

Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae.

IV. Further observations on *Schizaea*¹.

BY

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With three Figures in the Text.
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IN a previous paper on the anatomy of the Schizaeaceae (Boodle, 1901, p. 373) the vegetative structure of *Schizaea digitata*, Sw., was treated at some length, and a few observations were added regarding *S. dichotoma*, Sw., and *S. fistulosa*, Labill. The two latter species could not be dealt with fully, as small pieces of the dried rhizome formed the whole of the available material.

Further material of *Schizaea* has since been examined, namely, additional specimens of *S. digitata*, several plants of *S. dichotoma*, and of *S. bifida*, two specimens of a small form of *S. dichotoma*, and some seedling-plants of *S. pusilla*, Pursh. The structure observed in these species will now be described.

SCHIZAEA DICHOTOMA.

The general structure of the rhizome of *S. dichotoma* has already been referred to (Boodle, '01, p. 378, Pl. XIX, Fig. 11, and Pl. XX, Fig. 15), but certain important features, which occur locally in parts of the stem of this species, call

¹ From the Jodrell Laboratory, Royal Botanic Gardens, Kew.

for special description. These are: dichotomous branching, nodal endodermal pockets, internal endodermis, and internal tracheides.

1. **Branching.** Among the specimens of *S. dichotoma* there were two or three with branched rhizomes. The branching has every appearance of being dichotomous, both on external examination and also in the behaviour of the stele. When

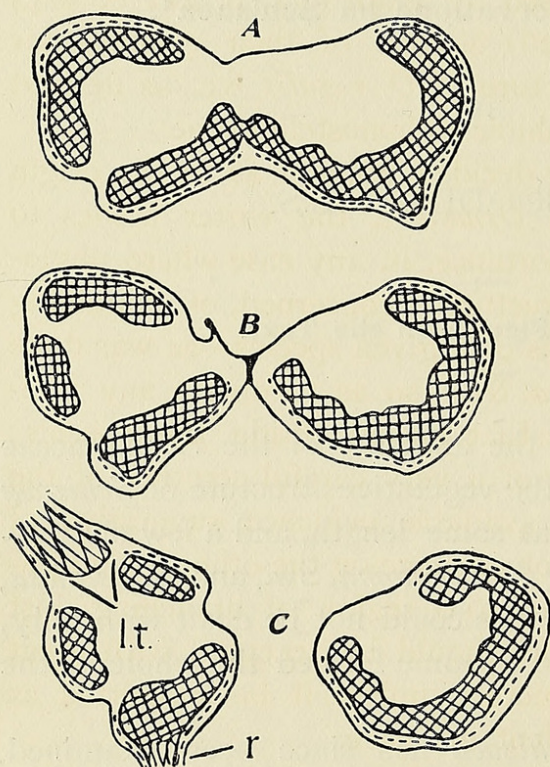


FIG. 24.—Dichotomy of the stele of *S. dichotoma*. A, B, C, three stages in acropetal order. $\times 9$. Endodermis represented by bounding line; xylem cross-hatched; phloem shown as a broken line. In C, leaf-trace and root at *lt.* and *r.*

preparing for dichotomy the stele becomes elongated in the horizontal plane and then divides into two in a simple manner¹. Three stages of its division are shown in Fig. 24. In this series, after the elongation of the stele, a leaf-trace is given off on the upper side leaving a gap in the xylem and phloem, which becomes very wide (Fig. 24, A); the lower part of the band of xylem and phloem splits in the median plane; the endodermis becomes constricted and fuses in the same plane (Fig. 24, B), producing an hour-glass-shaped double stele, which then separates

into two by fission of the endodermal bridge at the neck. The dichotomy of the stele is thus complete (Fig. 24, C). No branching other than apparent dichotomy was observed.

The mode of division of the stele (assuming that the latter

¹ Internal endodermis and internal tracheides may be present in the region of dichotomy, but do not affect the mode of division of the stele.

is bounded by the endodermis) resembles the dichotomy of the stele of *Lygodium* (Boodle, '01, p. 365), and the behaviour of the phloem in the region of branching gives no evidence for reduction from solenostely. Attention is drawn to this, because in *Osmunda cinnamomea* the special behaviour of the phloem in the region of forking (viz. the presence of internal phloem there and its continuity at times with the outer phloem) has been used by Faull ('01, p. 411 et seq.) and by Jeffrey ('02, p. 126) as one of their grounds for regarding the present structure of *O. regalis*, &c., as derived from a solenostelic (amphiphloic siphonostelic) type.

Without giving any very decided opinion as to the origin of the stelar structure of *Osmunda*, the writer wishes to emphasize: firstly, the importance, in any case where phylogenetic consideration of structure is concerned, of examining a large number of specimens of a given species—as was done by Faull in *O. cinnamomea*, &c.—so as to obtain any individual structural variation that occurs within the species; and secondly, the necessity of a very careful scrutiny of the results in the light of all available evidence suggestive of reduction on the one hand or advance on the other. Complication of structure restricted to a region of branching, just like complication at a node, should be accepted with great caution as a primitive structure, unless it be supported as such by weighty independent evidence.

While acknowledging the excellence of the observations detailed in Faull's paper, it may be pointed out as a serious omission that the seedling-stem of *Osmunda cinnamomea* is not described in greater detail. One gathers from the statements on pp. 396 and 410 of Faull's paper, and on p. 125 of Jeffrey's paper (Jeffrey, '02), that internal phloem is not present in the transitional region of the stem, but only occurs near the region of branching of the stem¹. This being so, a grave difficulty arises, for we have two alternative views.

¹ In *Osmunda regalis* Leclerc du Sablon ('90) found in the transitional region a pith with no internal phloem, and Seward ('03, p. 241) found the same in *Todea hymenophylloides*.

(1) If we accept the evidence derived from the seedling as thoroughly reliable, the absence of internal phloem in it proves that *Osmunda* has not been derived from an amphiphloic siphonostelic form, and that the local occurrence of internal phloem in the mature stem has been entirely misinterpreted by Faull and Jeffrey.

(2) If, on the other hand, one accepts their interpretation of the internal phloem, occasionally present in the mature stem, as a primitive structure, then the absence of a stage in the seedling showing similar structure proves that the ontogeny is not reliable as an index of structural phylogeny. This would strike at the root of Jeffrey's whole generalization (which is chiefly founded on ontogeny) as to amphiphloic siphonostely being the type of structure which succeeded protostely in Ferns, and gave place in certain cases to medullated monostely by reduction¹. For if the seedling-stem is at all dependable in repeating the structural history of the mature stem, one might of necessity count on *Osmunda cinnamomea* to show clear ontogenetic evidence of the previous existence of internal phloem, as, on our present assumption, it is a plant so little removed from the solenostelic condition that certain individuals of the species actually produce, by reversion in their mature stems, well differentiated local solenostelic structure. Thus it appears that either the basis of Jeffrey's theory, referred to above, is unsound, or the structure of *Osmunda* does not bear out Jeffrey's interpretation of it, and this genus forms an exception to his generalization.

The disagreement between Jeffrey's deductions from the anatomy of the mature plant and the evidence derived from the seedling, has already been pointed out by Scott ('02, p. 209) in a review.

The case of *Osmunda* has been referred to thus fully, because evidence of a similar nature has to be dealt with below in the case of *Schizaea*.

¹ There is certainly no sufficient evidence for regarding an inner endodermis as proving, in cases where it occurs, the previous existence of internal phloem.

2. Endodermal pockets. These are formed in connexion with some of the leaf-traces. One is seen in the transverse sections of the node represented by diagrams *A-D* in Fig. 25, which are arranged in acropetal order. In *A* two small endodermal pockets are shown cut transversely (e_1). They

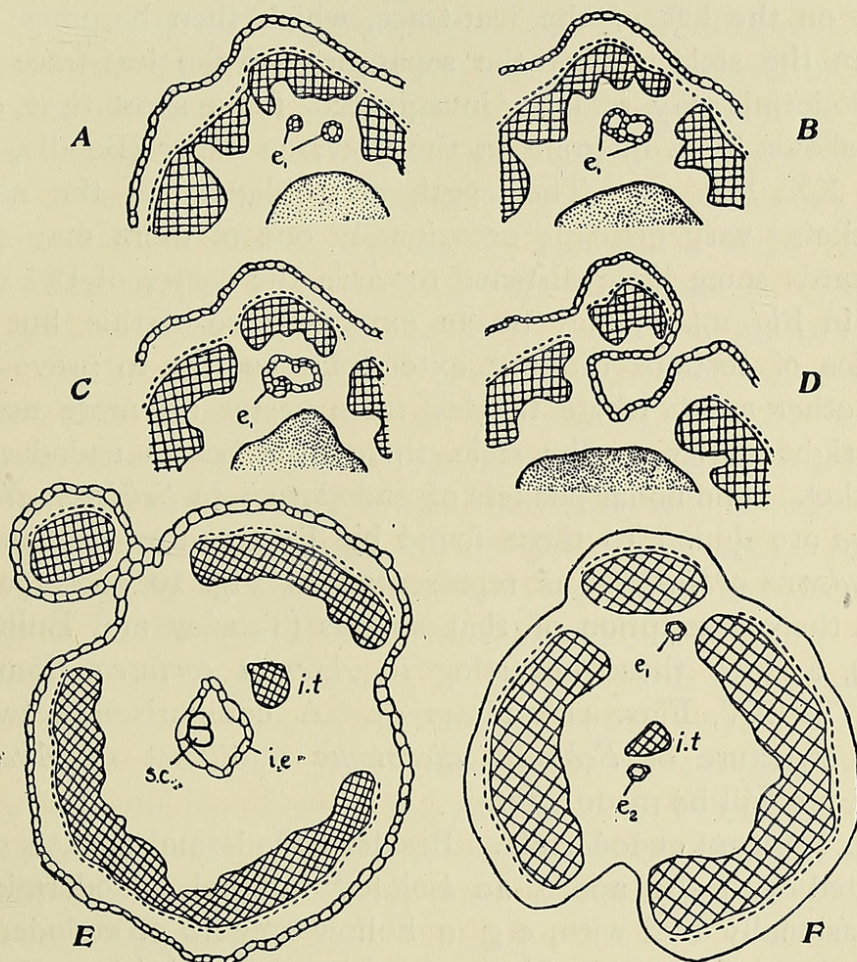


FIG. 25.—*Schizaea dichotoma*. *A, B, C, and D*, diagrams showing endodermal pocket (e_1) connected with departing leaf-trace. Position of sclerotic tissue shown by dotted area. *E*, stele showing internal tracheides (*i.t.*) and internal endodermis (*i.e.*); *s.c.*, two sclerotic elements. *F*, stele showing internal tracheides (*i.t.*), nodal endodermal pocket (e_1) and probably a second pocket (e_2). All \times about 23.

soon fuse to form one, two stages of the fusion being shown by diagrams *B* and *C*. In *C* the mass of xylem belonging to the leaf-trace has become detached, while in *D* it has moved further outwards, and the endodermal pocket has

become connected with the outer endodermis, so as to form an involution of the latter, the tissue contained in the pocket thus becoming continuous with the cortex. A little higher up the loop of endodermis, thus formed, becomes connected with the outer endodermis across the other gap in the xylem, i. e. on the left of the leaf-trace, which then becomes free from the stele. After the separation of the leaf-trace the endodermis may remain 'invaginated' for a short time, e. g. as shown by a diagram in the previous paper (Boodle, '01, Pl. XX, Fig. 15). The length and obliquity of the nodal pockets¹ vary greatly; occasionally one of them may pass inwards some little distance towards the centre of the stele (e_2 in Fig. 25, *F*, may be an extreme case of this, but the series of sections did not extend far enough to prove it); at other nodes, where the leaf-trace passes off more nearly at right angles to the stele, there may be no endodermal pocket. The nodal pockets of endodermis in *Schizaea dichotoma* are similar to those found by Tansley and Lulham in *Lindsaya orbiculata*, as represented in Fig. 10 accompanying their description of that species (Tansley and Lulham, '02), and to those occurring in *Anemia coriacea* (Boodle, '01, Pl. XV, Figs. 41 and 42 *e'*). A comparison between the structure of *Schizaea dichotoma* and that of *Anemia coriacea* will be made later.

3. Internal endodermis. Besides endodermal pockets connected with the nodes, an isolated internal endodermis is occasionally met with, e. g. a hollow spindle of endodermis tapering and closed both above and below, and lying vertically in the central tissue of the stele. Thus in Fig. 25, *E*, there is an inner endodermis (*i. e.*), which encloses a group of soft-walled cells (left blank) and two brown sclerotic elements

¹ The form of an ordinary endodermal pocket may be pictured by supposing a conical-tipped rod of cortical parenchyma provided with a sheath of endodermis to be pushed into the stele obliquely inwards and downwards from what may be called the axil of stele and leaf-trace, the endodermal sheath mentioned being continuous with the outer endodermis, which sheathes stele and leaf-trace. The endodermal pocket shown in Fig. 25 differs from the form above described in that it is forked at its base.

(s.c.). The inner endodermis in this case remains near the centre of the stele throughout its course, and only for a short distance encloses 1-2 sclerotic elements, resembling cells of the outer cortex; elsewhere it surrounds soft-walled cells only, like those forming the inner part of the cortex. Another case of a well-developed internal endodermis should be referred to. It differs from the one just described in the following characters: it attains a greater size, and, in the region where it is best developed, contains a fairly large group of brown sclerotic elements (a maximum of about 15) together with a certain amount of thin-walled tissue; for the greater part of its course it lies not far within the xylem-ring, and opposite a gap in the latter; for a certain distance it lies *in* this gap, and at one point a bridge of 1-2 endodermal cells connects this inner endodermis with the outer endodermis of the stele. There is, however, no communication between the ordinary cortical tissue and the parenchyma or sclerenchyma contained within the inner endodermis. Although the following fact probably has little importance, it should be mentioned that, in this series of sections, the phloem curved slightly round one of the ends of the open xylem-band, and that, when the gap in the xylem became closed, two or three sieve-tubes were shut in, but only persisted in the periphery of the pith for a short distance.

Deductions from the mode of occurrence of internal endodermis, &c., will be reserved until the internal tracheides have been described.

Internal endodermis in *Schizaea* was first discovered by Professor Tansley, viz. in *S. malaccana*; the inner endodermis of *S. dichotoma* was found by the writer subsequently.

4. **Internal tracheides.** The remaining peculiarity of *S. dichotoma* is the occurrence, in certain parts of the mature stem, of internal tracheides¹, of which two examples are

¹ There is no constant relation of internal tracheides either to nodes or to the branching of the stem. In two cases of dichotomy some internal tracheides were present, and in one of these an inner endodermis also, in the region of forking, but in other cases, where internal tracheides were present, there was no branching near.

represented in Fig. 25, *E* and *F* (at *i.t.*). The group of tracheides and the adjacent endodermal ring, shown diagrammatically in Fig. 25, *F*, are represented in detail, with the adjacent parenchymatous cells, in Fig. 26, *G*. Internal tracheides are not often found. When present, they may behave in different ways, as will be seen from the two following cases. The strand of tracheides, represented in Fig. 25, *E*, was followed through a series of sections and was found to become gradually reduced to only two or three elements, and then to disappear both above and below, the tracheides being at no time very far from the centre of the stele. In the second case, there were a few tracheides at some little distance within the ring of xylem, but when followed in the acropetal direction they were found to decrease in number to one or two, which then passed outwards and joined the xylem-ring just where a gap in the latter became closed. In both these cases, in the region where the tracheides are most numerous, they form a solid strand, but, when the tracheides are reduced in number, they become separated from one another by parenchymatous elements (this separation has begun in Fig. 26, *G*).

Thus the internal tracheides may or may not have a connexion with the tracheides of the ring.

5. Deductions from the anatomy of the mature plant. We may now enter into a discussion of the conclusions to be drawn from the occurrence of internal endodermis and tracheides.

Jeffrey ('02, p. 129), applying the conclusions he reached in the Osmundaceae to the Schizaeaceae by analogy, regards it as probable that the type of central cylinder found in *Schizaea* is derived by reduction from that which is characteristic of *Mohria* and *Anemia* (i. e. from dialystelic structure). This view is not accepted here (though the theory put forward by the writer is similar in some respects), firstly, because the case of *Osmunda* is not admitted as proved, and secondly, on account of the nature of the structural evidence derived from *Schizaea* itself.

Endodermal pockets, if they occurred alone, need not, according to our present knowledge, affect the question of the phylogenetic history of the stelar structure, for they may penetrate a solid stele as in the case of *Lindsaya*, described by Tansley and Lulham and referred to above. That is to say, so far as one knows, they need not be vestigial structures, but might perhaps arise for mechanical reasons¹. Thus no certain conclusion can be drawn from the presence of endodermal pockets alone.

The isolated internal endodermis, however, is difficult to explain except as a reduced structure. An argument which is practically based on the apparent impossibility of attributing a function to a given structure in its present condition is naturally inconclusive, but absence of function is also suggested by the apparently hap-hazard occurrence of the structure in question (without definite relation to nodes or branching).

Under these circumstances the following views are brought forward, while fully recognizing the tentative nature of some of them.

1. The internal endodermis described above, being isolated and apparently functionless, is probably reduced from some better developed structure.

2. Where the internal endodermis is best developed, it may be regarded as least reduced. And, as in that case it encloses two kinds of elements similar to the cells of the inner and outer cortex respectively, there is some probability that these two tissues were at one time (in the phylogenetic history) continuous with the cortex², on the ground that continuity

¹ It is conceivable that certain strains, liable to occur in the leaf-trace (perhaps before the sclerification of the cortex), might be capable of tearing the endodermal sheath of the vascular system at its 'axillary' point, while the elongation of this part of the endodermis as a hollow tapering tube dipping into the stele might prevent rupture between endodermal cells. The fact that leaf-traces, which leave the stele nearly at right angles instead of at a more acute angle, do not have well-developed endodermal pockets, may have some such significance, though it would not, on the other hand, be incompatible with a vestigial nature of the endodermal pockets.

² Such continuity would prove nothing as to the homology of the tissues concerned.

generally goes hand in hand with physiological and structural identity. On the other hand, it is just possible that the presence of cortex-like elements within the inner endodermis may be due to a certain correlation in tissue-development¹, the formation of an endodermis leading to the production, on its inner side, of elements similar to those on the outer side of the outer endodermis.

3. Comparison with *Anemia* (which belongs to the same Order) is of considerable value. Certain forms of that genus (in Prantl's sub-genus *Aneimiorrhiza*), which have a creeping rhizome and solenostelic structure, appear to form a series of reduction, the more xerophilous forms, some of which are adapted to growth on rocks, having thinner rhizomes. It is highly probable that the structure of the latter should be regarded as reduced from the type found in the larger forms of this series. To take two examples, which were partially investigated, *Anemia mexicana* has solenostelic structure, and central sclerotic tissue continuous with the cortex through the leaf-gaps, while *A. coriacea*, which is a plant with a smaller rhizome than that of *A. mexicana*, has in its stele a central core of sclerotic tissue surrounded by an inner endodermis, and also has endodermal pockets (see Boodle, '01, Pl. XXI, Figs. 41 and 42, e'), which are independent of the inner endodermis². The most natural conclusion is that the endodermal pockets in *A. coriacea* are reduced remnants of previous funnel-like connexions between outer and inner endoderms at each node, i. e. of typical foliar gaps, such as are found in species with a thicker rhizome, e. g. in *A. mexicana*. Now as the two structural features just referred to in *A. coriacea* are paralleled in *Schizaea dichotoma*

¹ The writer hopes to publish at a later date some facts, which probably find their explanation in a correlation of this kind. As an example of correlation of a different kind, but also apart from function, one may quote the dorsiventrality of the floral organs of certain Podostemaceae as explained by Willis ('02, p. 438).

² These facts are based on the examination of a small amount of dried material, so it cannot be said whether important variations of structure may not occur within these two species, but the occurrence of the structure described in them is sufficient for our present purpose.

by the quite similar endodermal pockets and the internal endodermis enclosing sclerotic tissue (although of local occurrence), and as the form of the inner endodermis in *S. dichotoma* suggests reduction from a more extended tissue, the most satisfactory explanation of the facts is that the stelar structure of *S. dichotoma* is due to reduction from a type in which the endodermis had the same distribution as in *Anemia mexicana*. This view does not involve reduction from solenostely, but only from ectophloic siphonostely, because there is no sufficient evidence that *Schizaea* or its ancestors ever had internal phloem. Nor does it directly touch the question of the morphology of the central tissues. That, on the present supposition, could only be attacked by an examination of forms (if such were extant) transitional in structure between a protostelic type and the supposed 'siphonostelic' ancestor of the *Schizaeas*.

The structure of *S. dichotoma* is, however, of interest in relation to the general question of the morphology of tissues. For, if one attempts to assign morphologic value to the endodermis as would be implied by using the word 'phloeoterma,' the natural inference is that the spindle-shaped sheath of inner endodermis, referred to above, contains cortical tissue, that in Fig. 25, *E*, where this endodermis is present, the bulk of the central tissue (that between inner endodermis and xylem) is stelar, and that, where the inner endodermis, after thinning off, comes to an end, *all* the central tissue must be regarded as stelar. It is difficult to see how an exponent of the morphological importance of the endodermis can avoid this conclusion.

The writer's view may be stated here: (1) that the local complications of structure in the rhizome of *S. dichotoma* are reversional phenomena occurring at certain periods in the life of the plant, probably when nutritive conditions were at their best, as indicated by Thomas ('02, p. 344 et seq.), in the case of local reversional complication of sporophylls in *Tmesipteris*; (2) that the structure of *Schizaea* has probably been derived from protostelic structure by the following stages, (*a*) appear-

ance of a parenchymatous pith, (*b*) differentiation from part of this parenchyma of a central strand of sclerotic tissue surrounded by an endodermis and continuous with the cortex at the nodes¹, (*c*) reduction in size of the central core of sclerotic tissue, and severing of its connexion with the cortex, leaving endodermal pockets as a vestige of the previous connexion between inner and outer endodermis, (*d*) disappearance of brown sclerotic tissue and of inner endodermis, leaving a parenchymatous pith, (*e*) transformation of the latter into sclerotic tissue (as found in most parts of the stem of *S. dichotoma* and always (?) in *S. digitata*).

If one now turns to a consideration of the internal tracheides, it is important to remember their relation to the inner endodermis. The two best-developed strands of tracheides were associated with the two best-developed examples of internal endodermis. One tracheide-strand, being quite unconnected with the xylem-ring, appears to be a vestigial structure; the association with the inner endodermis also points to the same conclusion, for the tracheide-strand is an added structure in a part of the stem, which is presumably reverting to earlier characters.

The exact significance of the tracheide-strands must be left an open question, but one may say that they probably indicate that the tissue within the xylem-ring (exclusive of the area taken up by the inner endodermis) is potentially xylem-tissue. This is suggested also by the fact that, apart from these definite strands of tracheides, one or two tracheides sometimes branch off from the inner face of the xylem-ring and pass a short way into the pith. This and other features often cause an indefiniteness of demarcation between the xylem-ring and the central parenchyma, such as impressed Prantl ('81, p. 24) in *S. Pennula*, and gave one of his reasons for regarding the central parenchyma or sclerenchyma of *Schizaea* as belonging to the 'bundle,' and not representing a 'true pith.' His other reason was the absence of an endo-

¹ The change described in (*b*), and possibly in (*a*) also, might begin at the nodes and spread to the internodes.

dermis separating this tissue from the xylem, and this fact also determined Russow ('72, p. 97) and De Bary ('77, p. 344) to regard the central tissue as belonging to the bundle-tissue.

STRUCTURE OF THE MATURE PLANT IN OTHER SPECIES.

Schizaea bifida need not be specially described. In structure it resembles *S. dichotoma*, but its parts have smaller dimensions. Endodermal pockets are present, but neither inner endodermis nor internal tracheides were found. Further material of *S. digitata* has also been examined, but none of the complications of structure shown by *S. dichotoma* were present in the specimens sectioned.

YOUNG PLANT OF SCHIZAEA PUSILLA.

The life-history of this species has been described by Britton and Taylor ('01). A figure of the mature stem (in transverse section) of this species is given by these authors ('01, Pl. V, Fig. 80), but the transitional region is not dealt with. Seedling-plants of *S. pusilla* were sectioned with the microtome. The largest of these plants, examined in an acropetal series of sections, shows the stele becoming immature between the fourth and fifth leaf, but previously the mature type of structure usual in the genus had been practically attained, so a description of the series is worth giving.

The main root appears to be diarch; the transition to protostelic stem-structure takes place in the usual way, the tracheides becoming more uniform in size and surrounded by phloem (Fig. 26, *A*). When the first leaf-trace separates from the stele, it leaves only three tracheides; on the separation of the second leaf-trace 6-8 tracheides remain in the stele; these increase, after the attachment of the second lateral root, to about 15, the xylem of the stele being still solid. Parenchymatous cells next make their appearance in the xylem (at first only two of them), and they and some of the tracheides undergo change of position, so that the parenchyma-cells are sometimes completely shut in, sometimes not. When the xylem of the third leaf-trace separates

(Fig. 26, *B*), it leaves a horseshoe-shaped mass of xylem in the stele. The xylem becomes nearly closed again and the fourth leaf-trace passes off; after which the stele possesses a fair-sized group of central parenchyma surrounded by a ring of tracheides (Fig. 26, *C*), thus agreeing with the structure of the mature stem in other species of the genus. The xylem is now not quite mature, lignification not being complete in the two tracheides with dark walls in the diagram. One of the central parenchymatous elements in the same diagram is shown with dotted contents to represent mucilage. This cell differs from the other cells of the central parenchyma in possessing mucilage, and in this resembles the cells of the endodermis. It may quite possibly be a rudimentary vestige of a nodal endodermal pocket. Or probably a more correct statement of this supposition would be to say that this cell may represent part of an endodermal pocket, but has been differentiated (owing to correlation) in connexion with a node in a region of the stem, which probably never possessed complete endodermal pockets.

The central parenchyma in the part of the seedling we have been considering, gives no indication of being of the nature of phloem, so that from the young plant we obtain no suggestion of reduction from solenostely.

The petiolar bundles of the first and second leaf of *S. pusilla* are shown in Fig. 26, *E* and *D* respectively. The bundle of the first petiole, in the basal region of the latter, has two or three sieve-tubes and is collateral, but higher up (Fig. 26, *E*) sieve-tubes are not present. Fig. 26, *D*, is the collateral petiolar bundle of the second leaf. Thus there is no indication in the early leaves of the collateral bundles of the leaf having been derived from concentric ones by reduction in this phylum.

Britton and Taylor ('01) give three figures of leaf-bundles. The structure of the largest of these appears to be of the same type as that found in other species of the genus, and fibres appear to be present in the usual position.

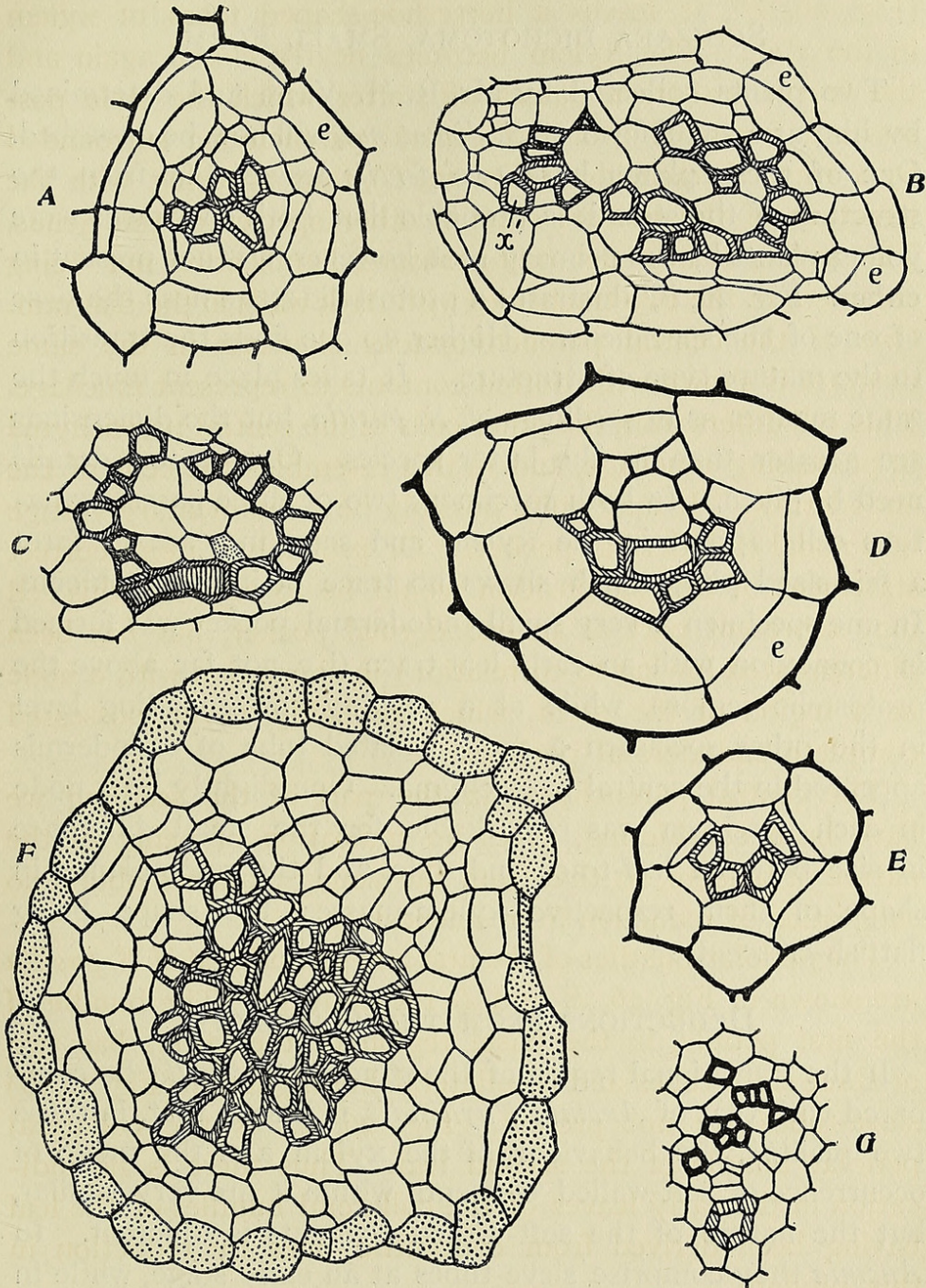


FIG. 26.—A-C, transverse sections of the seedling-stem of *Schizaea pusilla*: A, close above the primary root and before the separation of the first leaf; B, separation of the third leaf-trace (x' , xylem of the latter); C, after departure of the fourth leaf-trace. D and E, petiolar bundles of second and first leaf respectively of *S. pusilla*. F, *S. dichotoma*, small form, protostelic region of the stem. G, central tracheides and endodermis of *S. dichotoma* from Fig. 25, F. A, B, C, F, G, $\times 260$; D, E, $\times 600$.

SCHIZAEA DICHOTOMA, SMALL FORM.

Two plants, collected by Mr. R. H. Yapp and determined by him as a small form of *S. dichotoma*, will now be described. One of these plants bore two *fertile* leaves, but from the structure of the stem it is probable that both specimens were young plants¹; the primary root, however, was not present in either. Fig. 26, *F*, illustrates a protostelic stage near the base of one of the specimens. Higher up one finds the transition to the mature type of structure. It takes place in much the same manner as in seedlings of *S. pusilla*, but the dimensions are greater than in the latter species. Only a few details need be given. In both specimens two or three parenchymatous cells appear in the xylem and soon increase to form a fair-sized pith, which shows no trace of internal phloem. In one specimen a very small endodermal pocket was formed in connexion with an early leaf-trace (i. e. not far above the protostelic region), while at a roughly corresponding level in the other specimen a small isolated tube of endodermis appeared in the central parenchyma. One slightly later node in each specimen was remarkable for the small difference in size between leaf-trace and stele, and the resemblance in shape of their respective xylem-masses, the shape being flattish-crescentic².

DEDUCTIONS FROM THE ONTOGENY.

If the transitional region of the stem of *S. pusilla* be compared with that of *Anemia Phyllitidis*, it is seen that, in these two plants³, the behaviour of the xylem and the mode of occurrence of soft-walled elements within it are very similar, but the nature of the soft-walled elements is different. In *Anemia* they comprise sieve-tubes at an early stage, while in *Schizaea pusilla* this is not the case. Nor does phloem occur

¹ They may be simply young plants of the typical *S. dichotoma*.

² One of these nodes when first examined was taken for a dichotomy.

³ Examination of the structure of older seedlings of *S. pusilla* than that described in the present paper, and of known seedlings of *S. dichotoma*, is of course highly desirable.

in the pith of the supposed seedling-plants of *S. dichotoma*. These facts do not suggest a solenostelic ancestry for *Schizaea*, nor derivation from the *Lindsaya*-type.

The first two petiolar bundles are collateral ; hence there is no ontogenetic evidence for the petiolar bundles of *Schizaea* being reduced from the concentric type, and this fact favours the conclusion that the stem-structure has not been derived from a solenostelic type.

If one brings the supposed seedlings of *S. dichotoma* into consideration, the early appearance in them of small endodermal pockets and of rudiments which may represent an inner endodermis, while internal phloem is absent, would favour the view of reduction from ectophloic phyllosiphony.

ONTOGENY AND STRUCTURE OF MATURE PLANT.

The structure of the young plant of *Schizaea* has been insufficiently examined owing to lack of material, but such data as were obtained, are in agreement with the view derived from a consideration of the typical mature structure together with its variations in *S. dichotoma*. This is stated before giving an opinion as to what relative importance should be attached to different kinds of evidence.

A few words may now be said on this subject. Firstly, a study of the development of the tissues from the apical region, as Schoute ('02, p. 90 et seq.) has shown, does not give a morphological criterion. Secondly, the structure of the seedling-stem *may* give a clue to the phylogenetic origin of the mature structure, but probably what is found in the seedling requires great care in interpretation. Assuming that the transitional region of the stem repeats to some extent the phylogenetic history of the mature structure, it is extremely likely that there may be disturbing factors, which would at times make the evidence quite misleading. Thus certain kinds of reduction in the structure of the mature stem might be attained by one of the stages of the transitional region being continued unchanged in the mature stem, so that the plant would be a kind of permanently embryonic form.

If this were to take place the ontogeny would give no clue to reduction. On the other hand a correlation in development, that is to say a tendency to uniformity of structure at all nodes¹ or in all parts of the stem, may cause the appearance of certain tissues precociously (i. e. at too low a level in the seedling-stem). Thus it is possible that in plants, where the possession of internal phloem is a well-established character in the mature stem, the internal phloem may spread downwards below its proper ontogenetic level. If this were to take place, all deductions from the seedling as to phylogenetic priority of internal phloem as compared with a pith would be quite unreliable². To turn to the Dicotyledons for an illustration, the presence of internal phloem in the pith of the primary root of *Asclepias obtusifolia* (see Scott and Brebner, '90, p. 272) is almost certainly due to a downward extension (speaking metaphorically) of the inner phloem of the hypocotyl, and it is not an improbable assumption that the internal phloem in the lower part of the hypocotyl itself has originated in a similar way; otherwise, on ontogenetic grounds, one would have to assume that the ancestry of the plant in question did not include forms devoid of inner phloem.

Having pointed out one or two reasons for doubting the value of evidence derived from the stem-structure of the young plant, it will be as well to state what class of data appear to the writer to be important in elucidating a problem like that presented by *Schizaea*. The following is the method suggested:—

1. Any variations in the different parts of the mature stem or in the stems of different individuals should be noted.
2. Special attention should be paid to the structure of the node (because complications of advance or reversion, or more correctly retension, are to be sought here).

¹ Some features in the seedlings of some plants seem to point to the existence of such correlation.

² The writer does not wish to imply that in every case pith preceded internal phloem. Uniformity in this respect in different phyla is perhaps improbable on general grounds.

3. The structure of nearly allied species should be carefully compared with that of the species dealt with.

4. The structure of the young plant should be examined, chiefly to see whether it gives evidence of reduction not indicated by the mature plant, in the form of tissues not represented in a corresponding position in the mature stem.

5. In interpreting all such data obtained, both internal evidence and also independent clues should be sought as tests of advance or reduction.

GENERAL THEORY.

In the previous paper on the Schizaeaceae, as the forms included in that Order were found to possess features of special interest in relation to the stele, a discussion of some of the points at issue was given (Boodle, '01, p. 403 et seq.). It will be well to put together some further considerations on this subject and to restate others.

Tansley and Chick ('01) deduce, from their researches on some of the Bryophyta and from the probability of similarity of physiological requirements in the unknown primitive ancestors of the Pteridophyta, that in the latter the stem possessed a solid central strand of conducting tissue of the protostelic type and having acropetal development, that leaf-traces were developed independently of this protostele, and that their connexion with it was only a secondary phenomenon. This view appears well founded on theoretical grounds, and receives a certain amount of support from the fact that most cases of protostelic stems are found among the more primitive Ferns, and that as one passes from the lower to the higher forms the leaf-trace appears to exert more and more influence on the structure and development of the stele (cf. Gwynne-Vaughan, '01, p. 87). If one adopts this view, the tissues of the stele and leaf-trace are not strictly homologous¹.

¹ Hence the writer prefers to retain the terms 'leaf-trace' and 'petiolar bundle,' rather than replace them by the word 'meristele,' suggested by Brebner ('02, p. 523) for use in an extended sense.

Starting with a small protostele and a simple type of petiolar bundle, the following appears a probable course of advance in structure among the Ferns. Increased leaf-surface necessitated increase in sectional area of stele and petiolar bundle. But this was achieved in two different ways, viz. simply by greater diameter in the case of the protostele, and by elongation into a band-shaped structure in the case of the petiolar bundle¹. For mechanical reasons the peripheral part of the petiole had to be occupied by sclerenchymatous tissue; so, to avoid too great diameter in the petiole, the band-shaped bundle became arched. To admit of the insertion of a number of large arched bundles, the stele increased its diameter beyond the size required by the exigencies of water-conduction, and the central part of the xylem of the stele was transformed into parenchyma or other tissues. Such central tissue might be parenchymatous or sclerenchymatous at its origin and remain so in certain phyla (especially where the leaf-traces were collateral); in other cases it might be parenchymatous at first, and afterwards have its peripheral part converted into phloem; or inner phloem and pith might arise simultaneously; or possibly inner phloem might be produced without an ordinary pith (see Tansley and Lulham, '02).

To return to the petiole, its arched bundle was able to increase its sectional area² by an incurving of its ends, thus producing the horseshoe-type, which is of such frequent occurrence among Ferns as pointed out by Gwynne-Vaughan ('01, p. 95), and as seen by reference to the table of diagrams given by Parmentier ('99, p. 340). The division of the petiolar bundle into two or more portions, as found in many Polypodiaceae, &c. (see Bertrand et Cornaille, '02, pp. 53, 207, &c.), may be connected with the downward extension of the leaf-gap in the stem, or may have originated for mechanical reasons, because a large petiolar bundle would be subjected to consider-

¹ Convenient for the insertion of numerous distichous branch-bundles. Whether the primitive petiolar bundle was concentric or collateral must be left an open question, but probably both types existed at a fairly early stage.

² Without increasing the diameter of the petiole.

able strains unless the petiole possessed almost complete rigidity, and the latter would be unsuitable for positions exposed to wind.

Thus the theory suggested with regard to the origin of a bundle-system like that found in the petiole of *Pteris aquilina*, is that a band-shaped primitive bundle became arched and afterwards convoluted and divided¹.

We therefore arrive at a different view as to the origin of the vascular bundles in the petiole of *Pteris aquilina* from that which the writer would suggest for the vascular system of the stem of the same species² (see Jeffrey, '00, pp. 10-11).

Jeffrey in his recent paper ('02, p. 143) states that it is not easy to see why on the views put forward (Boodle, '01) 'the same view [that applied to the bundles in the adult stem of *Pteris aquilina*] should not be taken of the equally complex arrangement of bundles in the petiole.' What has been said above explains the writer's view³. It should be pointed out that, when one is dealing with a question of morphology and comparing the tissues in two different organs, it is necessary to form a definite theory as to the phylogenetic history of the tissues in *both* organs before formulating their morphological relations.

FURTHER ANATOMICAL DETAILS.

The resistance to strong sulphuric acid shown by cell-walls in the cortex, pith, &c., of *Schizaea digitata* has already been

¹ A petiolar bundle of the horseshoe-type may also become closed (presumably by the conversion of the tissue between its ends into vascular tissue), e. g. in some species of *Gleichenia* (Boodle, '01 a, Pl. XXXIX, Fig. 19). In this case the central tissue of the bundle is regarded as belonging to the historically non-vascular portion of the petiole, which has been invaginated; so the view corresponds to that held by Jeffrey for the solenosteles in stems.

² For the stem the theory suggested is that if one could follow the stages in the evolution of its structure, one would find a protostele converted into a solenostele by the replacement of its central tissue by parenchyma and phloem (the two tissues appearing successively or simultaneously), and then by the conversion of part of the central parenchyma into vascular strands.

The non-stelar nature of the petiolar bundle is not insisted on here, but simply the theoretical view that the centrally placed parenchyma in the petiole has not been directly derived from vascular tissue.

mentioned (Boodle, '01, p. 376). *S. dichotoma* was found to behave in a similar way. A transverse section of the rhizome was placed in strong sulphuric acid, with a section of *Cucurbita* as a control. Some time after the greater part of the cellular tissue in the control had swelled up and disappeared, a very different result was seen in the section of *Schizaea*. The walls of the tracheides were considerably swelled, but sharply outlined walls remained representing practically all the rest of the cells. Previous boiling of the material in water did not alter the effect of the acid.

The differentiation of the xylem, as seen in a microtome-series of sections of the stem-apex of *S. dichotoma*, is irregular. Thus, taking one particular part of the stele as an example, no tracheides were differentiated except one at the extreme outside and one at the extreme inside of the young xylem-ring, while, in other parts of the ring of xylem, tracheides in an intermediate position may be the first to differentiate. The differentiation may also be much further advanced on one side of the stele than on the other, in relation to the nearest leaf-trace.

The sieve-tubes of *S. dichotoma* appear to be of a fairly normal Fern-type.

The petiolar bundle of *S. dichotoma* is of a similar type to that of *S. elegans* figured by Prantl ('81, Taf. IV, Fig. 40). Fibres are present in the usual position, and protoxylem appears to lie at two points on the upper side. In the leaf the stomata are placed in two neat longitudinal rows, just as in *S. pusilla* (Britton and Taylor, '01, p. 14). In the flattened part of the leaf the bundle is similar to that of the petiole, the epidermal cells are very thick-walled, and the stomata are raised.

RECENT WORKS TREATING OF THE MORPHOLOGY OF TISSUES.

Reference should now be made to certain views regarding the stele and the morphology of tissues, which have been recently published. Farmer and Hill ('02, pp. 396 and 400)

regard the pith as not belonging to the stele. They recognize the difficulty in estimating the morphological nature of a tissue, and state that 'our criteria only become applicable as the adult condition is reached' or approached.

A thoroughly consistent and strictly morphological treatment of tissues is probably an impossibility, and in any case the subject is rather elusive, but in many cases one can draw an opinion from the position of a certain tissue, though suppositions as to the exact mode of its first origin may become necessary. Two cases may be brought forward in which the morphological nature appears fairly certain. The cortical sieve-tubes of *Cucurbita* must be regarded as derived from cortical cells; morphologically they are part of the cortex. Secondly, the trabeculae in the sporangium of *Isoetes* have probably been derived from the sporogenous tissue and, morphologically speaking, represent part of it, —not ingrowths of the surrounding tissue.

We will now turn to the stele. It is exceedingly probable that the solid protostele was the universal primitive type, that the more complicated types were moulded from it, and that it never passed through a stage of flattening and rolling round, such as is assumed by the writer for the petiolar bundle of many Ferns. Consequently, whatever tissue is found within the xylem is presumably morphologically stelar. Assuming an exarch protostele, a pith may have originated by incomplete differentiation of the xylem-mass. At any rate if one regards the pith or other central tissue as having arisen in the first place by the transformation of potential tracheides into other tissue elements, these latter should be treated morphologically as part of the stele.

The different types of stem-structure in Ferns have probably been derived by a differentiation of the protostele into vascular and non-vascular parts, hence, although the possibility of there being exceptions is kept in view, the writer agrees with Schoute's conclusion ('02, p. 163) as a provisional generalization that a single type of stele is found in the stem and root of the vascular plants, viz. monostely; that is to say, taking

'stele' and 'monostely' in a morphological sense, applying as strict morphology as is possible in the case of tissues, and working on the hypothesis set forth in the present paper.

As a consequence of this conclusion the description and classification of different types of stelar structure have at present no morphological basis, but only a physiological one, because they refer to specializations of tissue within the morphological unit with which we started.

Brebner ('02, p. 548) recognizes the physiological nature of the descriptive terms, which he applies to different types of stelar structure. In the writer's opinion, also, terms defined as referring to definite types of tissue-arrangement within the stele are useful, and in some cases necessary, but a constant morphological distinction between the different kinds of tissue concerned is not upheld. As to the terms to be employed many already in use are sufficiently suitable. Thus 'solenostele' as defined by Gwynne-Vaughan ('01, p. 73) describes a special arrangement of tissues; its derivation signifies 'tube-stele,' and whether one regards the stele itself as being tubular, or the vascular part of the stele as being tubular, does not interfere much with the appropriateness of the term.

Farmer and Hill ('02, p. 398, &c.) decide to take the vascular strand as their unit for comparative considerations, both pith and the parenchyma forming the leaf-gaps of a solenostelic or dialystelic type being excluded. This is excellent as a physiological treatment of the tissues, but, in accordance with the views adopted in the present paper, the writer holds that it obscures the homologies of the tissues concerned. Leaf-gaps are held to have been originally formed by the replacement of vascular tissue by ordinary parenchyma, the first stage possibly consisting in the incomplete differentiation of the tracheides in the region afterwards occupied by the leaf-gap; and the same view is held with regard to the pith¹. To exclude part of a given tissue as soon as it changes its structural nature does not appear to be a morphological treatment.

¹ Cf. the case of arrested roots, &c., in *Gleichenia* (Boodle, '01 a, p. 732).

SUMMARY.

The mature rhizome of *Schizaea dichotoma* exhibits apparent dichotomy. In the region of dichotomy the stele (as seen in transverse section) undergoes elongation, constriction, and fission. The ring of xylem is open during the process, but no internal phloem is present.

In the mature rhizome of *S. dichotoma* endodermal pockets are often present at the nodes; an isolated internal endodermis is occasionally found and may contain brown sclerotic elements; isolated internal tracheides sometimes occur.

In the stem of the young plant of *S. pusilla* no internal phloem is present in the transitional region.

In two specimens of a small form of *S. dichotoma*, which are probably seedling-plants, and at any rate have protostelic structure in their basal region, no internal phloem was present in the transitional region, but endodermal pockets or rudiments of them were present early in the medullated stage.

The deduction, which appears most natural, in the light of the various facts recorded, is that the inner endodermis is a vestigial structure, and that *S. dichotoma* owes its typical (or more usual) structure to reduction from a medullated form with inner endodermis ('ectophloic siphonostelic'). The same would probably be true for the other species of *Schizaea*. There is no evidence for the previous presence of an internal phloem.

CONCLUSION.

It is likely that a further structural examination of sufficiently numerous specimens of *S. dichotoma* and of other specimens of *Schizaea* may give more safe grounds, than were obtainable from the material examined, for elaborating a theory as to the phylogenetic history of the stele of *Schizaea*; and this may be helped by an extended comparison with certain species of *Anemia*, when their structure also has been examined in a large number of individuals. Both genera will

probably be productive of further data, useful in considerations on stelar morphology¹.

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¹ The writer hopes shortly to be able to publish some further observations on two or three species of *Anemia* and on *Gleichenia pectinata* in continuation of the present series.

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