, p. 693, fig. 4: rhizome creeping, with a dorsiventral solenostele; leaf-trace simple.

H. repens (Linn.) Presl.
D. T. Gwynne—Vaughan, p. 693, fig. 6: rhizome creeping, with a dorsiventral solenostele; leaf-trace simple.

H. tenuifolia (Forst.) Bernhardi.
D. T. Gwynne—Vaughan, 1903, p. 693, fig. 5: rhizome creeping, with a dorsiventral solenostele; leaf-trace double.

H. punctata (Thunberg) Mettenius.
D. T. Gwynne—Vaughan, 1903, p. 694 (Polypodium punctatum): rhizome creeping, with a dorsiventral solenostele; leaf-gaps nearly one internode long; leaf-trace simple. (see F. O. Bower, 1918, p. 55, C. Christensen, 1920, p. 127.)

74. Llavea Lagasca.

L. cordifolia Lagasca.
J. M. Lean Thompson, 1918, p. 373, fig. 8. pl. VI,

fig. 34: rhizome short, inclined, with a solenostele with short and wide leaf-gaps; leaf-trace simple.

76. **Cryptogramma** R. Brown.

C. crispa (Linn.) R. Brown.

P. Lachmann, 1889, p. 47, pl. II, fig. 6 (Allosorus crispus): rhizome short, with a radical dictyostele with relatively short gaps; leaf-trace simple.

77. **Plagiogyria** Mettenius.

P. adnata (Blume) Beddome.

Y. Ogura, 1921, p. 121: rhizome erect, short, with a radial dictyostele; leaf-trace simple.

P. pycnophylla (Kunze) Mettenius.

F. O. Bower, 1910, p. 429, fig. 5: rhizome erect, short, with a radial dictyostele; the pith large, the leaf-gaps relatively short, the leaf-trace simple.

P. semicordata (Presl) Christ.

A. de Bary, 1877, p. 297 (Plagiogyria biserrata): rhizome erect, short, with a radial dictyostele.

D. T. Gwynne—Vaughan, 1903, p. 698, fig. 10 (Lomaria semicordata): stem with a radial dictyostele; leaf-gaps relatively short.

3. ADIANTINAE.

78. **Adiantum** Linnaeus.

§ 1. Euadiantum.

A. lunulatum Burm.

D. T. Gwynne—Vaughan, 1903, p. 698; rhizome creeping, with short internodes; with a radial dictyostele, leaf-gaps little longer than one internode; leaf-trace simple.

A. macrophyllum Swartz.

P. Lachmann, 1889, p. 41, pl. I, fig. 15: rhizome creeping, with a dorsiventral dictyostele with leaf-gaps little longer than one internode; leaf-trace double.

A. monochlamys Eaton.

Y. Ogura, 1921, p. 114: rhizome creeping, with distinct internodes with a solenostele transitional to a dictyostele; leaf-trace simple.

A. peruvianum Klotzsch.
P. Lachmann, 1889, p. 41, pl. I, fig. 26; structure as in A. macrophyllum, but leaf-gaps shorter.

A. petiolatum Desvaux.
D. T. Gwynne—Vaughan, 1903, p. 695 (Adiantum Kaulfussi): rhizome creeping, with a dorsiventral solenostele; leaf-gaps but little longer than one internode; leaf-trace simple.

A. trapeziforme Linn.
P. Lachmann, 1889, p. 31, pl. I, fig. 12: rhizome creeping, with a dorsiventral solenostele.
T. D. Gwynne—Vaughan, 1903, p. 695: rhizome creeping, with a dorsiventral dictyostele; leaf-gaps but little longer than one internode; leaf-trace simple.

§ 2. Adiantellum.

A. aethiopicum Linn.
D. T. Gwynne—Vaughan, 1903, p. 720: rhizome erect, with short internodes; the gaps in the xylem overlap; the endodermis does not dip in through the leaf-gap or is decurrent for a slight distance only; internal phloem reduced; leaf-trace simple.

A. neoguineense Moore.
P. Lachmann, 1889, p. 81, pl. III, fig. 19: rhizome erect, with a radial dictyostele; leaf-trace double.

A. patens Willd.
P. Lachmann, 1889. p. 31: rhizome creeping, with a dorsiventral solenostele.

A. pedatum Linn.
E. C. Jeffrey, 1903, p. 133, pl. V, fig. 40: rhizome creeping, with a solenostele; inner phloem reduced.
Y. Ogura, 1921, p. 117: rhizome with short internodes, rarely with long internodes; with a dorsiventral solenostele. In the first case the leaf-gaps sometimes overlap.

A. gracillima Moore
P. Lachman, 1889, p. 80, pl. II, fig. 16—18: stem with a radial dictyostele; leaf-trace double or forked at the base.

A. Farleyense Moore.
P. Lachmann, 1889, p. 30; rhizome creeping, with a dorsiventral solenostele.

4. PTERIDINAE.

81. **Anopteris Diels.**
A. hexagona (Linn.) C. Christ.
D. T. Gwynne—Vaughan, 1903, p. 697; stem slender, erect, with a radial dictyostele; leaf-gaps but little longer than one internode.

83. **Pteris Linnaeus.**

§ 1. Eupteris.

P. arguta Ait.
P. Lachmann, 1889, p. 83: rhizome with a radial solenostele; leaf-trace simple.

P. cretica Linn.
D. T. Gwynne—Vaughan, 1903, p. 697; rhizome creeping, with short internodes, with a radial dictyostele; leaf-gaps but little longer than one internode.

P. dentata Forsk.
D. T. Gwynne—Vaughan, 1903, p. 697 (Pteris flabellata): rhizome short, with a radial dictyostele; leaf-gaps but little longer than one internode.

P. longifolia Linn.
P. Lachmann, 1889, p. 48, pl. II, fig. 7: rhizome short, with a radial solenostele, transitional to a dictyostele.

P. pellucida Presl.
D. T. Gwynne—Vaughan, 1903, p. 698: rhizome with a radial dictyostele; leaf-gaps but little longer than one internode.

P. tremula R. Bown.
D. T. Gwynne—Vaughan, 1903, p. 697: rhizome with a radial dictyostele; leaf-gaps but little longer than one internode; leaf-trace simple.

P. umbrosa R. Brown.
P. Lachmann, 1889, p. 82: In the young stem a radial solenostele is present with a double leaf-trace.

§ 1a. Campteria.

P. biaurita Linn.

P. Lachmann, 1889, p. 83, pl. III, fig. 2 (Pteris argyrea): rhizome with a radial solenostele; leaf-trace simple.

F. O. Bower, 1918, p. 36; rhizome with a dictyostele; leaf-gaps but little longer than one internode; leaf-trace simple.

§ 2. Heterophlebium.

P. grandifolia Linn.

F. O. Bower, 1918, p. 36: rhizome with a solenostele; leaf-trace simple.

§ 3. Lithobrochia.

P. gigantea Willden.

H. Karsten, 1847, p. 192; in the stele of this plant an internal system is to be found: in the lower part as a solid bundle, at a higher level as a hollow tube; leaf-trace simple.

P. Kunzeana Agardh.

G. Mettenius, 1864, p. 535, pl. VI, fig. 12—14 (Pteris elata, var. Karsteniana); stem with a solenostele with an internal system.

D. T. Gwynne—Vaughan, 1903, p. 702, fig. 14 (Pteris elata, var Karsteniana): rhizome with a radial solenostele with short leaf-gaps and with an internal system, consisting of a cylindrical tube with gaps just above the insertion of a strand, which is given off from the stelar tube above the leaf-gaps; sometimes the gaps in the internal system overlap, even an internal strand is formed, fusing with the margins of the lacunae of the inner tube.

P. orizabae Mart. et Galeotti.

H. Karsten, 1837, p. 193: structure as in Pteris gigantea.

P. podophylla Swartz.

G. Mettenius, 1864, p. 535: structure as Pteris Kunzeana.

F. O. Bower, 1916, p. 37, fig. 26—28: young plants with a protostele, in the higher parts with a solenostele; in the mature stem with an internal system.

84. Histiopteris J. Smith.

H. incisa (Thunbg) J. Smith.

P. Lachmann, 1889, p. 36: (Lithobrochia vesper-

tilionis): rhizome long-creeping, with a solenostele.
D. T. Gwynne-Vaughan, 1903, p. 691 (Pteris incisa): rhizome with a dorsiventral solenostele; leaf-trace simple, obliquely inserted.
A. G. Tansley and R. B. Lulham, 1903, p. 3—13, fig. 4 (Pteris incisa): solenostele with an internal system, derived from the lateral bays of the leaf-trace.
F. O. Bower, 1918, p. 29, fig. 23: young plant in the lower parts with a protostele, then with a Lindsaya-stele; in the higher parts a solenostele with a simple leaf-trace occurs.

85. **Lonchitis** Linnaeus.

§ 1. **Eulonchitis.**

L. aurita Linn.
F. O. Bower, 1918, p. 27: rhizome strong, erect, with a radial solenostele and a double leaf-trace.

§ 2. **Anisosorus.**

L. hirsuta Linn.
F. O. Bower, 1918, p. 27: rhizome strong, erect, with a radial solenostele with some perforations; leaf-trace double.

86. **Pteridium** Gleditsch.
P. aquilinum (Linn.) Kuhn.
K. G. Stenzel, 1861, p. 37, pl. 5, fig. 5—17 (Pteris aquilina): rhizome underground with long internodes; with a perforated dictyostele with internal system; leaf-trace bundles numerous.
P. Terletzki, 1884, p. 484 (Pteris aquilina): gives histological details.
A. Trécul, 1885a, p. 918 (Pteris aquilina): stem with mesarch protoxylem strands.
E. C. Jeffrey, 1899, p. 605, pl. VII (Pteris aquilina): ontogeny.
S. Kisch, 1907, p. 366, fig. 1—25, phot. 1—12: gives histological details.

87. **Paesia** St. Hilaire.
P. scaberula (Rich.) Kuhn.
D. T. Gwynne-Vaughan, 1903, p. 691 (Pteris scaberula):

rhizome creeping, with distinct internodes, with a dorsiventral solenostele; leaf-trace simple.
F. O. Bower, 1918, p. 24; idem.

P. viscosa St. Hilaire.
F. O. Bower, 1918, p. 24; F. O. Bower, 1923b, p. 74, fig. 68 VI: structure as in P. scaberula.

VII. VITTARIEAE.

1. VITTARIINAE.

89. Vittaria Smith.

§ 1. Euvittaria.

V. elongata Swartz.
G. Poirault, 1893, p. 179: vascular bundle of the stem without internal phloem or endodermis.
E. C. Jeffrey, 1903, p. 132: rhizome dorsiventral, the leaves arranged in 2 rows; a solenostele without internal phloem but with internal endodermis.
D. T. Gwynne—Vaughan, 1903, p. 719: in this plant the ground tissue is sometimes not decurrent through the leaf-gap at all; often the inner phloem at the ventral side is wanting, but sometimes the structure is wholly dictyostelic.

§ 2. Haplopteris.

V. lineata (Linn.) Smith.
E. C. Jeffrey, 1903, p. 132: rhizome short-creeping, with a solenostele.

V. stipitata Kunze.
D. T. Gwynne—Vaughan, 1903, p. 718: rhizome creeping, with short internodes, with a small solenostele; leaf-trace double; gaps in the xylem longer than one internode, those in the endodermis shorter; ground-tissue decurrent through the leaf-gap but not continuous, being replaced by an amount of pericyclic parenchyma; internal phloem slightly developed or wanting at the ventral side.

2. ANTHROPHYINAE.

91. **Anthrophyum** Kaulfuss.
A. plantagineum (Cavan.) Kaulfuss.
E. C. Jeffrey, 1903, p. 132, pl. V, fig. 38: rhizome short, creeping, with a solenostele; no internal endodermis; internal phloem reduced.
D. T. Gwynne-Vaughan, 1903, p. 720: stem with a dorsiventral dictyostele; inner phloem absent on the lower side.

A. reticulatum (Forst.) Kaulfuss.
E. C. Jeffrey, 1903, p. 132, pl. V. fig. 39: rhizome short, creeping, with a solenostele; internal endodermis and phloem wanting; leaf-trace simple.

A. semicostatum Blume.
E. C. Jeffrey, 1903, p. 132, pl. V. fig. 35—37: rhizome short, with a solenostele without internal phloem; leaf-trace double.

A. spec.
G. Poirault, 1893, p. 179: internal endodermis and phloem wanting.

VIII. POLYPODIEAE.

1. TAENITIDINAE.

93. **Drymoglossum** Presl.
D. heterophyllum (Linn.) C. Christensen.
W. Schütze, 1905, p. 343, fig. 4: rhizome creeping, with long internodes, with a dorsiventral perforated dictyostele.

96. **Taenitis** Willdenow.
T. blechnoides (Willden.) Swartz.
D. T. Gwynne—Vaughan, 1903. p. 698; rhizome creeping, with a radial dictyostele; leaf-gaps little longer than one internode.

2. POLYPODIINAE.

100. Polypodium Linnaeus.

§ 1. Eupolypodium.

P. paradiseae Langsd. et Fischer.
G. Mettenius, 1865, p. 555, pl. IX, fig. VII: rhizome short, creeping with a dorsiventral dictyostele, the lower part of which is perforated; leaf-trace bundles numerous.

P. vulgare Linnaeus.
K. G. Stenzel, 1861, p. 42, pl. 5, fig. 1—4: rhizome creeping with a dictyostele; accessory gaps present in the lower part.
G. Mettenius, 1864, p. 555, pl. IX, fig. VIII: stem with a dorsiventral dictyostele, the lower part (Unterstrang) with perforations.
L. Klein, 1881, p. 373, pl. 4, fig. 4—6: the same result as Mettenius.

§ 1a. Grammitis.

P. caespitosum (Bl.) Mett.
G. Mettenius, 1864, p. 553, pl. IX, fig. IV: rhizome creeping, with a dorsiventral dictyostele, the lower part of which has many perforations; leaf-trace bundles four in number.

§ 2. Goniophlebium.

P. fraxinifolium Jacquin.
H. Link, 1836, p. 378 (Polypodium deflexum): rhizome creeping, with a dictyostele.
G. Mettenius, 1864, p. 554, pl. IX, fig. V: stem with a dorsiventral perforated dictyostele; leaf-trace bundles numerous.

P. latipes Langsd. et Fischer.
G. Mettenius, 1864. p. 555, pl. IX, fig. VI: structure much resembling that of P. fraxinifolium.

P. loriceum Linn.
H. Link, 1836, p. 378, pl. I, fig. 1 (Polypodium ramosum): rhizome creeping, with a dictyostele.

§ 3. Marginaria.

P. ciliatum Willdenow.

G. Mettenius, 1864, p. 552, pl. IX, fig. I. (Polypodium cajennense): rhizome creeping, with long internodes, with a dorsiventral dictyostele, the lower part of which is perforated; leaf-trace simple.

P. piloselloides Linnaeus.

G. Mettenius, 1864, p. 552: structure as in P. ciliatum.

P. tectum Kaulfuss.

G. Mettenius, 1864, p. 552 (Polypodium aurisetum): structure as in P. ciliatum.

§ 4. Phlebodium.

P. aureum Linnaeus.

H. Link, 1836, p. 378: rhizome thick, creeping, with solenostele.

G. Mettenius, 1864, p. 557, pl. X fig. II; stem with a dorsiventral dictyostele with perforations; leaf-trace bundles numerous, the anterior coming from the anterior margin of the gap.

L. Klein, 1881, p. 373, pl. III, fig. 16—17: idem.

E. C. Jeffrey, 1903, p. 131, pl. V, fig. 34: stem with a radial dictyostele.

S. E. Chandler, 1905, p. 381, fig. 91—126: stem with a dictyostele.

§ 5. Campyloneuron.

P. angustifolium Swartz.

L. Klein, p. 364, pl. III, fig. 6—8, 12 (Polypodium taeniosum): rhizome short, creeping, with a perforated dictyostele.

P. Lachmann, 1889, p. 31 (Polypodium taeniosum): stem with a dictyostele.

P. decurrens Raddi.

G. Mettenius, 1864, p. 558, pl. X. fig. I: rhizome creeping, with a dorsiventral dictyostele, the lower part of which is perforated; leaf-trace bundles numerous, the anterior fusing with the anterior margin of the gap.

§ 6. Pleopeltis.

P. musifolium Blume.

L. Klein, 1881, p. 373: rhizome with a dictyostele.

P. percussum Cavanilles.
H. Link, 1836, p. 378: rhizome creeping, with long internodes, with a dictyostele.

P. persicariaefolium Schrader.
H. Link, 1836, p. 378: structure as in P. percussum.

P. punctatum (Linn.) Swartz.
rhizome creeping, with a dorsiventral perforated dictyostele; leaf-trace bundles numerous.
(see also Hypolepis punctata).

P. squamulosum Kaulfuss.
G. Mettenius, 1864, p. 553, pl. IX, fig. II: rhizome creeping, with long internodes with a dictyostele the lower part of which is perforated; leaf-trace double.

§ 9. **Myrmecophila.**

P. heracleum Kunze.
G. Mettenius, 1864, p. 558, pl. X, fig. IV, rhizome creeping, with a perforated dictyostele.
L. Klein, 1881, p. 439, pl. IV, fig. 1—3, 10—16: stem with a dorsiventral perforated dictyostele, leaf-trace bundles numerous; ontogeny.

P. sinuosum Wallich.
R. H. Yapp, 1902, p. 208, fig. 36; rhizome dorsiventral, with a dorsiventral dictyostele, the lower part of which is perforated; leaf-trace bundles numerous.

103. **Lecanopteris** Reinwardt.
L. carnosa (Reinwardt) Blume.
R. H. Yapp, 1902, p. 193, fig. 33—35 (Polypodium carnosum): rhizome creeping, with a dorsiventral dictyostele, the lower part of which is perforated; leaf-trace bundles numerous.

104. **Dryostachyum** J. Smith.
D. drynarioides (Hooker) Kuhn.
F. O. Bower, 1917, p. 24, fig. 11: rhizome creeping, with a dorsiventral dictyostele with numerous perforations.

106. **Drynaria** J. Smith.
D. quercifolia (Linn.) J. Smith.
G. Mettenius, 1864, p. 558 (Polypodium quercifolium): rhizome creeping, with a perforated dictyostele. H. Klein, 1881, p. 364, pl. III, fig. 1—4, 10—11; idem.

IX. ACROSTICHEAE.

1. ACROSTICHINAE.

107. **Elaphoglossum** Schott.

E. brevipes (Kunze) Moore.

G. Mettenius. 1864, p. 546, pl. VIII, fig. 2 (Acrostichum brevipes): stem creeping, with a dorsiventral dictyostele; leaf-trace bundles usually 5 in number. P. Lachmann, 1889, p. 33 (Acrostichum brevipes): stem with a dorsiventral dictyostele.

E. hybridum (Bory) Moore.

G. Mettenius, 1864, p. 546 (Acrostichum melanopus): structure as in E. brevipus.

E. latifolium (Swartz) J. Smith.

F. O. Bower, 1917, p. 27, fig. 13; rhizome creeping, with a dorsiventral solenostele transitional to a dictyostele; leaf-trace bundles numerous.

E. lingua (Raddi) Brackenridge.

G. Mattenius, 1864, p. 546, pl. VII, fig. VII (Acrostichum Lingua): rhizome creeping, with a dorsiventral dictyostele; leaf-trace bundles 3 in number. P. Lachmann, 1889, p. 33 (Acrostichum Lingua): stem with a dorsiventral dictyostele.

E. Sieberi (Hooker et Greville) Moore.

P. Lachmann, 1889, p. 33, pl. I, fig. 15 (Acrosticum coriaceum): rhizome creeping, with a dorsiventral dicdyostele.

E. simplex (Swartz) Schott.

G. Mettenius, 1864, p. 547 (Acrostichum simplex): structure as in E. brevipes.

E. tomentosum (Bory) Christ.

E. N. Thomas, 1905, p. 185 (Acrostichum tomentosum): rhizome creeping with a dictyostele; leaf-trace bundles usually 3 in number.

109. **Acrostichum** Linnaeus.

A. aureum Linnaeus.

G. Mettenius, 1864, p. 535, pl. VI, fig. 17 (Chrysodium vulgare): rhizome strong, erect, with a soleno-

stele with an internal system, constisting of a compensatory strand springing from the upper margin of the leaf-gap, and of free bundles of the leaf-trace running through the gap.
E. N. Thomas, 1905, p. 179, fig. 27—33, 38: stem with a solenostele with internal strands.
E. Schumann, 1915, p. 211: stem with a solenostele with internal bundles.

2. PLATYCERINAE.

110. **Cheiropleuria** Presl.
C. bicuspis (Blume) Presl.
F. O. Bower, 1915; see this memoir, p. 196.

112. **Platycerium** Desvaux.
P. bifurcatum (Cavanilles) C. Christensen.
G. Mettenius, 1864, p. 556, pl. VIII, fig. VII (Platycerium alcicorne): rhizome with a dorsiventral dictyostele, the lower part perforated; leaf-trace bundles numerous.
P. Lachmann, 1889, p. 31, pl. I. fig. 13, 14 (Platycerium alcicorne): stem with a dictyostele with perforations.
D. T. Gwynne-Vaughan, 1903, p. 698: rhizome with a dorsiventral dictyostele with leaf-gaps little longer than one internode; the larger ventral gutter shaped strand broken up by perforations into an irregular network of strands.
F. O. Bower, 1915, p. 508, fig. 9 A (Platycerium alcicorne): stem with a highly perforated dictyostele.
P. stemaria (Beauv.) Desvaux.
F. O. Bower, 1915, p. 508, fig. 9 B: rhizome with a perforated dictyostele with a complex medullary system.
H. von Straszewski, 1915, p. 279, fig. 17, 20: rhizome in the young plant with a solenostele, in the higher parts with a dictyostele with a medullary system.

Though this list shows that of large groups of Ferns relatively little is known, the facts already at our disposal are sufficient to show, that the anatomical characteristics in many cases are valuable for the study of the interrelationship of the different genera. Some of the most striking points of correlation between the anatomical features and the systematic position will be mentioned here.

In the first group, the Woodsieae, the Woodsiinae are characterised by their rhizome being erect, with short internodes; they possess a well-developed dictyostele with a double leaf-trace; in Acrophorus there is a larger number of leaf-trace bundles.

An aberrant structure is found in Hypoderris Brownii; the dictyostele is here dorsiventral, while in the upper, as well as in the lower part, perforations occur. According to Diels (1899, p. 163) the exact position of this Fern is uncertain; it is placed in the Woodsieae on account of the structure of the indusium, though in its habit it has many points in common with the Aspidieae.

Diacalpe foeniculacea (Diels, 1899, p. 159) is better to be considered as a Polystichum.

In the Onocleineae there is much agreement in internal structure.

Of the Aspidieae the genus Dryopteris is an interesting one; in this large genus there are some forms, the isolated position (as is shown by their synonymy) is in perfect correlation with their internal structure. In the section Eudryopteris the rhizome is erect with short internodes, a radial dictyostele is found. In the species of the subgenus Phegopteris, Leptogramme, Cyclosorus and Meniscium the internodes are longer; in these plants too there is a radial dictyostele, but the leaf-gaps are very small and narrow.

Exceptions are: D. thelypteris from the section Eudryopteris has a creeping rhizome with long internodes and a radial dictyostele; according to Diels (1899, p. 172) this form is somewhat isolated among the group Furcato-veniae of the subgenus Eudryopteris by the reduction of the fertile pinnae. Therefore Newmann makes it into a separate genus, — Hemestheum —, which has been accepted by Parmentier, (1899, p. 337) who studied the leaf-trace of this and allied forms. Dryopteris punctata (Thunberg) C. Christensen (Index Fil.) has a dorsiventral solenostele with a simple leaf-trace; this structure is not found in the other species of the group Phegopteris in which it has been placed, which is regarded by Hooker and Baker to belong to Polypodium, while Christensen includes this group in the genus Dryopteris. It is interesting to see, that both Mettenius and Kuhn have considered this plant as a Hypolepis with reduced sori, which view has lately been supported by Bower on arguments derived from the development of the sori. In his monograph of the genus Dryopteris C. Christensen (1920, p. 127) draws the same conclusion. The internal structure quite agrees with that in the genus Hypolepis, where a dorsiventral solenostele with a simple leaf-trace is found. Thus the combination Hypolepis punctata (Thunbg.) Mettenius should be restored.

A similar case is Dryopteris orientalis (Gmel.) C. Christensen. It has a dorsiventral dictyostele and agrees in this and in a number of morphological features with the species of the genus Arthropteris; these characteristics will be discussed later on.

While in the genus Dryopteris the radial structure of the dictyostele is still present in the creeping forms, this is not the case in the genus Polystichum; the dictyostele is here radial in the forms with an erect rhizome, dorsiventral in the creeping species. Polystichum foeniculaceum has been considered by Beddome and Diels (1899, p. 159) as a Diacalpe; this supposition is not supported by the anatomical structure, since this agrees with that of the other species of Polystichum.

Neocheiropteris palmatopedata was at first described as a Polypodium by Baker on characteristics derived from the sorus; H. Christ has founded the genus Neocheiropteris on it, which he considers to be allied to Polypodium. Diels believes that there is an affinity between this form and the Aspidiinae because of the characteristics of the leaf and on the lack of an articulation at the base of the petiole. But the internal structure shows the presence of a dorsiventral dictyostele with the lower part much perforated and a divided leaf-trace; in these characteristics there is much agreement with Polypodium. Bower supports this belief; according to him its nearest allies are amongst the section Phymatodes of the latter genus.

In the genus Polybotrya the species are according to Diels (1899, p. 195) isolated in the subgenera; the interrelation of these groups ought to be investigated. The anatomical structure is in agreement with these views, the two species of which the internal structure is known belong to two different sections; one of them has a radical dictyostele with numerous leaf-trace bundles, the other has a dorsiventral solenostele with a simple leaf-trace.

In the Davalliaeae the genus Arthropteris J. Sm. is characterised by a creeping rhizome, with the leaves placed in two rows; the petiole is articulated at the base or higher on; the leaves are pinnate, the pinnae being entire or lobed, the veins simple or forked, with concretions of carbonate of lime on the upper surface of their ends.

The indusium is very variable in this genus, according to this great variability the various species have been placed in different genera. In A. tenella (Forst.) J. Sm. the indusium is wanting, its synonym is Polypodium tenellum Forst. In A. obliterata (R. Br.) J. Smith it is cordate, delicate and soon falls off, its synonyms are Nephrodium obliteratum R. Br. and Nephrolepis ramosa Moore. A. altescandens (Colla) J. Smith too has been considered as a

Nephrodium. These three species in which the structure of the involucre is so different, agree, not only in the morphological features mentioned, but also in having a dorsiventral dictyostele with a double leaf-trace.

This structure is also to be found and has been described by Mettenius in Aspidium albo-punctatum Bory, so named after the white dots (a secretion of carbonate of lime) on the upper surface of the leaf. This species is identical with Polypodium orientalis of Gmelin, which C. Christensen (1905, p. 581) placed among the Dryopteris. The habit agrees with that of the species mentioned above, by having a creeping rhizome with long internodes, an articulated petiole (which is not found in the other Dryopteris), and in the venation. Thus the opinion of J. Smith, who considered this species to be an Arthropteris seems to me fully justified, so that this species should be named Arthropteris orientalis.

In Davallia as in Humata a dorsiventral dictyostele with a large number of leaf-trace bundles is to be found, except in the section Prosaptia of the former genus, where a radial dictyostele is present. It is remarkable to see, that this group has been considered by some authors as a group of the genus Polypodium. The structure of the sorus in Prosaptia shows some pecularities the real nature of which is not yet clear. The idea that Prosaptia is allied to Polypodium has lately been stated by B. Hayata, (1915) but neither in anatomical characters is there any agreement with the latter genus, nor with the other species of Davallia.

In the group embracing the genera Microlepia, Leptolepia, Odontosoria, Tapaenidium and Lindsaya a creeping rhizome occurs with the leaves arranged in two rows on the upper surface.

In the genus Lindsaya and the section Stenoloma of the genus Odontosoria there is a Lindsaya stele; in the genus

Tapaenidum a transition between the Lindsaya-stele and the solenostele is to be found, while in Leptolepia, Microlepia, and in Odontosoria, sect. Euodontosoria there is a solenostele. In the genus Lindsaya a different structure has been noted in L. cultrata and L. repens, but the statements on these species differ. Dennstaedtia possesses a dorsiventral solenostele with a simple leaf-trace, but an internal system sometimes occurs. A similar structure is to be found in Saccoloma.

The structure of Monachosorum is different from the former plants, but the affinities of this plant are still very doubtful.

In the Aspleniinae the dictyostele is radially built, ever in those with a creeping rhizome. The leaf-trace is mostly divided, it is simple in the section Acropteris of the genus Asplenium.

The only exception is the structure in Asplenium obtusifolium Linn., of which Mettenius mentions a dorsiventral dictyostele, but it should be remarked that Giesenhagen states that there is a solid vascular strand in this plant.

The Blechninae are a homogenous group, they all have a radial dictyostele with a large number of leaf-trace bundles, not only in the forms with an erect rhizome but also in those with a creeping or scandent rhizome. Stenochlaena has the same type of structure.

In the Pterideae a solenostele or a dictyostele with relatively short gaps is found in the Gymnogramminae. The stem is erect in the genera Hemionitis, Ceropteris, and Trismeria, and the stele is radially built; in the other genera the solenostele is dorsiventral in a creeping rhizome. In a specialised form as Coniogramme japonica a few perforations may occur in the stele. The leaf-trace is simple or double.

The Cheilanthinae have as a rule a creeping rhizome with a dorsiventral solenostele or a dictyostele with relatively short gaps. This structure is found in Pellaea, Doryopteris, Hypolepis (H. punctatum included), Llavea and Notholaena. This structure is also to be found in the genus Cheilanthes, except in Ch. persica, the only Palaeotropic form of this genus of which the structure is known. In Cryptogramme too a radially structure is seen, as in Plagiogyria, the natural position of which however is still doubtful.

The section Euadiantum of the genus Adiantum has a creeping rhizome with a dorsiventral solenostele or a dictyostele with short gaps; the leaf-trace is simple or divided. In the section Adiantellum some species have an erect rhizome with a radial stele.

In the Pteridinae there is a solenostele or a dictyostele with short leaf-gaps; in the section Lithobrochia of the genus Pteris an internal system occurs, which is built up in the same way as in Saccoloma and in Thyrsopteris. Pteridium also has as internal system, which is probably built up in the same way but the outer vascular cylinder has many perforations. The genus Lonchitis also has some perforations.

The Vittarieae posses a solenostele, which may be more or less reduced.

The structure in the Polypodieae is a dorsiventral dictyostele, in the lowest part of which there are perforations so that in transverse section a large number of bundles is seen. The leaf-trace bundles are numerous.

Taenitis blechnoides is an exception as it has a radial dictyostele with the leaf-gaps but little longer than one internode.

The Acrosticheae contain a number of genera, the mutual affinities of which are not yet sufficiently well known.

In Elaphoglossum a dorsiventral dictyostele is found with numerous leaf-traces. In Acrostichum a radial solenostele with an internal system occurs. In the second division, the Platycerinae, the genus Platycerium has a dorsiventral dictyostele with numerous perforations; P. Stemmaria has an internal system. Cheiropleuria possesses has a haplostele with a leaf-trace, which is mesarch in its lowest part.

The extension of the sori on the lower surface of the leaf may take place in different ways. The group of the Acrosticheae therefore is an artificial one. The different genera of this group have their nearest allies in several other groups. Formerly Stenochlaena, Leptochilus and Polybotrya were also included amongst them. Of the four genera mentioned above, Acrostichum shows in the development of the sorus certain characteristics which point to an affinity with Pteris; the internal structure (an internal system is found, with reparatory strand springing from the anterior margin of the leaf-gap), makes this hypothesis probable. The affinities of Cheiropleuria are very doubtful, a remarkable combination of primitive and more advanced characteristics being present in it. It is supposed, that its nearest ally is Platycerium, but the conclusion made by v. Straszewki is that Cheiropleuria has only the venation in common with Platycerium. The latter genus is, according to him, most closely allied with Polypodium, (in which as in Platycerium a dorsiventral dictyostele with numerous perforations is found present). The affinity of Platycerium with the other Acrosticheae is remote.

CHAPTER VI.

The Stelar Morphology of the Cyatheaceae.

The Cyatheaceae are divided into the subfamilies the Dicksoniaea, the Thyrsopterideae and the Cyatheae. The first two groups have according to Bower (1913, p. 474) their nearest affinity with the Marginales in the Polypodiaceae. To the latter group belong e. g. Saccoloma, Dennstaedtia, Lindsaya and the Pterideae. The Cyatheae, to which belong the genera Cyathea, Hemitelia and Alsophila, are considered to be allied to the Superficiales on account of the development of the sporangia, their nearest allies being the Aspideae and the Asplenieae in the Polypodiaceae (Bower 1912, p. 319).

With this classification corresponds a difference in anatomical structure. The Dicksonieae-Thyrsopteridineae have as a rule a dictyostele which is but little different from a solenostele. If, as in Thyrsopteris, an internal system is present, it is built up in the same way as in Saccoloma, Dennstaedtia and Pteris Kunzeana.

In the Cyatheae an internal system often occurs too. But it is built up in a different way: some of the elementary bundles of the petiolar trace retain their individuality and pass through the gap into the pith, were they may anastomose with similar bundles or end blind. In some cases cortical bundles are to be found.

I. DICKSONIEAE.

2. **Dicksonia** l'Heritier.

D. antarctica Labill.

A. de Bary, 1877, p. 297: a tree-fern, with a radial dictyostele.

D. Karsteniana (Klotzsch) Moore.

G. Nördlinger, 1856 (Balantium Karsteniana): a radial dictyostele.

H. W. Reichardt, 1859, p. 38, pl. II, fig. 32, 33 (Balantium Karsteniana): stem with a radial dictyostele.

A. de Bary, 1877, p. 297: a tree-fern with a radial dictyostele.

W. Schütze, 1905, p. 337, fig. 2: stem with a radial dictyostele with a large pith; leaf-trace bundles numerous.

D. squarrosa (Forst.) Swartz.

P. Lachmann, 1889, p. 84, fig. 3, pl. IV, fig. 1, 2 (Balantium squarrosum): a tree-fern with a radial dictyostele, the gaps relatively narrow, the pith large; leaf-trace bundles numerous.

G. B. Stephenson, 1908, p. 9, fig. 85—88: ontogeny.

3. **Cibotium** Kaulfuss.

C. barometz (Linn.) J. Smith.

A. de Bary, 1877, p. 297: stem erect with a radial dictyostele.

D. T. Gwynne—Vaughan, 1903, p. 691, fig. 7 (Dicksonia barometz): a radial dictyostele, the leaf-gaps but little longer than one internode; leaf-trace simple near its insertion, divided at a slightly higher level.

C. Schiedei Schlechtend. et Chamisso.

A. de Bary, 1877, p. 297: a large tree-fern, with a radial dictyostele.

II. THYRSOPTERIDEAE.

4. **Thyrsopteris** Kunze.
T. elegans Kunze.
F. O. Bower, 1913, p. 454, textfig. A, pl. XXXIII, fig. 14, 15; pl. XXX: in the runner in the base a solenostele is found; in the higher parts there is a medullary strand springing from the upper margin of the leaf-gap, often ending blind in the pith, when the runner is small; in stronger axes it may connect up with that from the next lower leaf-gap and constitute a continuous rod. In larger shoots the medullary strands form a hollow tube with interruptions above the insertion of the bundle, which comes from the upper margin of the leaf-gap. In this part of the stem this compensation strand separates from the solenostele after its fusion with the leaf-trace, in distinction from the lower parts of the runners. Leaf-trace simple at the base.

III. CYATHEAE.

5. **Cyathea** Smith.
C. arborea (Linn.) Smith.
P. Lachmann, 1889, p. 93, fig. 6: a tree-fern with a radial dictyostele with narrow leaf-gaps and a large pith; leaf-trace with numerous bundles; intracortical strands.
D. T. Gwynne—Vaughan, 1903, p. 708; stem with a radial dictyostele with narrow leaf-gaps with outwards turned margins; leaf-trace bundles numerous, some of them but temporary touching the margins of the gap or quite free from it, then passing through the gap and running down as central strands in the pith, ending blind, mesarch in their lower parts; the other ones fusing with the margins of the leaf-gaps, joining and rapidly disappearing after the leaf-gap has closed.

C. aurea Klotzsch.
H. Karsten, 1847, p. 195: a tree-fern with a radial solenostele; leaf-trace simple or double.

C. ebenina Karsten.
H. W. Reichardt, 1859, p. 30, pl. I, fig. 5—7: a tree-fern with a radial dictyostele with vascular bundles, situated in the pith.

C. glauca Bory.
D. T. Gwynne—Vaughan, 1903, p. 708: a tree-fern with structure as in Cyathea moluccana, but with more internal strands.

C. Macarthurii (F. Muell.) Baker.
E. C. Jeffrey, 1903, p. 130, fig. 32, 33: a tree-fern with a radial dictyostele with narrow leaf-gaps; leaf-trace double.

C. medullaris (Forst.) Swartz.
P. Lachmann, 1889, p. 93, pl. V, fig. 6, 7: a dwarf tree-fern with a radial dictyostele and a large pith; leaf-trace bundles numerous; internal strands passing from the margins of the gap into the pith and ending blind.
G. B. Stephenson, 1908, p. 9, fig. 25—29: ontogeny.

C. mexicana Cham. et Schlechtend.
H. W. Reichardt, 1859, p. 31, pl. I, fig. 10, 11: a tree-fern with a radial dictyostele with internal strands.
F. O. Bower, 1913, p. 452: the runner at the base with a solenostele.

C. moluccana R. Brown.
D. T. Gwynne—Vaughan, 1903, p. 707, fig. 15 (Cyathea Brunonis): a tree-fern; structure as in C. arborea.

C. Tussacii Desvaux.
A. de Bary, 1877, p. 305, fig. 138—142 (Cyathea Imrayana): a tree-fern with a radial dictyostele with internal strands; leaf-trace bundles numerous.
W. Schütze, 1905, p. 345 (Cyathea Imrayana): stem with a radial dictyostele with internal strands.

C. usumbarensis Hieronymus.
W. Schütze, 1905, p. 339, fig. 3—5; a tree-fern, with a radial dictyostele with narrow gaps; leaf-trace bundles

numerous, some of them passing through the gap into the pith.

6. Hemitelia R. Brown

§ 2. Euhemitelia.

H. multiflora (Sm.) R. Brown.
H. W. Reichardt, 1859, p. 33, pl. I, fig. 15—19 (Alsophila multiflora): a tree-fern with a radial dictyostele with internal bundles.

H. setosa (Kaulf.) Mettenius.
F. O. Bower, 1913, p. 450: a tree-fern with a radial dictyostele with internal strands; the horizontal runners, when smaller in size, protostelic below, later on with a solenostele; leaf-trace bundles numerous.

H. speciosa (H. B. Willd.) Moore.
H. Nördlinger, 1859 (Hemitelia integrifolia): stem with a radial dictyostele with internal strands.

§ 3. Amphicosmia.

H. capensis (Linn. fils) R. Brown.
G. Mettenius, 1864, p. 525, pl. V. fig. 1: a tree-fern; in the young plant two of the leaf-trace bundles pass through the gap into the pith.
W. Schütze, 1995, p. 340: stem with a radial dictyostele.

7. Alsophila R. Brown.

§ 1. Species Americanae.

a. Amphidesmium.

A. blechnoides (Rich.) Hooker.
F. O. Bower, 1913, p. 444 (Metaxya rostrata): rhizome creeping, the internodes varying in length, with a solenostele; leaf-trace bundle simple, facing the apex.

d. Dicranophlebium.

A. armata (Swartz) Presl.
H. W. Reichardt, 1859, p. 36, pl. II, fig. 24, 25 (Alsophila aculeata): stem with a radial dictyostele with cortical bundles; leaf-trace bundles numerous.
K. G. Stenzel, 1861, p. 16, pl. I, fig. 1 (Alsophila aculeata): stem with a radial dictyostele, the pith large, the leaf-trace bundles numerous.

A. caracasana Klotzsch.
H. W. Reichardt, 1859, pl. II, fig. 26, 27: stem with a radial dictyostele, with cortical bundles; leaf-trace bundles numerous.

A. microphylla Klotzsch.
H. Karsten, 1847, p. 195: stem with a radial solenostele; leaf-trace simple or divided.

A. paleolata Martius.
P. Lachmann, 1889, p. 49, p. 97, fig. 7, IV, fig. 8—14 (Alsophila eriocarpa): stem with a radial dictyostele, the pith large, with narrow leaf-gaps and numerous mesarch cortical bundles, forming a network, not in connection with the stele but with the numerous leaf-trace bundles.

e. Chnoophora.

A. villosa (H. B. Willd.) Desvaux.
H. W. Reichardt, 1859, p. 34. pl. II, fig. 20—23: stem with a radial dictyostele with internal bundles; leaf-trace bundles numerous.
G. Mettenius, 1864, p. 525: stem with internal strands.

f. Lophosoria.

A. quadripinnata (Gmelin) C. Christensen.
H. Karsten, 1847, p. 195, pl. IX, fig. 1—14 (Alsophila pruinata): stem with a radial solenostele; leaf-trace simple.
G. Mettenius, 1864, p. 520 (Alsophila pruinata): stem with a radial solenostele; leaf-trace simple.

g. Alsophilopsis.

A. aspera (Linn.) R. Brown.
H. W. Reichardt, 1859, p. 32. pl. I, fig. 12—14 (Cyathea aspera): stem with a radial dictyostele, with internal strands; leaf-trace bundles numerous.

§ 2. Species asiaticae et oceanicae.

A. australis R. Brown.
P. Lachmann, 1889, pl. IV, fig. 3—4: stem with a radial dictyostele with a large pith; leaf-trace bundles numerous.

A. crinita Hooker.

W. Schütze, 1905, p. 342, fig. 6: stem with a radial dictyostele with a large pith; inner bundles of the leaf-trace passing through the gap into the pith.

A. excelsa R. Brown.

P. Lachmann, 1889, p. 93, fig. 5, stem with a radial dictyostele with a large pith; leaf-trace bundles numerous.

D. T. Gwynne—Vaughan, 1903, p, 709, fig. 18: in the lowest part of the young plant a haplostele is found; in the higher by pocketing a Lindsaya-stele, then a solenostele is formed.

A. extensa (Forst.) R. Brown.

G. Mettenius 1864, p. 535, pl. VI, fig. 3—13 (Alsophila Haenkei): stem with a radial dictyostele with a large pith; leaf-trace bundles numerous, the inner ones passing through the gap into the pith.

A. Leichhardtiana F. Muell.

P. Lachmann, 1889, p. 93, pl. IV, fig. 5, (Alsophila Moorei): stem with a radial dictyostele; leaf-trace bundles numerous.

CHAPTER VII.

The Stelar Morphology of the Spermophyta.

Of this large group the structure of only a few forms will be considered here. The vast majority of living plants belongs to this group, but representatives are undoubtedly present in Upper Palaeozoic strata, perhaps even in Devonian rocks.

The stem-structure in recent forms presents considerable variations. It can be described as built up from leaf-traces, which pass through the cortex and run down in the stem for some distance, fusing laterally with the trace of the leaf next below. The differences in the structure are caused by the varying number of bundles of which the trace is composed and by the number of internodes through which it passes. Among the fossil Spermophyta some are known, in which the structure is somewhat aberrant, if compared with the normal structure in the group; they enable us to form conclusions about the primitive form from which the several types of structure may be derived. The structure of Lyginodendron Oldhamium will first be considered and compared with that of Heterangium; afterwards they will be compared with the anatomical features present in some other fossil representatives of the group.

Lyginodendron Oldhamium Williamson, (1873, p. 377, pl. 22-28, Williamson and Scott, 1895, p. 705-744, pl. 18-20). This plant is well known from the coal-balls of the English coal-measures; it has also been found in similair concretions in the Carboniferous of Westphalia and Bohemia. Their preservation is often so very perfect, that many structural details can be elucidated. Thus it happens that Lyginodendron is one of the relatively few fossil plants, of which not only the structure of the stem, but also that of the leaves, roots, and reproductive organs has been ascertained. It is well fitted therefore as a starting point for the discussion of the other representatives of the Spermophyta.

Its habit was that of a climbing plant, of the scrambler type, leaning upon and holding itself in an upright position by clinging to trees and shrubs of stronger build. The leaves were rather numerous, placed spirally on the stem and the internodes are distinct but rather short. The main petiole was of a large size, sometimes reaching a diameter of 1 c.M.; they were much branched, the ultimate ramifications bearing the leaflets, which are deeply lobed, with veins diverging from each other at an acute angle. The vascular bundles of the smaller rachises are concentric, the protoxylem placed in the interior of the xylem, towards its lower margin. In the petiole the xylem is V-shaped in transverse section, with the convex side of the bundle directed towards the lower side of the petiole; in these bundles usually three groups of protoxylem are present, one in the middle and one towards the end of each arm.

At the top of the vlins the xylem is commonly dilated. All these characteristics, the considerable thickness of the leaflets, their incurved margins, the presence of a hypodermis, the dilated ends of the vascular bundles, have also been observed in the xerophytic leaves of the Mangrove plants of tropical sea-shores, and possibly indicate a similar habitat. The stem contains a rather large pith (chiefly parenchymatous but containing scattered groups of dark sclerotic tissue) surrounded by a number of distinct xylem-strands, varying from about 5 to 8 or more. This primary xylem consists of collateral mesarch vascular bundles. Outside the ring of vascular bundles is a zone of secundary wood, produced by a cambium, which is sometimes preserved; beyond this cambium there is a well marked zone of phloem, for the most part of secundary origin, but in well preserved specimens a group of primary phloem may be recognized opposite to each of the primary xylem strands. The primary xylem structure of the stem of Lyginodendron is typical of some Gymnosperms, e.g. Taxus, where there is a ring of collateral bundles, situated round a parenchymatous pith and secundary wood and bast, formed by means of a cambium. The pericycle often contains certain groups of thick-walled elements, like those which occur in the pith. The outer cells have generally formed a few layers of periderm, which does not however reach any great development. The inner cortex is parenchymatous, the outer cortex, which is very characteristic, consists of anastomosing strands of fibrous sclerenchyma, forming a network, with the meshes occupied by cellular tissue.

Towards the exterior a few parenchymatous layers terminate the cortex. The petiole was forked a short distance above the insertion. The two bundles of the dichotomy enter the petiole, but remain distinct; they sometimes fuse however after their entry into the cortex but more often after they have entered the pericycle. This double leaf-trace traverses the cortex rather horizontally, but after having entered the pericycle it passes steeply downwards.

But not until some five internodes lower is it united tangentially to an adjacent strand. Consequently the successive stages of the leaf-trace development can be studied in one and the same transverse section.

If the figure, published by Williamson and Scott, (1895, fig. 1. Scott, 1909, p. 359, fig. 129,) be considered, we see 8 vascular bundles situated round the pith and 5 more towards the periphery of the stem; the outer ones are double. Starting from the outermost bundle we see the next situated $^2/_5$ of the circumference further round the stem and lying a little nearer the axis. If the bundles be numbered in this way and the regularity of their disposition, which is caused by the phyllotaxis being about $^2/_5$, be taken into account, the disposition will appear as given in fig. 18. The phase of the bundle which is numbered as 13 will be similar to that of number 12 one internode lower down; two internodes lower down it will be similar to 11 and so on. If we consider the vascular cylinder to be rolled out into one plane, the arrangement of the phases in the bundles may be indicated by the following scheme:

13	5	10	2	7	12	4	9	1	6	11	3	8
12	4	9	1	6	11	3	8	13	5	10	2	7
11	3	8	13	5	10	2	7	12	4	9	1	6
10	2	7	12	4	9	1	6	11	3	8	13	5
9	1	6	11	3	8	13	5	10	2	7	12	4
8	13	5	10	2	7	12	4	9	1	6	11	3
7	12	4	9	1	6	11	3	8	13	5	10	2
6	11	3	8	13	5	10	2	7	12	4	9	1
5	10	2	7	12	4	9	1	6	11	3	8	13
4	9	1	6	11	3	8	13	5	10	2	7	12
3	8	13	5	10	2	7	12	4	9	1	6	11
2	7	12	4	9	1	6	11	3	8	13	5	10
1	6	11	3	8	13	5	10	2	7	12	4	9
13	5	10	2	7	12	4	9	1	6	11	3	8

If we take into account the fact that 1 is fusing with 6, as is shown in the figure, and we use this in the reconstruction of the developped cylinder, the scheme in fig. 19 results.

It is thus clear that the vascular system in Lyginodendron consists of a number of leaf-traces, double in their upper part, which enter the stem and run down for some distance in it, thereafter fusing with the trace belonging to the leaf, which is inserted on the stem 5 internodes higher.

The strand resulting from this fusion follows its downward course in the stem and fuses 5 internodes further down with the trace of the leaf next below. Thus the vascular system is built up from 5 independent systems, formed by the fusion of the leaf-traces of the leaves placed on the same orthostichy. These 5 compound strands have no communication with each other as far as the primary xylem is concerned. This arrangement wholly agrees with that present in the stems of some Gymnosperms and is also the plan on which the more elaborate structure in other Gymnosperms and Angiosperms may be based.

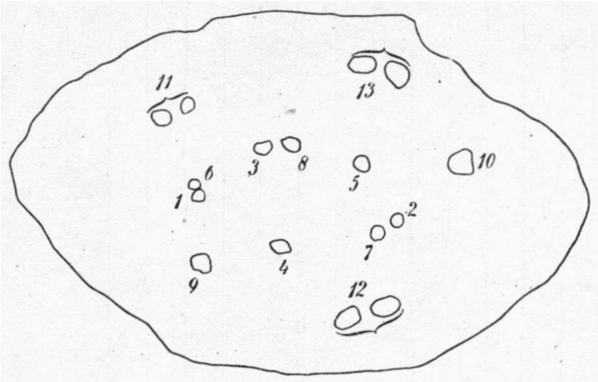

Fig. 18. Lyginodendron Oldhamium Will. Transverse section of the stem, showing the arrangement of the vascular bundles (after Scott, modified).

The arrangement of the tissues in the leaf-traces in Lyginodendron is somewhat different from that in the majority of recent Spermophyta, though it is shown in some Cycadaceae. The small spiral elements (protoxylem) are placed in the interior of the vascular bundle, but nearer its outer than its inner margin. The greater part of the primary wood was thus developed centripetally, i. e. on the inner side of the protoxylem. A smaller portion of xylem occurs on the outer side, — the centrifugal wood —. The protoxylem consists of spiral and annular elements; the tracheids adjacent to it are scalariform, but the bulk of

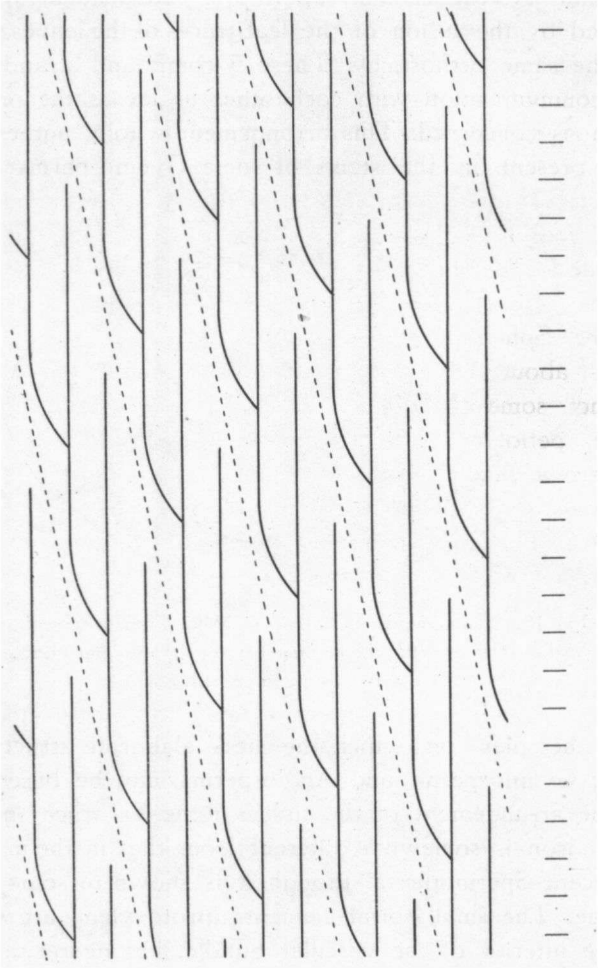

Fig. 19. Lyginodendron Oldhamium Will. Arrangement of the vascular bundles of the stem. The figure shows the absence of a connection between the five sympodia.

the primary wood, especially its centripetal portion is composed of tracheids with bordered pits. On the inner side of the protoxylem some parenchymatous elements are seen. This parenchyma situated in the immediate neighbourhood of the protoxylem can also be distinguished in allied forms.

The other species of Lyginodendron, which are known, have essentially the same structure. In L. heterangioides Kubart tracheids have been observed, scattered in the pith.

Heterangium Corda. Representatives of this genus have been found in Carboniferous strata in France, England, Scotland and Bohemia.

They are characterised by the possession of large leaves of the Sphenopteris type. They possessed long angular stems about $1^1/_2$ cM. in diameter. The internodes are distinct, some cM. long. The leaves were spirally arranged, large, petiolate, the rachis being repeatedly forked with numerous finely segmented leaflets. They have long been known as Sphenopteris, a well known species being S. elegans. The inner cortex of the stem and petiole contains numerous horizontal plates of cells with dark contents, which gives a characteristic transverse striation to the specimens, when that part of the tissue is exposed to view. This characteristic feature is also shown in the petiole of the above mentioned leaves of the Sphenopteris type. This fact has led to the supposition that the plant was closely allied to the Filices, the more so since the anatomy of the stem on account of its solid central xylem-core shows a slight resemblance to the structure present in some Gleicheniaceae and Hymenophyllaceae.

The discovery of the reproductive organs of Lyginodendron, which in spite of differences in structure, is to be regarded as a closely allied form, makes it very probable that here also seeds in actual connection will be found.

The internal structure is well known. For our purpose it will be desirable to take H. Grievii Williamson (Williamson 1873, p. 394, pl. 28—31, Williamson and Scott, 1895, 745—759, pl. 26, 27) as the typical form.

The habit of this plant has been mentioned above; the outer surface of the stem was distinctly ribbed, the ribs corresponding to the decurrent leaf-bases. The cortex clearly shows a division into two parts: the outer cortex of the Sparganium type (i. e. a meshwork of sclerenchyma-bundles, long and narrow, the meshes filled up by parenchymatous tissue), and the inner cortex, which is much wider and consists of thin-walled parenchyma, interrupted by very regular horizontal plates of characteristic dark-celled tissue.

The leaves, which were spirally arranged with $^3/_8$ phyllotaxis in larger stems and a $^2/_5$ phyllotaxis in smaller stems, each received a single bundle. The traces passed very gradually through the cortex and joined the central cylinder at a distance of 6 to 10 internodes below the level at which the leaf is free. The central part of the stem was occupied by a mass of tracheids and parenchyma, extending to the centre. This primary wood consists of anastomosing groups of tracheids interspersed with conjunctive parenchyma. The structure of the primary wood is however not uniform in all its parts. Around the periphery definite clusters of tracheids may be distinguished, each of which corresponds to one of the primary bundles in Lyginodendron. The smallest elements of the clusters are internal, lying at a short distance from its outer limit; these smallest elements are shown in longitudinal sections to be tracheids with a lax spiral tickening; they thus constitute the protoxylem of the bundle. These protoxylem elements are associated with a little parenchyma; towards the external periphery of the bundle they are succeeded by more densely spiral or reticulate tracheides with multiseriate bordered pits; similar pitted elements extend throughout the whole interior of the stele, forming the mass of the primary wood.

If we examine these clusters of tracheids, provided with a protoxylem strand, in a series of successive transverse sections, we find that they continue outwards into the cortex and forms the xylem of the leaf-traces. These leaf-trace bundles have the same structure as the clusters lower down, and are also similar to the leaf-trace in Lyginodendron. Lower down in the stem however they become indistinct and at a somewhat lower level the protoxylem is no longer visible, the lower part of the leaf-trace having lost its individuality.

The phloem is continuous all round the xylem. The outgoing leaf-trace bundles are collateral in their lower part, they become concentric however in the cortex and in the leaf-trace. As a rule a little secundary wood is present in the stem only, not in the leaf-trace.

The arrangement of the leaf-trace and their downward extension is well shown in the figure given by Scott (1904, p. 404, fig. 155), see fig. 20. In another species, H. tiliaeoides Williamson (1887, p. 281, pl. 21, 22; W. and Scott, 1895, p. 760, pl. 29) the structure is essentially similar to that of H. Grievii. The mesarch primary xylem bundles at the periphery of the wood are more distinct and at once strike the eye as discrete bundles, separated from one another by bands of conjunctive tissue.

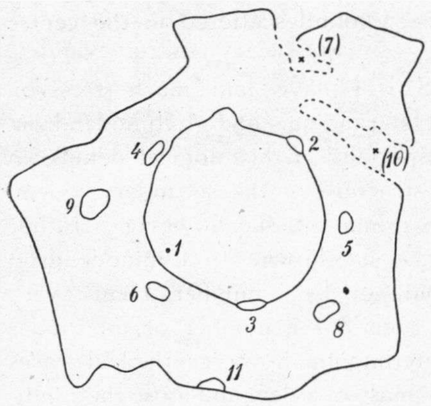

Fig. 20. Heterangium Grievii Will. Transverse section of the stem showing the arrangement of the leaf-trace (after Scott, modified).

The primary phloem corresponding to the more internal xylem strand can be easily recognized. The leaf-trace is double where it enters into the stele and this character is also present in all Heterangiums from the coal balls, except in H. minimum. Scott (1917, p. 90) classes all species with a double leaf-trace in his subgenus Polyangium, while those with a trace, simple at its insertion, are placed in the subgenus Eu-Heterangium.

Other representatives of the genus have been described by Renault from the Permian of France; they all belong to the subgenus Polyangium; Kubart had recorded other forms from the Carboniferous of Bohemia, which belong to Eu-Heterangium; one of them, H. Andraei, being in many respects an intermediate form between Heterangium and Lyginodendron, especially Lyginodendron heterangioides, where tracheids have been found scattered in the centre of the pith.

Williamson and Scott have laid much stress on the affinity between Heterangium and Lyginodendron. This affinity appears especially in histological details, in the leaves, and in the structure of the secundary xylem. In the structure of the primary tissue however a rather large important difference is shown. In Lyginodendron the vascular system is built up by a number of leaf-traces, which run down in the stem for a number of internodes and fuse laterally. In Heterangium, however, the leaf-traces are inserted into a solid mass of xylem and loose their individuality at a somewhat lower level. The two forms agree in the structure of the leaf-traces, which are mesarch in both. The structure of Lyginodendron indeed may be considered as derived from Heterangium by the reduction of the central xylem and by the downwards extension of the leaf-traces. The tracheids situated in the centre of the stem are no longer developed and the lower parts of the leaf-traces are prolonged and are connected with others by lateral fusion. If this supposition be true, a number of transitional stages might be expected. The presence of detached tracheids in the pith may be considered as a remnant of the former central xylem-tissue. In Heterangium tiliaeoides the central xylem is less well developed than in H. Grievii, and the contrast between the peripheral parts of the leaf-traces and the central xylem-tissue is much greater than in H. Grievii. In Megaloxylon Scottii Seward central xylem-tissue is also present and the lower part of the leaf-trace merges gradually into the stem-xylem. In Calamopitys the leaf-traces are prolonged, so that their lower parts fuse laterally, nevertheless in some species of this genus tracheids are found scattered in the pith. In one species of Lyginodendron, L. heterangioides, internal tracheides occur also.

Transitional stages between the structure of Lyginodendron and Heterangium may also be seen in the degree of the downward prolongation of the leaf-traces throughout the groups of plants to which these genera belong. In Heterangium the traces end blind; in Megaloxylon this is also the case; the lower parts of the leaf-traces are still functionally united by the central xylem.. In Pitys antiqua, however, the leaf-bundles enter into the pith and end blind in that tissue. In Poroxylon this also seems to be the case, but in contrast with the structure in Pitys, the leaf-traces are always situated on the margin of the pith in contact with the secundary wood. The cambium in the vascular bundle in Poroxylon seems to have been formed between the xylem and the phloem of the primary bundle, but this does not appear to have been the case in Pitys. In Cordaites and Mesoxylon the leaf-traces seem to loose their individuality in their lower part. Thus all conditions occur which may be considered as transitional between a stele with a solid central xylem and leaf-traces, which end blind in their lower parts, and a vascular system composed of a number of leaf-traces in which the lower parts fuse laterally, to form a system of compound bundles lying around a pith, occupying the place of xylem, which has disappeared by reduction.

If the type of structure, which is supposed to be primitive in the Spermophyta, be compared with that, which has been considered in the former chapters as the basic form in the Filices, it is evident that they are essentially alike. In both the primitive form of the stem structure is supposed to have been a solid mass of xylem of which the differentation is independent of the leaf-trace. The leaf-traces, each composed of a number of elementary bundles, are inserted into the stem-xylem and the differentiation of the tissues near the insertions of the traces is independent of any differentation in the xylem of the stem itself. From both primitive types a similar type of structure is formed, viz. a system of vascular bundles situated round a mass of parenchymatous tissue, either the whole surrounded by a single endodermis (Osmunda, Lyginodendron), or each bundle marked off from the central parenchymatous tissue by a separate endodermis (most Polypodiaceae, some Primula spec.). The way in which this process takes place is however very different in the two groups. In the Filices, as far as they have been considered, the xylem adaxial to the protoxylem strands is reduced first of all. The reduction of this xylem to parenchyma affects the xylem of the stem. A reduction of the central part of the stem-xylem may also take place independently; in the former case the pith is produced by the downward prolongation of the funnels. The result is a hollow tube, the wall of which is pierced by numerous perforations, situated above the insertions of the leaf-traces.

In the Spermophyta however, the reduction of the stem-xylem has taken place in another way. It is not in relation to the leaf-trace, nor is the central part of the xylem more reduced than the outer layers. The stem-xylem is reduced as a whole and the connection between the lower part of the leaf-traces is effected not through the remnants of the stem-xylem as in the Filices, but by the downwards prolongation of the leaf-traces themselves.

Certain characteristics of the leaf-traces may be correlated with the other mode of reduction of the xylem of the stem. The protoxylem in the Filices is associated with some parenchymatous cells. These always occur, but are separated from the stem-xylem or from the pith in the forms, discussed above, by tracheids, which are situated adaxially to this parenchyma, the centripetal wood.

In all cases where the stem-xylem or its remnants are present, this centripetal xylem is also found. In recent Spermophyta, except in the Cycadaceae, it is wanting, but its presence in the latter group and in many fossil forms is an argument for the supposition that the reduction of the stem-xylem is not connected with the reduction of the centripetal xylem of the leaf-trace, for the latter has been reduced after the atrophy of the elements of the stem-xylem.

The centripetal wood separated the parenchyma, which is situated near the protoxylem of the leaf-trace, from the xylem of the stem. It thus prevented the gapping of the stem by the incoming leaf-traces. The reduction of the centripetal xylem began in the lower parts of the leaf-trace and proceeded upwards; the last remnant may still be found in the petioles and the leaves.

Thus the centripetal xylem, which has been named the "cryptogamic wood, the old wood", is characteristic of the Spermophyta and not of the Pteridophyta, as has formerly been supposed.

The affinity of the Filices and the Spermophyta thus appears to be a remote one. They differ not only in their reproductive organs, but also in the essential features of their anatomical structure. The supposed affinity between the Ferns and such plants as Lyginodendron (which led to the formation of the group of Pteridosperms) was based upon the superficial resemblance of the leaves of this group with those of the Ferms. This close affinity was also expressed in the phylum Pteropsida, defined by E. C. Jeffrey (1903, p. 144). But from the above considerations it is clear that the interruption in the vascular tissue in Lyginodendron, resulting from the insertion of the leaf-trace, is quite different from the leaf-gap present in the Ferns. In the former they 'are really the spaces between the bundle systems of the leaves, situated on one and the same ortostichy, and are not limited above or below.

Put otherwise, the leaf-traces are inserted through a primary medullary ray.

It is very interesting to see, that the structure most closely resembling that of the Spermophyta may be found in the Lycopodiales. It is also interesting to note that only in this group the presence of seed-like organs has been demonstrated in other plants than the Spermophyta e.g. in Lepidocarpon and Mazocarpon. The tendency towards the seed-habit in a group in which the stelar-morphology is similar to that of the Spermophyta, seems to strenghten the supposition, that the affinity between the Lycopodiales and the Spermophyta is a closer one than that between the Spermophyta and the Filices. Because the similarity is shown in those essential features, which characterise the primitive forms in each group, e. g. in the way in which the stem-xylem is reduced and the position of the protoxylem in the leaf-trace.

After this has been printed the third edition of Scott, Studies in fossil botany, Vol. II, 1923 came in my hands. His figg. 17, pg. 31 is essentially the same as fig. 19 of the present memoir.

Summary of the results.

Regarding the anatomical structures in the forms mentioned above, the following conclusions may be drawn:

a. concerning Vascular Plants in general:

1. The vascular system in Ferns and Spermophyta is built up of stem xylem and leaf-trace xylem and surrounding tissues; the differentiation in each is independent of that of the other.
2. The stem xylem is situated in the central part of the axis and confined to it; its first formed elements may be arranged in different ways.
3. The vascular system of the leaf is composed of a number of elementary bundles, which originate in the leaf and run downwards, nearly always reaching the insertion into the stem xylem and running for a short distance in this part of the stem; the differentiation here is continuous with that in the leaf-trace. They consist of an originally mesarch xylem bundle, surrounded by an endodermis and phloem; they may remain separate or form a continuous bundle; lower down their number is reduced by fusion; their arrangement gives the different forms of transverse sections.
4. The originally mesarch protoxylem of the elementary bundle is associated with an amount of parenchyma, situated at its adaxial side.

b. concerning Ferns in general.

5. In the Ferns this parenchyma is well developed and the metaxylem at the adaxial side is reduced; lower down this parenchyma diminishes in size and ends blind; a funnel is thus formed in the metaxylem.

6. This funnel extends towards the insertion of the leaf-trace into the stem-xylem; its lowest point may be at different levels; it may even penetrate the stem xylem causing the leaf-trace to be endarch over its whole length and the stem xylem in the axil of the leaf-trace to be reduced; a groove or interruption is then formed in it opposite the leaf-trace.
7. The central part of the stem xylem may be reduced or not; in the first case the funnels may in their higher part pierce through into the hollow cylinder of the wood, thus forming a gap above the insertion of each leaf-trace; the lowest part of this gap is seen as a little funnel decurrent into the stem xylem; the protoxylem is imbedded in the metaxylem below this level. In the second case the funnels penetrate into the solid stem xylem and those of successive leaves may unite, thus hollowing the xylem and forming a tubular bundle with gaps above the insertions of the leaf-traces. The protoxylem decurrent from the leaf-trace is never imbedded in the metaxylem and a small funnel is never formed below the insertion of the leaf-trace into the stem xylem.
8. In such gaps other elements may be differentiated, such as phloem, endodermal cells and sclerotic tissue, similar to that of the cortex.
9. The lateral fusion of the elementary bundles, the size of the funnels, the reduction of the stem xylem and the length of the internodes are independent of each other; the relationship between these factors brings about the difference in the various structures.

c. concerning Spermophyta in general:

10. In Spermophyta the parenchyma at the adaxial side of the protoxylem is less developed; it does not break through the centripetal xylem, neither does it reduce the stem xylem.

11. The stem xylem is reduced here as a whole. not in relation to the insertions of the leaf-traces. The leaf-traces may be prolonged downwards and fuse laterally; in the simplest case they form a number of sympodially arranged bundles; the "interruption" in the vascular tissues opposite the incoming leaf-trace (in transverse section) is simply the space between these sympodia.
12. The centripetal xylem is often reduced later, after the reduction of the stem xylem and independent of it; this reduction is most obvious in the lowest part; in the higher portions of the leaf-trace the centripetal xylem may still be present; this centripetal wood, the so-called "cryptogamic wood" is found in Spermophyta only.

d. concerning both groups:

13. In both groups the result is similar: the formation of a number of vascular strands, situated round or in a parenchymatous tissue.

e. concerning some groups of Ferns:

14. In the Osmundaceae the leaf-trace consists in the lowest part of only one elementary bundle, except in Osmunda javanica, where there are two; the central part of the stem xylem is mostly reduced. The following main structural types may be distinguished: In Thamnopteris the funnel does not reach so far as the stem xylem, its lowest point is still above the insertion. In Osmundites Dunlopi the funnel penetrates into the stem xylem, but does not break through the wood of the cylinder; in O. Kolbei this is interrupted, a "gap" is formed, the lowest margin of which lies above the insertion; in Osmunda regalis this margin usually lies below it. In Osmunda javanica two groups of protoxylem remain distinct, each ending with a separate funnel. In Osmundites Kolbei, in Osmunda

regalis and in Osmunda javanica loose tracheides may be found scattered in the pith; they may be considered as remnants of the former central xylem, the factors influencing their differentiation reaching in abnormal circumstances the "threshold" value. In the young plants similar structures may be found.

15. In the Gleicheniaceae the xylem in the stem is solid; in the axil of the leaf-trace a funnel is formed; in Gleichenia pectinata a pith is formed by reduction of the stem xylem and in the lowest part of the leaf-trace, which has three protoxylem strands, a funnel is found near each group and ending blind and separate. In Stromatopteris this funnel does not reach the insertion of the leaf-trace into the stem xylem; in Platyzoma it reaches the stem xylem but does not interrupt it, the centra portion of the stem xylem may be more or less reduced.
16. In the Dineuroidaceae the peculiar form of transverse sections of the petiole is caused by the different orientation of the pinnae to the petiole; the parenchyma adaxially to the protoxylem strands interrupts the peripheral loop; this parenchyma is decurrent into the petiolar strand for a short distance above the insertion into the stem xylem; it is associated with the protoxylem and ends blind as a funnel. In the Clepsydropsidaceae the structure is built up otherwise.
17. In the Polypodiaceae and the Cyatheaceae the central part of the stem xylem is never reduced. It may be solid, as in Cheiropleuria, where the funnel scarcely penetrates into the stem xylem, or hollowed by fusion of the funnels of successive leaf-traces. The structure varies much in accordance with the different size of the gaps, the length of the internodes, and the number of elementary bundles in the lowest part of the leaf-trace.

f. concerning some Spermophyta.

18. In the Spermophyta the simplest structure is found in Heterangium which has a solid stem xylem; the leaf-traces become indistinct some distance below their insertion. In Poroxylon the stem xylem is reduced; the bundles are but slightly fused in their lower parts. In Lyginodendron they are wholly fused, forming a number of sympodially arranged strands round the pith. Scattered tracheides as a remnant of the stem xylem have been found in the pith of some species of Calamopitys and Lyginodendron.

g. concerning the relation between the Filices and Spermophyta.

19. The structure in Ferns and Spermophytes is built up along different lines; grouping them together into the Pteropsida seems to me unjustifiable.

h. general remarks.

20. No conclusions have been drawn from the position of the phloem; its study will no doubt give interesting results.
21. The position of the endodermis is of a secundary morphological importance.
22. The constant orientation of the parenchyma, which is associated with the protoxylem to the adaxial side of the leaf-blade has perhaps some physiological meaning.

LIST OF LITTERATURE.

A. de Bary, 1877. Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne. Handb. der Phys. Bot. Bd. III, Leipzig, 1877.

P. Bäsecke, 1908. Beiträge zur Kenntniss der physiologischen Scheiden der Filicinen-Achsen und -Wedel, sowie über den Ersatz des Korkes bei den Fillicinen. Diss. Marburg, 1908. Bot.-Zeit., Bd. 88, p. 25—88, with 3 pl.

R. Beck, 1920. Ueber Protothamnopteris Baldaufii, einen verkieselten Farn aus dem Rotliegenden der Chemnitzer Gegend. Abh. der Sächs. Acad. der Wiss. Math.-Phys. Kl., Bd. 36, 1920, Nr. 5, with 1 pl.

H. Beddome, 1883. Handbook of the Ferns of British India, Ceylon and the Malay Peninsula. Calcutta, 1883.

C. Eg. Bertrand, 1880. Theorie du faisceau. Bulletin scientifique du département du Nord. 2me sér. 3me ann., 1880.

C. Eg. Bertrand et F. Cornaille, 1902. Étude sur quelques caractéristiques de la structure des Filicinées actuelles. I. La masse liberoligneuse élementaire des Filicinées actuelles et ses principaux modes d'agencement dans la fronde. Trav. et Mém. de l'Univ. de Lille. T. X. Mém. 23. Lille, 1902. 220 p.

P. Bertrand, 1909. Études sur la fronde des Zygopteridées. Thèse Lille, 1909, with atlas.

P. Bertrand, 1911. Nouvelles remarques sur la fronde des Zygopteridées. Bull. de la Soc. d'hist. nat. d'Autun, T. 25, 1911, p. 18—23 with 2 plates.

P. Bertrand, 1912. L'étude anatomique des Fougères anciennes et les problèmes qu'elle soulève. Progr. rei, Bot. Bd. 4, 1912, p. 182—302.

L. A. Boodle, 1899. Stem-structure in the Schizaeaceae, Gleicheniaceae, and Hymenophyllaceae. Ann. of Bot., vol. 13, 1899, p. 624—626.

L. A. Boodle, 1901. On the Anatomy of the Gleicheniaceae. Ann. of Bot., vol. 15, 1901, p. 703—749, with 2 pl.

L. A. Boodle and W. E. Hiley, 1909. On the Vascular Structure of some Species of Gleichenia. Ann. of Bot., vol. 23, 1909, p. 419—432, with 1 pl.

F. O. Bower, 1908. The Origin of a Land-Flora. A Theory based upon the fact of alternation. London, 1908.

F. O. Bower, 1910. Studies in the Phylogeny of the Filicales. I. Plagiogyria. Ann. of Bot., vol. 24. 1910, p. 236—239.

F. O. Bower, 1912. Studies in the Phylogeny of the Filicales. II. Lophosoria, and its relation to the Cyatheoideae and other Ferns. Ann. of Bot., vol. 26, 1912, p. 269—324, with 7 pl.

F. O. Bower, 1913. Studies in the Phylogeny of the Filicales. III. On Metaxya and certain other relatively primitive Ferns. Ann. of Bot., vol. 27, 1914, p. 444—478, 3 pl.

F. O. Bower, 1914. Studies in the Phylogeny of the Filicalis. IV. Blechnum and allied Genera. Ann. of Bot., vol. 128, 1914, p. 363—423, 11 pl.

F. O. Bower, 1915. Studies in the Phylogeny of the Filicales. V. Cheirophleuria bicuspis (Bl.) Presl., and certain other related Ferns. Ann. of Bot., vol. 29, 1915, p. 496—529, 2. pl.

F. O. Bower, 1916. On leaf-architecture as illuminated by a study of Pteridophyta. Trans. Roy. Soc. Edinburgh, vol. 51, 1916, p. 657—708, with 1 pl.

F. O. Bower, 1917. Studies in the Phylogeny of the Filicales. VI. Ferns showing the Acrostichoid condition with special Reference to Dipterid derivates. Ann. of Bot., vol. 31, 1917, p. 1—40, 2 pl., 13 fig.

F. O. Bower, 1918. Studies in the Phylogeny of the Filicales. VII. The Pteroideae. Ann. of Bot., vol. 32. 1918, p. 1—69, 43 fig.

F. O. Bower, 1920. Size, a neglected Factor in Stelar Morphology. Proc. Roy. Soc. Edinburgh, vol. 41, 1920, p. 1—26.

F. O. Bower, 1923*a*. Studies in the Phylogeny of the Filicales. VIII. On Loxsoma and Loxsomopsis. Ann. of Bot., vol. 37, p. 349—354. 1923.

F. O. Bower, 1923*b*. The Ferns. I. Cambridge, 1923.

G. Brebner, 1902. On the Anatomy of Danaea and the other Marattiaceae. Ann. of Bot., vol. 16, 1902, p. 516—552, 2 pl.

J. Briquet, 1917. Les nervures incomplètes des lobes dans le corolle dans le genre Adenostylis. C. R. de la Soc. phys. et d'Hist. nat. de Genève. vol. 32, 1916, p. 23—26. Genève, 1917.

H. de Bruyn, 1911. The Ontogenetic Development of the Stele in Two Species of Dipteris. Ann. of Bot., vol. 25, 1911, p. 761—772, 2 pl.

D. H. Campbell, 1887. The development of the Ostrich Fern, Onoclea struthiopteris. Mem. Boston Soc. Nat. History, vol. 4. Boston, 1887, p. 17—53.

D. H. Campbell, 1918. The structure and development of mosses and Ferns (Archegoniates). Third Ed. New-York, 1918.

S. E. Chandler, 1905. On the arrangment of the Vascular Strands in the "Seedlings" of Certain Leptosporangiate Ferns. Ann. of Bot., vol. 19, 1905, p. 365—408, with 3 pl.

R. Chodat, 1908. Les Pteropsidées des Temps Palaeozoiques. Étude critique. Arch. Sc. phys. et nat. CXIII ann., 4me per., t. 26, 1908. p.

H. Christ, 1987. Die Farnkräuter der Erde. Jena, 1897.

H. Christ, 1910. Die Geographie der Farne. Jena, 1910.

C. Christensen, 1906. Index Filicum. Hafniae, 1906.

C. Christensen, 1920. A. Monograph of the Genus Dryopteris. Part II. The tropical American bipinnate-decompound species. Mem. Acad. Roy. des Sc. et des Lettres de Danemark. Sect. des Sciences. Kopenhague. 8me Serie T. VI. no. I. 1920.

G. Colomb, 1888. Essai d'une classification des Fougères basée sur leur étude anatomique et morphologique. Bull. Soc. Bot. de France, T. 35, 1888, p. 98—103.

R. H. Compton, 1909. The Anatomy of Matonia sarmentosa Baker. New Phyt. vol. 8, 1909, p. 299—301.

H. Shoemaker Conard, 1908. The structure and Life History of the Hay-scented Fern. Carnegie Inst. Washington. Publ. no. 94. Washington, 1908, 56 p., 25 pl.

E. B. Copeland, 1907. Pteridophyta Halconensis: A List of the Ferns and Fern-Allies collected by Elmer D. Merril on Mount Halcon, Mindoro. Philippine Journ. of Science, C. Botany, vol. II, 1907, p. 119—150, with 4 pl.

E. B. Copeland, 1909. The Ferns of the Malay-Asiatic Region, Part. I. Philippine Journ. of Science, C. Botany, vol. IV, 1909, p. 1—67, with 21 pl.

A. J. Corda, 1867. Flora Protogaea. Beiträge zur Flora der Vorwelt. Neue Ausgabe. Berlin 1867.

F. Cornaille see C. Eg. Bertrand.

J. E. Cribbs, 1920. Early stem-anatomy of Todea barbara. Bot. Gaz., vol. 70, 1920, p. 279—294, with 4 pl.

S. C. Dale see A. C. Seward.

R. C. Davie. The structure and affinities of Peranema and Diacalpe. Ann. of Bot., vol. 26, 1912, p. 245—268, with 2 pl.

R. C. Davie, 1917. On the leaf-trace in some pinnate Leaves. Trans. Roy. Soc. Edinburgh, vol. 52, 1917, p. 1—37, with 1 pl.

R. C. Davie, 1918. A comparative List of Fern Pinnatraces, with some Notes on the Leaf Trace in the Ferns. Ann. of Bot., vol. 32, 1918, p. 233—245.

J. W. Dawson, 1881. On new Erian and Devonian Plants. Quart. Journ. of Geol. Soc., London, vol. 37, 1881.

L. Diels, 1899. Loxsoma, Cyatheaceae, Polypodiaceae, in Engler und Prantl. Die natürliche Pflanzenfamilien. I. Teil, Abt. IV, 1899, p. 112—336.

H. Douliot see Ph. Van Tieghem.

C. Dunzinger, 1901. Beiträge zur Kenntniss der Morphologie und Anatomie der Genera Hemionitis, Gymnogramme, und Jamesonia. Diss. Erlangen, 1901. 48 p., with 4 pl.

D. C. Eaton, 1879. The ferns of North-America. 2 vol. Salamanca, 1879—1880.

J. H. Faull, 1901. The anatomy of the Osmundaceae. Bot. Gaz., vol. 32, 1901, p. 381—420, with 4 pl. (University of Toronto studies. Biol. stud. No. 2, Toronto, 1902).

J. H. Faull, 1909. The stele of Osmunda cinnamomea. Trans. Canadian Inst., vol. VIII, 1909, p. 515—535, with 3 pl.

S. O. Ford see A. C. Seward.

K. Giesenhagen, 1892. Ueber Hygrophile Farne. Flora, Bd. 76, 1892, p. 157—182.

K. Göbel, 1913. Loxsoma und das System der Farne. Flora, Bd. 105, 1912, p. 33—52.

W. T. Gordon, 1911 *a*. On the Structure and Affinities of Diplolabis Römeri (Solms). Trans. Roy. Soc. of Edinburgh, vol. 47, 1911, p. 711—736, with 4 pl.

W. T. Gordon, 1911 *b*. On the Structure and Affinities of Metaclepsydropsis duplex (Williamson). Trans. Royal Soc. of Edinburgh, vol. 48, 1911, p. 163—190, with 4 pl.

D. T. Gwynne—Vaughan 1901 *a*. Observations on the Anatomy of Solenostelic Ferns. I. Loxsoma. Ann. of Bot., vol. 15, 1901, p. 71—98, with 1 pl.

D. T. Gwynne—Vaughan, 1901 *b*. Some observations upon the Vascular Anatomy of the Cyatheaceae. Ann. of Bot., vol. 15, 1901, p. 776.

D. T. Gwynne—Vaughan. 1903, Observations on the Anatomy of Solenostelic Ferns. II. Ann. of Bot., vol. 17, 1903, p. 689—742, with 3 pl.

D. T. Gwynne—Vaughan, 1905. On the possible existence of a Fern-Stem, having the form of a lattice-work tube. New Phyt., vol. 4, 1905, p. 211—216.

D. T. Gwynne—Vaughan, 1911. Some Remarks on the Anatomy of the Osmundaceae. Ann. of Bot., vol. 25, 1911, p. 525—536.

D. T. Gwynne—Vaughan, 1914. On a mixed Pith in Osmunda regalis. Ann. of Bot., vol. 28, 1914, p. 351—354, with 1 pl.

D. T. Gwynne—Vaughan, 1916 a. Observations on the Anatomy of the Leaf in the Osmundaceae. Ann. of Bot., vol. 30, 1916, p. 487—493, with 1 pl.

D. T. Gwynne—Vaughan, 1916 *b*. On some climbing Davallia's and the petiole of Lygodium. Ann. of Bot., vol. 30, 1916, p. 495—706, with 1 pl.

D. T. Gwynne—Vaughan see R. Kidston.

C. Haberlandt, 1918. Physiologische Pflanzenanatomie. 5. Aufl., Leipzig, 1918.

B. Hayata, 1915. Can Prosaptia properly be placed under Davallia? i.e. is it really distinct from Polypodium? Bot. Mag., Tokyo, vol. IX, p. 161—168.

W. E. Hiley see L. A. Boodle.

A. Hillmann, 1910. Vergleichend-Anatomische Untersuchungen über das Rosaceenhypanth. Beih. zum Bot. Centralbl. Bd. 26, 1910, p. 377—421.

W. J. Hooker and J. G. Baker, 1874. Synopsis Filicum. Sec. London, 1874.

E. C. Jeffrey, 1897. The Morphology of the Central Cylinder in Vascular Plants. Rep. British Assoc. Toronto, 1897, p. 869—870.

E. C. Jeffrey, 1899. The Morphology of the Central Cylinder in the Angiosperms. Trans. Canadian Inst., vol. VI, 1899, p. 599—636, 5 pl.

E. C. Jeffrey, 1901. The Anatomy and Development of the Stem in the Pteridophyta and Gymnosperms. Ann. of Bot., vol, 15, 1901, p. 779—781. Proc. Roy. Soc., vol. 69, 1901.

E. C. Jeffrey, 1902. The structure and the development of the stem in the Pteridophyta and Gymnosperms. Phil. Trans. Roy. Soc. London. (B), vol. 195, 1902, p. 119—146, with 6 pl.

E. C. Jeffrey, 1910. The Pteropsidae. Bot. Gaz., vol. 50. 1910, p. 401—414.

E. C. Jeffrey, 1918. The Anatomy of Woody Plants. Chicago, 1918.

M. Jossa, 1914. Le developpement de l'appareil conducteur dans les rhizomes des Osmundacées et des Gleicheniacées. Univ. de Genève. Inst. de Bot.; 6me sér., T. XII. Genève, 1914, p. 1—42.

G. Karsten, 1849. Die Vegetations organe der Palmen. Abh. königl. Akad. der Wiss. Berlin. (1847) Berlin 1849, p. 73—236. with 9 pl.

E. M. Kershaw, 1910. A Fossil Solenostelic Fern. Ann. of Bot., vol. 24, 1910, p. 683—691, 1 pl.

R. Kidston. 1908. On a new species of Dineuron and of Botryopteris from Pettycur, Fife. Trans. Roy. Soc. Edinburgh, vol. 46, 1908, p. 361—363, with 1 pl.

R. Kidston, 1910. Note on the petiole of Zygopteris Grayi Will. Ann. of Bot., vol. 24. 1910, p. 451—455, with 1 pl.

R. Kidston and D. T. Gwynne—Vaughan. 1907. On the Fossil Osmundaceae. Part I. Trans. Roy. Soc. Edinburgh, vol. 45, 1907, p. 759—780, with 6 pl.

R. Kidston and D. T. Gwynne—Vaughan, 1908. On the Fossil Osmundaceae. Part. II. Idem, vol. 46, 1908, p. 213—232, with 4 pl.

R. Kidston and D. T. Gwynne—Vaughan, 1909. On the Fossil Osmundaceae. Part. III. Idem, vol. 46, 1909, p. 651—668, with 8 pl.

R. Kidston and D. T. Gwynne—Vaughan, 1910. On the Fossil Osmundaceae. Part. IV. Idem, vol. 47, 1910, p. 455—478, with 4 pl.

R. Kidston and D. T. Gwynne—Vaughan, 1914. On the Fossil Osmundaceae. Part. V. Idem, vol. 50, 1914, p. 469—480, with 4 pl.

R. Kidston and D. T. Gwynne—Vaughan, 1908 a. On the Origin of the adaxially curved Leaf-trace in the Filiclales. Proc. Roy. Soc, Edinburgh, vol. 28, p. 433—436.

S. Kisch, 1907. On the Development and Function of certain structures in the Stipe and Rhizome of Pteris aquilina and other Pteridophyts. Proc. Trans. Roy. Soc. Canada. 3d ser., vol. I., 1907, p. 353—412, with 21 phot.

L. Klein, 1881. Bau und Verzweigung einiger dorsiventral-gebauter Polypodiaceen. Nova Acta, Bd. 42, 1881, p. 333—396, with 4 pl.

B. Kubart, 1908. Pflanzenversteinerungen erhaltende Knollen aus dem Ostrauer-Tarnowitzer Kolenbecken. Sitzungsber. kaiserl. Akad. der Wiss., math. naturwiss. Kl.. Bd. 117, Abt. I. 1908, p. 571—578, 1 pl.

B. Kubart, 1911. Corda's Sphaerosiderite aus dem Steinkohlenbecken Radnitz-Braz in Böhmen nebst Bemerkungen über Chorionepteris gleichenioides Corda. Sitzungsber. kaiserl. Akad. der Wiss. math. naturw. Klasse, Bd. 120, Abt. I. 1911, p. 1035—1048, 2 p.l

R. Kuhn, 1889. Untersuchungen über die Anatomie der Marattiaceen und andere Gefäszkryptogamen. Flora, Bd. 72, 1889, p. 457—504, 3 pl.

G. Kunze. 1848—1851. Die Farrnkräuter in kolorierten Abbildungen naturgetreu erlätert und beschrieben. Supplement zu Schkuhr's Farrnkräuter. Zweiter Band, Leipzig, 1848—1851, with 40 pl.

P. Lachmann, 1884. Recherches sur le système liberoligneux des Fougères. Bull. de la Soc. bot. de Lyon. 1884.

P. Lachmann, 1885. Recherches sur la morphologie et l'anatomie des Fougères. C. R. de l'Acad. des Sc. vol. 101, 1885, p. 603—609.

P. Lachmann, 1885. Sur la nature caulinaire des stolons de Nephrolepis. Bull. de la Soc. bot. de Lyon, 1885.

P. Lachmann, 1886*a*. Sur la structure du Davallia Mooreana. Bull. de la Soc. bot. de Lyon. 1886.

P. Lachmann, 1886*b*. Sur des racines gemmipares de l'Anisogonium seramporense. Bull. de la Soc. bot. de Lyon. 1886.

P. Lachmann, 1887. Stucture et croissance de la racine des Fougères. Origine des radicelles. Bull. de la Soc. bot. de Lyon. 1887.

P. Lachmann, 1889. Contributions à l'histoire naturelle de la racine des Fougères. Thèse Paris, 1889.

M. Leclerc du Sablon, 1890. Recherches anatomiques sur le formation de la tige des Fougères. Ann. des Sc. nat. Bot. 7me serie, t. 11, 1890, p. 1—17, 2 pl.

H. Link, 1837. Ueber den Bau der Farrnkräuter. I. Abh. kön. Akad. der Wiss. Berlin. (1834) Berlin 1837, p. 375—388, with. 2 pl.

J. P. Lotsy, 1909. Vorträge über Botanische Stammesgeschichte. Bd. 2, Jena, 1909.

H. Luthje, 1914. Beitrage zur Anatomie von Struthiopteris germanica (Willd.). Diss. Kiel, 1914, 38 p., 6 pl.

A. S. Marsh, 1914. The Anatomy of some Xerophilous Species of Cheilanthes and Pellaea. Ann. of Bot., vol. 28, 1914, p. 671—685.

G. Mettenius, 1864. Ueber den Bau von Angiopteris. Abh. math.-phys. Kl. der kön. Sächs. Ges. der Wiss. Bd. 6, 1864, p. 501—570, with 10 pl.

F. J. Meyer, 1917*a*. Die Stelärtheorie und die neuere Nomenclatur zur Beschreibung der Wasserleitungsbahnen der Pflanzen. Beih. Bot. Centralbl. Bd. XXXIII. I. Abt. 1917, p. 129—168.

F. J. Meyer. 1917*b*. Bau und Ontogenie der Wasserleitungsbahnen und der an diesen angeschlossenen Siebtheile in den vegetativen Achsen der Pteridophyten, Gymnospermen und Angiospermen. Progr. rei Bot. Bd. V. 1917, p. 520—588.

A. Nestler, 1894. Ueber Ringfasciation. Sitzungsber. kais. Acad. der Wiss., Math-phys. Kl. Bd. CIII, Abt. I, 1894, p. 153—168, 2 pl.

H. Nördlinger, 1859. Querschnitte von Hundert Holzarten, Zweiter Band. Stuttgart, 1859.

G. Ogilvie, 1859. On the Form and Structure of the Fern-Stems. Ann. Mag. of Nat. Hist., 1859.

Yudzura Ogura, 1921. On the Gaps in the Stele of some Polypodiaceae. Bot. Mag., Tokyo, vol. 35, 1921, p. 113—125.

E. M. Osborn, 1915. Preliminary observations on an Australian Zygopteris. Rep. British Assoc., Liverpool, 1915, p. 727.

P, Parmentier, 1899. Recherches sur la structure de la feuille des Fougères et sur leur classification. Ann. Sc. nat. Bot. 8me sér., T. IX, 1899, p. 290—363.

G. Poirault, 1892. Sur la structure des Gleicheniacées. C. R. l'Acad. des Sc. T. 115, Paris, 1892, p. 1100—1103.

G. Poirault, 193. Recherches anatomiques sur les Cryptogames vasculaires. Ann. Sc. nat. Bot. 7me série, T. XVIII, 1893, p. 113—256. Thèse Paris 1893/1894, no. 8.

O. Posthumus, 1923. Etapteris Bertrandi Scott, een nieuwe Etapteris van het Boven-Carboon van England (Lower Coal Measures), en zijne beteekenis voor de stelair-morphologie. Versl. Kon. Akad. van Wetensch. Amsterdam, deel XXXII, 1923, p. 850—855, 5 fig.

O. Posthumus, 1924. Osmundites Kidstoni Stopes. Ann. of Bot. vol. 38, 1924, p. 215.

H. W. Reichardt, 1859. Ueber die Gefäszbündelvertheilung im Stamme und Stipes der Farne. Denkschr. math.-naturw. Kl. der Kais. Akad. der Wiss. Bd. 17. Wien 1859, p. 21—48. with 3 pl.

B. Renault, 1896. Bassin houiller et Permien d'Autun et d'Epinac. Flore fossile. Fasc. IV. 1896.

A. Rippel, 1913. Anatomische und physiologische Untersuchungen über die Wasserbahnen der Dikotylen Laubblätter, mit besonderer Berücksichtigung der handnervigen Blätter. Diss. Marburg, 1913. Bibl. Bot. Heft 82, 1913, 74 p., with 4 pl.

B. Sahni, 1915. The anatomy of Nephrolepis volubilis J. Sm. With remarks on the Biology and Morphology of the Genus. New Phyt., vol. 14, 1915, p. 251—274.

B. Sahni, 1918. On the Branching of the Zygopteridean Leaf, and its Relation to the probable Pinna-nature of Gyropteris sinuoasa, Goeppert. Ann. of Bot. vol. 32, 1918, p. 364—381.

B. Sahni, 1919. On an Australian Species of Clepsydropsis. Ann. of Bot., vol. 33, 1919, p. 85—92, with 1 pl.

H. Schacht, 1856. Lehrbuch der Anatomie und Physiologie. Berlin, 1856.

J. C. Schoute, 1902. Die Stelär-Theorie. Groningen und Jena, 1902.

J. C. Schoute, 1914. Beiträge zur Blattstellungstheorie. II. Ueber verästelte Baumfarne und die Verästelung der Pteropsida im allgemeinen. Rec. Trav. Bot. Néerl. vol. XI. 1914, p. 94—195, with 21 pl.

E. Schumann, 1915. Die Acrosticheen und ihre Stellung im System der Farne. Flora, Bd. 108, 1915, p. 201—260.

W. Schütze, 1905. Zur physiologischen Anatomie einiger tropischen Farne, besonders der Baumfarne. Diss. Berlin, 1905; Beitr. zur wiss. Bot., Abt. 2. V. 1906.

D. H. Scott, 1902. The Old Wood and the New. New Phyt., vol. 1, 1902, p. 25—30.

D. H. Scott, 1903, Prof. Yeffrey's Theory on the Stele. New Phyt. vol. I. 1900. p. 207—212.

D. H. Scott, 1909. Studies in Fossil Botany, vol. II. Second Edition. London, 1909.

D. H. Scott, 1912*a*. A Palaeozoic Fern, the Zygopteris Grayi of Willamson. Ann. of Bot., vol. 26, 1912, p. 39—71, with 5 pl.

D. H. Scott, 1912*b*. The structure of Mesoxylon Lomaxii and Mesoxylon poroxyloides. Ann. of Bot., vol 26, 1912, p. 1011—1030, 4 pl.

D. H. Scott, 1917. The Heterangiums of the British Coal-Measures. Journ. Linn. Soc., vol. XLIV, Bot. 1917, p. 59—105, 4 pl.

D. H. Scott, 1918*a*. Note on Calamopitys Unger. Journ. Linn. Soc., vol. XLIV, Bot. p. 205—232, with 6 pl.

D. H. Scott, 1918*b*. The Structure of Mesoxylon multirame. Ann. of Bot., vol. 32, 1918, p. 437—458, with 4 pl.

D. H. Scott, 1920. Studies in Fossil Botany, vol. 1. Third Edition, London, 1920.

D. H. Scott see W. C. Williamson.

A. C. Seward, 1899. The structure and affinities of Matonia pectinata. Ann. of Bot., vol. 13, 1899, p. 319.

A. C. Seward, 1899. On the structure and affinities of Matonia pectinata R. Br., with Notes on the Geological History of the Matoninae. Phil. Trans. Roy. Soc. London. (B) vol. 191, 1899, p. 177—209, 4 pl.

A. C. Seward and S. C. Dale, 1901. On the structure and affinities of Dipteris, with notes on the Geological History of the Dipteridinae. Phil. Trans. Roy. Soc. London. (B) vol. 194, 1901, p. 487—53, 3 pl.

A. C. Seward and S. O. Ford, 1902. The Anatomy of Todea, with Notes on the geological history and affinities of the Osmundaceae. Trans. Linn. Soc., 2d. ser., Bot., vol. VI, 1902, p. 239—260, with 4 pl.

E. W. Sinnott, 1910. Foliar gaps in the Osmundaceae. Ann. of Bot., vol. 24, 1910, p. 197—218, with 2 pl.

E. W. Sinnott, 1914. Some Jurassic Osmundaceae from New-Zealand. Ann. of Bot., vol. 28, 1914. p. 471—479, with 1 pl.

H. Grafen zu Solms—Laubach. Ueber die seiner zeit von Unger beschriebenen strukturbietenden Pflanzenreste des Unterculm von Salfeld in Thüringen. Abh. Kön. Preuss. geolog. Landesanstalt. N. F. Heft 23, Berlin, 1896.

K. G. Stenzel, 1861. Untersuchungen über Bau und Wachstum der Farne. II. Ueber Verjüngungserscheinungen bei der Farnen. Nova Acta. Bd. 28, Jena 1861, 56 p. with 5 pl.

G. Stenzel, 1889. Die Gattung Tubicaulis Cotta. Bibl. Bot. Heft 12. Cassel, 1889.

B. G. Stephenson, 1907. Young Stages of Dicksonia and Cyathea. Trans. and Proc. New-Zealand Inst. vol. 40, 1907, p. 1—16.

M. C. Stopes, 1921. The missing link in Osmundites. Ann. of Bot., vol 35, 1921, p. 55—61 with 1 pl.

E. Strasburger, 1891. Histologische Beiträge. III. Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Jena, 1891.

H. von Straszewski, 1915. Die Farngattung Platycerium. Flora, Bd. 108, 1915, p. 271—310.

A. G. Tansley and R. B. Lulham, 1902. On a new type of Fern-Stele and its probable phylogenetic relations. Ann. of Bot., vol. 16, 1902, p. 157—164.

A. C. Tansley and R. B. Lulham, 1903. The vascular system of the rhizome and the leaf-trace of Pteris aquilina L. and Pteris incisa Thunberg, var. integrifolia Beddome. New Phyt., vol. 3, 1903, p. 1—18.

A. G. Tansley and R. B. Lulham, 1905. A study of the Vascular system of Matonia pectinata. Ann. of Bot., vol. 19, 1905, p. 475—519, 3 pl.

A. G. Tansley, 1907. Lectures on the Evolution of the Filicinean Vascular System. New Phyt. vol. VI, 1907, p. 25—34, 53—68, 109—120, 135—155, 186—203.

A. G. Tansley. 1908. Id. New Phytologist, vol. VII, 1908, p. 1—16, 29—40.

P. Terletzki, 1884. Anatomie der Vegetationsorgane von Struthiopteris germanica Willd. und Pteris aquilina L. Jahrb. für Wiss. Bot. Bd. 15, 1884, p. 452—502, 3 pl.

K. Thomae, 1886. Die Blattstiele der Farne. Jahrb. für wiss. Bot. Bd. 17, 1886, p. 99—161.

E. N. Thomas, 1905. Some points in the Anatomy of Acrostichum aureum. New Phyt. vol. IV, 1905, p. 175—190, with 2 pl.

J. M'Lean Thompson, 1916. The anatomy and affinity of Platyzoma microphyllum, R. Br. Trans. Roy. Soc. Edinburgh, vol. 51, 1916, p. 631—656, with 4 pl.

J. M'Lean Thompson, 1917*a*. The anatomy and Affinity of Stromatopteris moniliformis Mett. Trans. Roy. Soc. Edinburgh, vol. 52, 1917, p. 133—156, with 4 pl.

J. M'Lean Thompson, 1917*b*. A further contribution to the knowledge of Platyzoma microphyllum, R. Br. Trans. Roy. Soc. Edinburgh, vol. 52, 1917, p. 156—164.

J. M'Lean Thompson, 1919. The Morphology of the Stele of Platyzoma microphyllum R. Br. Trans. Roy. Soc. Edinburgh, vol. 52, 1919, p. 571—596, with 3 pl.

J. M'Lean Thompson, 1920. New Stelar Facts and their Bearing on Stelar Theories of the Ferns. Trans. Roy. Soc. Edinburgh, vol. 52, 1920, p. 715—736, with 4 pl.

Ph. Van Tieghem et H. Douliot, 1886*a*. Sur la Polystelie. Ann. Sc. nat. Bot. 7me ser., T. III, 1886, p. 275—322, with 3 pl.

Ph. Van Tieghem et H. Douliot, 1886*b*. Sur les tiges à plusieurs cylindres centraux. Bull. de la Soc. bot. de France, t. XXXIII, 1886, p. 213.

Ph. Van Tieghem, 1888. Sur la limite du cylindre central et de l'écorce dans les Cryptogames vasculaires. Journ. de Bot., vol. 2, 1888, p. 369—377.

Ph. Van Tieghem, 1891. Traité de Botanique. 2me éd. Paris, 1891.

A. Trécul, 1869*a*. Remarques sur la position des trachées dans les Fougères. Ann. Sc. nat., 5me sér., t. 12, p. 219—301.

A. Trécul, 1869*b*. Ramification des rhizomes de l'Aspidium quinqueangulare. Ann. des Sc. nat., 5me sér., t. 12, p. 365—372.

A. Trécul, 1885*a*. Nature radiculaire des stolons de Nephrolepis. Réponse à M. P. Lachmann. C. R. Acad. des Sc., vpl. 101, 1885, p. 915—920.

A. Trécul, 1885*b*. Observations sur la structure du système vasculaire dans le genre Davallia, et en particulier dans le Davallia répens. C. R. l'Acad. des Sc.. vol. 101, 1885, p. 1453—1459.

W. C. Williamson, 1873. On the Organisation of the Fossil Plants of the Coal-Measures. IV. Dictyoxylon, Lyginodendron and Heterangium. Phil. Trans. Roy. Soc., London, vol. 163, 1873, p. 377—408, 10 pl.

W. C. Williamson, 1887. On the Organisation of the Fossil Plants of the Coal-Measures. XIII. Heterangium tiliaeoides (Will.) and Kaloxylon Hookeri. Phil. Trans. Roy. Soc., London. (B). vol. 178, 1887, p. 289—304, 4 pl.

W. C. Williamson and D. H. Scott. 1895. Further Observations of the Fossil Plants of the Coal-Measures. III. Lyginodendron and Heterangium. Phil. Trans. Roy. Soc., London. (B). vol 186. 1895, p. 701—778, 1 pl.

W. C. Worsdell, 1902. The Evolution of the Vascular Tissues of Plants. Bot. Gez. vol. 34, 1902, p. 216—223.

W. C. Worsdell, 1902. The nature of the Vascular of the Stem in certain Dicotyledonous Orders. Ann. of Bot., vol. 16, 1902, p. 599—601.

R. H. Yapp, 1902. Two Malayan „Myrmecophilous" Ferns, Polypodium (Lecanopteris) carnosum Blume and Polypodium sinuosum Wall. Ann. of Bot., vol. 16, 1902, p. 185—231, 3 pl.

P. Zenettti, 1895. Das Leitungssystem im Stamme von Osmunda regalis und dessen Uebergang im Blattstiel. (Diss. Strassburg, 1895). Bot. Zeit., Bd. 53 1895, p. 53—79, with 1 pl.

CONTENTS.