Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae.

II. On the Anatomy of the Schizaeaceae¹.

BY

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With Plates XIX, XX, and XXI.
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THE Anatomy of the Hymenophyllaceae formed the subject of the first part of this paper, which was published last year². The present part is concerned with the anatomy of the Schizaeaceae. A monograph of this Order, which contained a large amount of valuable information regarding the anatomy, was published by Prantl ('81). As many of the observations to be described below are confirmatory of Prantl's statements, his work will be referred to at the end of the paper, so as to avoid too numerous references.

Of the anatomical points to be dealt with here, the structure of the vascular tissue of the stem and petiole occupy the chief place, and form in some respects a more interesting study than in the Hymenophyllaceae, on account of the very diverse types found within the Order. The simply constructed stele of *Lygodium* is not far removed in type from certain species of

¹ From the Jodrell Laboratory, Royal Gardens, Kew.

² Annals of Botany, vol. xiv, p. 455.

the Hymenophyllaceae, but the dialystelic stem of *Anemia Phyllitidis* has no counterpart in that Order. Seedling plants of both these types were examined, in order to trace the manner in which the structure of the mature stem is attained in the ontogeny of the plant, and if possible to draw some conclusion as to the homologies of the mature structure. Especially in the case of *Anemia* and *Schizaea* several anatomical points have been left for further investigation, and as new material of some species has recently been obtained, it is intended to publish some additional observations at a future date.

In the Schizaeaceae Hooker and Baker ('74) include five genera: *Schizaea*, Sm., *Anemia*, Sw., *Mohria*, Sw., *Trochopteris*, Gardn., and *Lygodium*, Sw. *Trochopteris*, which is represented by a single species, is placed by Prantl ('81) as a subgenus of *Anemia*¹, thus reducing the genera to four. Material of *Trochopteris* was not obtained, but the structure was investigated in *Lygodium*, *Schizaea*, *Anemia*, and *Mohria*, and the results will now be described, and will be arranged under each genus taken in the order just given.

Some further observations on the sieve-tubes and bundle-fibres of the Hymenophyllaceae are included towards the end of the paper, where a more general treatment of certain tissues, &c. is given.

LYGODIUM, habit.

The stem of *Lygodium* is a horizontal rhizome often much branched at short intervals, and apparently dichotomously, but with some of the branches occasionally arrested. The roots are borne on the lower surface, without marked regularity, but approaching distichous arrangement in places. The leaves are borne at short intervals on the upper surface of the rhizome, and according to Prantl ('81, p. 2) form a single row. This is often approximately correct, but especially where the leaves are rather crowded, they tend to distichous

¹ Prantl and other authors write the generic name *Ancimia*, in order to make its Greek derivation correct.

arrangement. The petiole is upright and is continued into the climbing rachis which has indefinite growth, and bears pinnae at intervals. The pinna is usually quite short and stalk-like and divides dichotomously to produce secondary pinnae, but frequently at its apical region, i.e. at the fork, a bud-like body is produced, which afterwards is circinate, and then lengthens to produce a secondary rachis. The secondary pinnae may be simple or may be further divided dichotomously or pinnately.

In all the genera of the Order the form of the leaves, venation, fructification, &c. are fully described in Prantl's monograph.

LYGODIUM, stem.

The rhizome of *Lygodium dichotomum*, Sw., has a thick cortex, in which three zones may be distinguished. The outer cells are thin-walled and brown, and graduate into the thick-walled sclerotic elements of the middle part of the cortex. The latter cells have dark reddish-brown walls with numerous pits and distinct stratification. A similar brown colouring matter present in the walls is familiar in the sclerotic tissue of most Ferns and has been shown by Walter ('90, p. 18) to be phlobaphene, which probably belongs to the group of humic substances. This colouring matter is slowly removed from the sclerotic tissue of *Lygodium* by the action of Eau de Javelle, and the decolourized walls then give the cellulose reaction with Schulze's solution. This agrees with what Poirault ('93, p. 127) found in certain other Ferns. Succeeding the sclerotic tissue abruptly is the third or innermost zone of the cortex, which consists of from three to five layers of rather thin-walled cells, whose walls are suberized. Many of these cells are slightly rounded off at the corners, when seen in transverse section. In a tangential section they are from two to five times as long as broad, and often show a chain of small oval intercellular spaces between their vertical walls, similar to those seen among the palisade-cells of some Angiospermous leaves. The intercellular spaces thus run in the

radial direction, and their function is probably connected with the aeration of the tissues of the stele. In Fig. 1, Plate XIX, the layer of suberized cells may be recognized by comparison with the high-power drawing, Fig. 2, where this tissue (*s. l.*) is seen to lie between the sclerotic middle cortex, one layer of which is shown at the top of the drawing, and the endodermis (*e.*). The endodermis is easy to distinguish; in young stems it shows the usual suberized bands in its cells, and in old stems all its cell-walls are suberized. Its cells become yellow or brownish. The pericycle is mostly from three to four cells thick. Its cells, at an early stage, show radial seriation with their radial walls corresponding with those of the endodermal cells (as seen to some extent in Fig. 3). This arrangement is, however, upset by subsequent displacement (Fig. 2). The protophloem forms a ring, broken here and there, and consists of rather small sieve-tubes, often flattened in old stems, and easily distinguished from the succeeding band of metaphloem, which is composed of large sieve-tubes and phloem-parenchyma. The walls of the sieve-tubes are rather thick, and stain strongly with haematoxyline (Fig. 2, *ph.*). In thick unstained transverse sections the sieve-tubes are seen to differ by their scanty contents from the phloem-parenchyma.

In longitudinal section the sieve-tubes, which are much elongated elements with oblique end-walls, appear empty except for the presence of numerous granules on the walls. Usually, at any rate, no nuclei are present. This character readily distinguishes the sieve-tubes from the pericyclic cells, which have evident protoplasm and nuclei. The walls of the sieve-tubes stain blue with Schulze's solution, often rather pale, but in some sections of the petiole they took an extremely deep-blue colour; in this case the conjunctive parenchyma-cells in the phloem and xylem were also deeply stained, but the pericyclic cells were scarcely coloured. The sieve-plates remain nearly unstained by Schulze's solution, and the granules turn slightly yellow. The latter are often nearly restricted to the sieve-plates, and probably consist of proteid.

Part of a small sieve-tube from the rhizome of *L. dichotomum* is shown in Fig. 7. In the largest sieve-tubes the sieve-plates on the vertical walls are often much more crowded than in the specimen figured; the thick parts of the wall, in consequence, have a reticulate arrangement. Sieve-plates in section and surface view are easily seen in unstained longitudinal sections. In structure the sieve-tubes of *Lygodium* agree with those of other Ferns, but callus, as will be described below, appears to be absent.

A layer of conjunctive parenchyma (1–2 cells thick) separates the phloem from the xylem. The xylem occupies the centre of the stele, and forms a solid rounded mass about $\frac{3}{4}$ mm. to $2\frac{1}{2}$ mm. in diameter (Fig. 1). It consists of tracheides and parenchyma, the latter occurring chiefly as tortuous chains of cells, which are mostly uniseriate (Fig. 2). Short rows of cells and isolated cells (as seen in transverse section) also occur, but it is probable that the parenchyma really forms a connected system. The smallest tracheides, which are also the first to differentiate, and must be described as protoxylem, are scattered round the periphery of the xylem, and are not arranged in definite groups; see Fig. 2, and also the young stem Fig. 3, where the protoxylem-elements are the only tracheides differentiated. Especially in large steles in this species the protoxylem-elements may be much more numerous on the lower than on the upper side of the xylem, and may differentiate earlier on the lower side. The first-formed tracheides differ from typical protoxylem in not being annular or spiral. They are finely scalariform. This character no doubt implies that the formation of the protoxylem is subsequent to the elongation of the tissues. The tracheides of the remainder of the xylem are scalariform, and their order of differentiation is not regularly centripetal, but a number of single tracheides scattered throughout the xylem become fully developed, while the intervening ones are still thin-walled. The latter become subsequently thickened and the mature structure is attained. The intermediate stage of development with internal scattered tracheides is described by Russow ('72,

p. 97); and Prantl ('81, p. 27) evidently referred to this stage when he described the protoxylem as 'regellos über den Strangquerschnitt zerstreut.'

Many of the conjunctive-parenchyma cells in the xylem and also those bounding its periphery contain irregular refractive bodies, which prove to be silica-nodules. Several are shown in Fig. 2; the one marked *si.* is adjacent to the nucleus of the cell. They show varied shape and texture, but a frequent type has a rod-like general outline, either blunt or pointed at both ends, the texture being sometimes loose and granular, but more often dense and solid-looking, with a botryoidal or mammillated surface. They occur singly in a large proportion of the cells mentioned above. The silica-nodule, when large, lies with its length along the length of the cell which contains it, and appears to be free in the cell cavity, but is possibly imbedded in a mucilaginous substance. In a piece of old rhizome the silica-nodules were specially well-developed, and many attained a length of $\frac{1}{10}$ mm. They can be isolated by boiling a piece of the stele in Schulze's macerating fluid till the tissues are completely dissolved, when the sediment consists entirely of silica-nodules. Fig. 5 is a drawing of a nodule isolated in this way. They are very distinct when mounted in methylated spirit or water, but almost unnoticeable in strong glycerine or sulphuric acid. This of course depends on the refractive index of the liquid. Decisive chemical tests were not employed, but it is easily shown, by rubbing them between a watch-glass and a glass-slide, that they are hard enough to scratch glass, hence it may be taken for granted that they consist of silica. The siliceous bodies were found to be about equally numerous and well developed in the rhizome of a plant grown at Kew and of one from Ceylon. Poirault ('93, p. 241) has described siliceous bodies of similar appearance in certain epidermal cells of the petiole in some species of Marattiaceae.

The structure of the node will be described later. The rhizome of *Lygodium* has a uniform type of structure in the species examined, and as it has been rather fully described in

L. dichotomum, it will only be necessary to mention a few differences of detail, observed in other species. The stele of *L. pinnatifidum*, Sw., is similar to that of *L. dichotomum*, but smaller. Silica-nodules are present, but in the specimen examined were less numerous. The walls of the suberized cells of the inner cortex become brown in the old rhizome. In *L. japonicum*, Sw., the protoxylem of the rhizome was seen to be similar to that of *L. dichotomum*. No siliceous nodules were observed. In *L. scandens*, Sw., the small scalariform tracheides are at the periphery of the xylem as in the other species, but they are less numerous and less regularly distributed than in *L. dichotomum*. The layer of suberized cells is several cells thicker than in that species, and much more lacunar in transverse section, adjacent cells being often completely rounded off from one another with the exception of a narrow neck-like prolongation connecting them and divided by a cross-wall at the middle point. Chains of intercellular spaces between the cells are seen in a tangential section as in the other species. In *L. palmatum*, Sw., the inner cortex instead of being represented by lacunar suberized cells, consists of sclerotic cells, which showed no intercellular spaces. In *L. reticulatum*, Schk., the tracheides of the rhizome are specially thick-walled, and no layer of suberized cells was observed. In *L. volubile*, Sw., the rhizome is of the usual type; the layer of suberized cells is yellowish and fairly lacunar.

The branching of the stem in *Lygodium* appears to be dichotomous, but no stage was met with, sufficiently early to prove whether it is a case of true dichotomy. The stele elongates so as to become oval, then becomes constricted into hour-glass form, and divides into two about equal-sized steles. No definite relation between the branching and the leaf-insertion could be made out, but in one or two cases a leaf-trace was attached to the stele just where it forked, in a median position, and the tracheides of the leaf-trace were attached to tracheides supplying the xylem of both branches. The apex of the rhizome, examined in the seedling of

L. japonicum, agreed with what Bower ('89, p. 322) found in *L. scandens*, i. e. it had a three-sided apical cell, and a comparatively flat apical cone.

LYGODIUM, petiole and node.

A transverse section of the petiole of *L. japonicum* is represented in Fig. 4. The xylem, which forms a solid mass at the centre of the bundle, has the same characters as in the rhizome, that is, it consists chiefly of large scalariform tracheides and chains of parenchymatous cells. It has three prominences, one median and two lateral, where the first formed tracheides occur. On the morphologically lower side (the upper side in Fig. 4) the prominence bears a pair of protoxylem-groups composed of spiral tracheides. Each of the two remaining prominences has one or two spiral tracheides connected with it, but most of the small peripheral tracheides in this region are scalariform. The protophloem forms a scarcely broken ring round the xylem, and the metaphloem attains its greatest thickness and includes its largest sieve-tubes in the three bays alternating with the three prominences of the xylem; the lateral bays being here considerably deeper than the median one. The pericycle is mostly from one to two cells thick. The endodermis is small-celled, and its cells contain a mucilaginous substance. The form of the xylem in transverse section varies according to the distance from the base of the petiole. Close to the base the xylem becomes much more rounded, while higher up in the petiole the prominences of the xylem become more and more pronounced. Some details on this point are given below under *L. dichotomum*. One or two granular bodies, probably siliceous, were observed in the petiole of *L. japonicum*.

In the petiole of *L. dichotomum* the structure is of the same type as in *L. japonicum* in the corresponding region, and the shape of the xylem-mass undergoes similar changes according to the level. Quite at the base of the petiole the xylem has an oval outline; at some little distance from the base (e. g. at

about one inch) it has a well-marked prominence on the morphologically lower side, while the outline of the xylem on the upper side is rounded, and the two lateral prominences are broad but only slightly raised. At a still higher level the xylem becomes three-lobed, much as in Fig. 4. In this upper region of the petiole spiral tracheides occur in connexion with all three prominences; one group near the lower corner of each lateral prominence, and one near each corner of the lower one. Towards the lower region of the petiole the two groups of spiral tracheides belonging to the lower side of the xylem are retained, but the other groups disappear, all the small peripheral tracheides of the lateral prominences being then scalariform. At a lower level still, close to the base of the petiole, spiral elements are absent altogether. The lower prominence is no longer broad and flattened, but forms a slight rounded angle with a single group of small scalariform protoxylem-elements forming its apex. This group becomes less and less marked as one passes downwards, so that the leaf-trace in passing through the cortex of the stem has a xylem of circular and then oval outline, and a nearly uniform layer of phloem surrounding the xylem. The position of the lower group of scalariform tracheides is still just distinguishable, and one is able to determine that the bundle does not undergo any great change in orientation during its passage through the cortex. The xylem of the leaf-trace passes in about radially until it is almost touching the stele, when it curves downwards and its tracheides join those of the stele. As stated above, there has been no important change in orientation, so the lower group of scalariform tracheides is probably continuous with some of the protoxylem-elements of the stele, though this cannot be stated with certainty. The node in longitudinal section shows a peculiar structure. A large number of branched tracheides occur, chiefly of a V- or Y-shape¹. They are arranged one above another and more or less fitting into one another, and are so placed that one arm of each tracheide

¹ A few similar tracheides occur at the node in *Trichomanes radicans*.

runs obliquely into the base of the leaf-trace, while the other arm is directed longitudinally forward in the stele. In this way the junction of the xylem of petiole and rhizome is effected. One of these nodal tracheides isolated by maceration is shown in Fig. 6. They occasionally have a more complicated and irregular form. Similar branched tracheides occur at the division of the stele when the stem dichotomizes.

In the petiole of *L. dichotomum* as in *L. japonicum* the proto-phloem forms a nearly continuous ring. The biggest sieve-tubes of the metaphloem and the greatest thickness of phloem occur in the three bays of the xylem. Spiral protoxylem-elements are present on the lower side of the xylem-mass. Examination of a young stage of the petiole proved that in the region, where the upper side of the xylem is rounded (without a median bay), two protoxylem-groups consisting of spiral elements on the lower side of the xylem were the first to differentiate. A good deal later two to three groups of 'protoxylem,' consisting chiefly at any rate of scalariform tracheides, were differentiated at each side of the xylem-mass, in the regions corresponding to the lateral prominences. Then subperipheral and peripheral tracheides were formed on the upper and lower sides, the elements opposite the two bays being late in differentiation. The development of tracheides in the interior is rather irregular, but appears to depend partly on the size of the mature elements to be formed. Siliceous nodules with a granular texture are fairly numerous in the xylem-parenchyma.

L. pinnatifidum has a petiole of the same type as the last species, but the bundle is smaller. The development is evidently fairly similar. In the region where the upper side of the xylem is rounded there are four protoxylem-groups, two on the lower side and two lateral. Their differentiation is probably more nearly simultaneous than in *L. dichotomum*.

In *L. scandens* the xylem of the petiole has a more rounded form than in the species described above. There are three protoxylems, one on the lower side and two lateral. Some

very thick-walled sieve-tubes are present, and resemble fibres, but were not lignified in the cases examined.

The petiole of *L. palmatum* is small compared with that of *L. dichotomum*, &c., and is of a somewhat different type. The xylem is shaped rather like an equilateral triangle with one protoxylem at each corner. The protoxylem-group on the lower side is distinctly not peripheral, but slightly embedded in the xylem. This fact and the peculiar rosette-like arrangement of the adjacent tracheides round the protoxylem-groups in this species were noticed by Prantl ('81, p. 27). Especially in this species the rule given by Bertrand ('81, p. 15), that in sections of appendicular organs the bundles show symmetrical arrangement in relation to a single straight line, does not at first sight appear to hold good, as the bundle has a nearly complete radial symmetry. But it must be noted that the median protoxylem ('centre de développement') is not quite peripheral, and that in *L. dichotomum*, at any rate, the bundle attains a bilateral symmetry at the base of the petiole by the disappearance of the lateral protoxylems.

There are three fair-sized bays of phloem, and the proto-phloem is continuous. The pericycle is from one to two cells thick, being one cell thick opposite the protoxylem-groups, and separated from them by parenchyma.

The petiole or rachis of *L. lanceolatum*, Desv., is of the usual type, except that it contains a large number of fibres chiefly in the neighbourhood of the protoxylem-groups. They are strongly lignified, and almost certainly produced by sclerosis of sieve-tubes. In addition, some of the large meta-phloem sieve-tubes situated in the bays of the xylem become lignified in different degrees. The chains of parenchyma-cells in the xylem have the walls separating them from one another considerably thickened and lignified. In the petiole of *L. heterodoxum*, Kze., the xylem-parenchyma also tends to be thick-walled, and fibrous sieve-tubes are present, but are not lignified. In *L. volubile*, while the petiole is typical, the rachis shows a structure approaching that of *L. palmatum*.

LYGODIUM, root.

The root of *L. dichotomum* has a diarch xylem-plate with sometimes two specially large tracheides in the metaxylem, as occurs in many other Ferns. The tracheides at each end of the xylem plate, including the protoxylem and a few other tracheides, are somewhat spread out as a tangential row of elements at right angles to the plane of the diarch plate. The two protoxylem-groups consist of a few small tracheides, and are in the usual position. After their differentiation the subsequent order of development of the xylem is tangentially outwards for the one or two larger tracheides completing the tangential rows mentioned above, and at the same time inwards (towards the centre of the root) for the remainder of the metaxylem. The development here and comparison with the structure in other species do not appear to give any grounds for distinguishing by a separate term the tangentially developed tracheides from the more central part of the xylem. Hence 'metaxylem' may be used for all the xylem other than protoxylem, as in the previous paper (Boodle, '00, p. 458). The endodermis consists in most cases of six flattish cells, whose radial walls correspond roughly with those of the cortical layer next outside; this layer also consists of six cells, which measure tangentially two to three times their radial depth, and have brown walls. Outside these cells there is a sudden change to many-celled layers, of which the next 1-3 layers are thick walled (according to the age of the root). The innermost of these may consist of very thick-walled cells with narrow radially elongated cavities. The remaining five or six layers of the cortex have comparatively thin brown walls. The pericycle is one cell thick in most places, and is a many-celled layer, but appears to have been formed by subdivision of a six-celled layer, whose radial walls at first corresponded with those of the endodermal cells.

The root of *L. pinnatifidum* is fairly like that of the species just described, but the endodermis consists of twelve or more cells. When the root-stele passes off from the stele of the

rhizome, it has a nearly longitudinal course until after passing through the phloem region of the rhizome. It then curves out more sharply. In *Lygodium japonicum*, at the junction of the xylem of the root with that of the stem, a few branched tracheides occur, but they differ from those at the node, in that their arms are scarcely divergent. This depends on the angle at which the root-stele separates. In all the species 'root-tracheides' are differentiated at the periphery of the stele a short distance before they 'pass out' to the root.

LYGODIUM, seedling.

The seedling¹ of *Lygodium japonicum* may now be described. The first leaf is simple and palmatipartite; the second leaf has its lamina dichotomously divided into two palmatipartite segments. In the next few leaves the petiole forks into two at the top with one pinnately lobed pinna on each fork. The later leaves have the growth of the rachis continued above the two pinnae as a circinate tendril-like projection or a bud. The appearance of the rhizome in oldish seedlings suggests that, after the first dichotomy of the rhizome, one branch does not develop far, and that growth is continued by forking of the other branch. The roots show distichous arrangement.

The structure of the seedling was examined by means of microtome-series. Several series were made, and showed differences in detail, but agreement in the main characters. The primary root is diarch. In the region of the foot the root-stele curves sharply (nearly horizontally) inwards towards the prothallus. Fig. 8 shows the arrangement of the foot (*f.*) and prothallus (*p.*) at the point where the root-stele, whose diarch xylem is shown diagrammatically at *x.*, is just beginning to curve inwards. After curving in, it turns upwards so as to become vertical again, and generally by that time has lost the distinctive characters of root structure,

¹ 'Sporeling' is of course the more reasonable term, but 'seedling' appears customary.

and may be regarded as belonging to the stem. To take one case as an example for the details:—during the double bending of the stele, the xylem-tracheides become more nearly uniform in size, and increase in number from 15 to about 36, at the same time the outline of the xylem becomes roughly circular, definite protoxylem-groups are not distinguishable, and the phloem becomes practically continuous. Then, to return to the general description, a few parenchyma-cells appear in the xylem, and a little higher up they increase in number, so that the structure of the rhizome of a mature plant is represented on a small scale, as seen in Fig. 9. This is from a section below the first leaf; *p.* is one of the xylem-parenchyma-cells. In Fig. 10 the xylem of the first leaf-trace has just separated from the xylem of the stele. From two to three leaf-traces and from one to three roots are given off (in the order of first a leaf-trace and then a root), the stele meanwhile retaining the type of structure shown in Fig. 9. After this the stem dichotomizes and leaves and roots are produced by the two branches of the stem, which grow as rhizomes. One of them is usually horizontal, while the other is inclined upwards, and, as stated above, one of them tends to be arrested. At this first dichotomy the branch cut transversely near its base shows the same type of structure as the rhizome of the mature plant; parenchyma is scattered among the xylem, and the largest tracheides are towards the centre of the latter, while the protoxylem is peripheral or nearly so. To return to one of the series for the orientation: the first leaf-trace separates from the stele on the side away from the prothallus, about in the position of an original root-protoxylem. The second leaf passes off towards the prothallus at a divergence of about 120 degrees. The stele of the stem elongates in a plane about perpendicular to one which includes the two leaves, and then dichotomizes. Each branch gives off a root on its lower side, and one branch close to its base produces a leaf-trace on its upper side.

It is clear from the above description that the structure

typical of the rhizome of *Lygodium* is attained in the seedling without any intermediate more complicated structure. Hence there are no grounds for assuming a reduction to have taken place.

With regard to the first and second leaf-trace of the seedling, although they pass off from the stele as collateral bundles, their phloem, though only containing a few sieve-tubes, spreads towards the inner side as they pass through the cortex of the stem, so that they become concentric or very nearly so, and the same structure appears to be continued in the petiole.

The leaves are radially arranged on the upright stem of the seedling, the dorsiventral arrangement of the mature plant beginning after the first dichotomy of the stem.

SCHIZAEA, habit.

The stem of *Schizaea digitata*, Sw., may be erect or obliquely ascending, or often in old plants the lower part of the stem is erect, and the upper part ascending or even horizontal. The leaves are crowded on the stem, and the roots attached between them; the phyllotaxy is difficult to determine and probably variable, but in some stems it appeared to be $\frac{1}{3}$ in places, but usually the orthostichies numbered more than three. In *S. fistulosa*, Labill., the leaves are, at any rate sometimes, dorsal and distichous. The leaves of *S. digitata* are narrow-linear, and grass-like, often over a foot in length. The petiole is triangular in section, and passes gradually into the lamina, which is flattish only in its upper region, where it shows a prominent midrib on the lower side. The leaves of certain other species are much broader and are dichotomously forked.

SCHIZAEA, stem.

In the rhizome of *Schizaea digitata*, Sw., the stele shows a marked difference from that of *Lygodium*. The distinguishing character is that the xylem consists of tracheides with usually no parenchyma among them, and forms a ring

surrounding a central pith. The ring of xylem is interrupted by the departure of the leaf-traces as seen in Fig. 11, which represents the node of *S. dichotoma*, Sw.

The rhizome of *S. digitata* has a cortex of 6–8 layers of brown sclerotic cells. The endodermis contains mucilage, and the pericycle is usually 2–3 cells thick and its cells are rather thick-walled. The outer pericyclic cells generally have their radial walls coinciding with those of the endodermal cells, and the sieve-tubes sometimes correspond with the inner pericyclic cells. The phloem consists of sieve-tubes and parenchyma, and is 2–4 or 5 cells in thickness. The sieve-tubes are sometimes tabular and three or four of them may form a neat radial row, at other times they are smaller, more rounded and irregularly placed, with parenchymatous cells among them. Some little doubt must be expressed as to the nature of the elements here spoken of as sieve-tubes. In longitudinal section they are at first sight considerably unlike the sieve-tubes of *Lygodium*. Some of them are short elements, of the same length as the pericyclic cells or slightly longer, with straight or slightly inclined end-walls; but others are a good deal longer and may have long pointed ends. The points in which they resemble the sieve-tubes of *Lygodium* are best seen in the more elongated elements, in longitudinal sections unstained and mounted in glycerine-jelly, and are as follows:—the walls are rather thick and refractive, and oval or rounded pits are seen on some of the longitudinal walls, and bear refractive granules. The phloem-parenchyma-cells have rather scanty contents, except for the presence of a distinct nucleus, and their walls do not stain quite so strongly with haematoxyline as those of the sieve-tubes. One meets with doubtful elements, which might be either sieve-tubes or phloem-parenchyma, but those which most suggest sieve-tubes are usually destitute of a nucleus.

The 'sieve-tubes' occupy the usual position for sieve-tubes, are differentiated early as in other Ferns, and also when first formed are well differentiated by haematoxyline. All the characters point to the elements in question being sieve-

tubes corresponding to those of other Ferns, but probably mixed with elements intermediate between sieve-tubes and phloem-parenchyma, and possibly somewhat reduced.

The xylem is separated from the phloem by the usual ring of conjunctive parenchyma, and forms a complete round or oval zone, which is interrupted by the departure of the leaf-trace. The xylem-ring in *S. digitata* is like that of the species figured (Fig. 11), but consists of a thinner layer of tracheides, which is usually 1-3 elements thick. The tracheides are scalariform with narrow pits, and are usually rather short, and often irregular. As in *Lygodium*, there are no definite protoxylem-groups, but the first formed tracheides are scattered. With such a thin ring of xylem it is difficult to determine whether the xylem is endarch or exarch, but Fig. 12, which represents the young node, shows that the development is irregular; *a.* and *b.* are examples of an outer and an inner tracheide respectively being the first to differentiate. Protoxylem-formation in this case progresses from one side of the stem to the other.

Within the xylem-ring is the pith, the cells of which are sclerotic, contain mucilage, and have numerous fine pits in their walls. The walls of the pith-cells adjoining the xylem are usually thinner than the rest, and remain unlignified longer, and in these cells mucilaginous contents are less or absent. There is no internal endodermis. In the region of the leaf-gap the pith becomes continuous with the pericycle, and its cells, especially the outer ones, resemble those of the pericycle, which become fairly thick-walled and occasionally show pitting like that in the pith. The inner cortical cells also possess pits just like those of the pith-cells, but their walls are brown. The pith-cells are not very much elongated, being shaped like rather long parenchymatous cells and having often flat ends.

There is a tendency to lignification in the pericycle and phloem. It was found by treating a section with phloroglucin and hydrochloric acid that the tracheides were very strongly lignified. The pith-cells were fairly strongly lignified,

except the outermost layer of the wall, which was not lignified; but the peripheral cells of the pith had hardly more than the middle lamella lignified. In the pericyclic cells the wall at the corners was often lignified, sometimes the middle lamella as well, or sometimes the greater part of the wall. The sieve-tubes sometimes had their walls lignified at the corners. The lignin stain was not seen in the sclerotic cortex. The middle lamellas of the cortical cells, pith and pericycle were curiously resistant to sulphuric acid, and were not dissolved by boiling for a short time in potash-solution.

The stem-structure of *S. dichotoma* and *S. fistulosa*, Labill., was examined in fragments of dried material. The figure *S. dichotoma* (Fig. 11), and the diagram of the same species (Fig. 15) will be referred to in the description of the node. The structure of *S. dichotoma* (Fig. 11) need not be described at length, as it is of the same type as *S. digitata*, but it should be mentioned that one or two fibrous sieve-tubes, apparently lignified, occurred in the phloem near the two ends of the arc of xylem belonging to the stem. The smaller tracheides are usually at or towards the periphery of the xylem. Two or three layers of thin-walled cells with small intercellular spaces at the corners lie between the brown outer part of the cortex and the endodermis.

In *S. fistulosa* there is a broad cortex consisting of fairly thin-walled cells, of which the outermost one or two layers only are coloured brown. The pith-cells are also fairly thin-walled, but have collenchyma-like thickenings at the corners. The xylem is only 1-2 tracheides thick, but where it is two-layered, if the tracheides differ in size, the smaller ones are nearly always at the outside; so the structure tends to be exarch. Another piece of rhizome of this species was probably a short distance behind a dichotomy, as it had two nearly equal-sized steles, both of which were slightly irregular, and the xylem was more or less interrupted by leaf-gaps. The two steles had been giving off leaf-traces; three had been derived from each stele and were found at different distances on their way out through the cortex.

In *Schizaea digitata* a comparison of transverse sections of the young stem at different stages of development points to a possibility that the endodermis, pericycle and phloem may be formed by subdivision of a single layer. This would be a very remarkable case of stelar endodermis, or cortical phloem, and it is intended to reinvestigate it.

SCHIZAEA, petiole and node.

A transverse section of the petiolar bundle of *Schizaea digitata* is represented in Fig. 13. The bundle is seen at once to be collateral. There is a band of xylem on the morphologically upper side, with no well-marked protoxylem, but judging by the size of the tracheides those laterally placed are probably the first to differentiate. This section was cut near the base of the petiole, and spiral elements appear to be absent in this region, the tracheides being scalariform. The phloem forms a band on the lower side (*ph'*), and consists of thick-walled sieve-tubes and a certain amount of parenchyma. A group of fibres (*f.*) is seen touching the xylem at each end of the bundle. Their end-walls resemble sieve-plates and they appear to represent lignified sieve-tubes. The pericyclic cells are rather thick-walled as in the stem, but have been represented as thin-walled in the figure. Sections of a young petiole cut higher up than the level of the section just described, prove that spiral protoxylem-elements are formed on the upper side of the bundle roughly in the median region (Fig. 14, *px'*) and the differentiation proceeds outwards on both sides along the periphery of the xylem, so that a crescent of tracheides is formed, the more centrally placed tracheides developing subsequently. The nearly median first-formed tracheides become crushed rather early, and are scarcely distinguishable in the mature petiole. In the lamina of *S. digitata* the bundle in the midrib resembles the bundle of the petiole, but has more numerous fibres. In the median region on the lower side, in the sections examined, three pericyclic cells had become much enlarged, and had crushed the greater part of the

phloem. If normal, this may be compared with 'cavity-parenchyma.'

At the node a segment of the xylem-ring separates for the leaf-trace, and carries with it the phloem on its outer side. The leaf-trace is seen cut rather obliquely in Fig. 12. In *S. dichotoma* the leaf-trace is seen separated from the xylem and phloem of the stem in Fig. 11, but still enclosed by the endodermis. Fibres occur in the leaf-trace. In the diagram, Fig. 15, the leaf-trace surrounded by its own endodermis is on its way out through the cortex, and the endodermis of the stele has dipped into the leaf-gap as far as the inner limit of the xylem. As far as was observed, the pith remains separated from the cortex by the endodermis in the nodal region. The xylem of the leaf-trace becomes detached from the xylem of the stem at one end first. In *S. fistulosa* the leaves are dorsal and apparently distichous, but in the specimen described above as preparing for dichotomy the phyllotaxy was $\frac{1}{3}$.

In *S. fistulosa* some of the leaf-traces in the cortex had an arched xylem-mass, with its convexity directed outwards. This type of structure is an approach to what is found in *Anemia*. The petiolar bundle resembles that of *S. digitata*.

SCHIZAEA, root.

In the root of *Schizaea digitata* there are only three layers of cells outside the endodermis. The outermost of these is the piliferous layer, and often peels off in the old root, then follows one layer of thin-walled cortex, and one layer of cells with their inner and radial walls very strongly thickened. In old roots the stratification of these walls is remarkably distinct. The endodermal cells are flattish. Both pericycle, endodermis and the layer of sclerotic cortical cells usually consist of six cells each, but sometimes of eight or nine cells, especially in the case of the pericycle. The xylem forms a typical diarch plate, with two large tracheides in the metaxylem. The structure is nearly identical with that

figured by Prantl ('81, Fig. 59) for *S. pennula*, Sw. The radial walls of the pericycle, endodermis and sclerotic layer of the cortex correspond, while the walls of the next cortical layer, which may consist of twelve cells, do not coincide with them. The pericycle therefore appears to be cortical.

ANEMIA, habit.

In *Anemia Phyllitidis*, Sw., the stem is obliquely ascending, the leaf-bases are crowded and leave scarcely any free surface to the stem. The roots are borne by the stem in longitudinal rows between the leaf-bases, and stick out through the narrow fissures left between the latter (Prantl, '81, p. 2). The phyllotaxy appears to be $\frac{2}{5}$ as stated by Prantl. Polystichous leaf-arrangement occurs in most species of *Anemia*, but seven species have a creeping rhizome, which bears distichous leaves, sometimes distant, on its upper side. These species are included by Prantl in the subgenus *Aneimiorrhiza* (*Anemirrhiza*, J. Sm. emend.), and the above characters form part of the diagnosis of the subgenus. *A. mexicana*, Klotzsch., and *A. cuneata*, Kze., are examples of this type.

The leaf in the genus is petiolate, and pinnate, the pinnae being nearly entire, pinnately lobed, or again pinnate in their basal region.

ANEMIA, stem.

Fig. 16 is a diagram of a transverse section of the stem of *Anemia Phyllitidis*, the vascular tissues or rather their endodermal sheaths being shown in outline. The structure is entirely different from what has been described in the stems of *Lygodium* and *Schizaea*, and may be called dialystelic, and the masses of vascular tissue represent steles, or meristeles, or bundles, according to what view one takes of their homology and of suitable terminology. In the particular case figured two leaf-traces (viz. *l.t.* and the bundle on the opposite side of the stem) are seen on their way in towards the interrupted vascular ring, which here consists of two parts. These latter represent the section of a hollow reticulate vascular

cylinder similar, except as to leaf-traces, to that of *Nephrodium Filix-mas*, Rich. In *Anemia* each mesh is a leaf-gap, and the leaf-trace is inserted about at its base as shown in Prantl's diagram (Fig. 27 A).

In the transverse section of the stem the ground-tissue appears as a uniform tissue of rounded, starch-containing, parenchymatous cells frequently with small intercellular spaces at the corners. In longitudinal section these cells are from two to six times as long as broad, and have flat or sometimes pointed ends. Three or four layers at the periphery may become sclerotic. In Fig. 16 two roots (*r.*) are seen on their way out through the ground-tissue. A cavity or pocket (not shown in Fig. 16) is present in the ground-tissue on the inner side of one of the incoming leaf-traces. A pocket which communicates with the exterior is present in connexion with each leaf. It is axillary in position, slit-shaped where the petiole joins the stem, but becoming triangular and decreasing in size in passing downwards, and disappearing before the leaf-trace joins the vascular cylinder. Three of these axillary pockets are represented in Prantl's Fig. 27 B. The tissue limiting them bears numerous hairs, and becomes sclerotic. The structure of the leaf-traces and of a large part of the vascular cylinder may be best described in reference to the petiolar bundle, but the structure of one of the flattish 'steles' forming part of the vascular ring in some sections may be described here, as more characteristic of the stem. A section of one such stele is really one of the strands composing the reticulate cylinder, cut near the base of a mesh. It has an elongated elliptical outline formed by the rather flat-celled endodermis (*e.* in Fig. 40, which represents a small piece of the stele). The pericycle forms a continuous layer about two cells thick, while the phloem consists of a band of sieve-tubes on the outer and inner side of the xylem (*ph.* and *i. ph.* in Fig. 40). On the inner side of the xylem the sieve-tubes form a continuous or nearly continuous band from one to two elements thick, but on the outer side of the xylem the sieve-tubes are less numerous and smaller and form only a broken

band, interrupted by parenchyma. The sieve-tubes are not present at the ends of the xylem-mass. The sieve-tubes are in most places separated from the xylem by conjunctive parenchyma, 1-2 cells thick; this tissue also is better developed on the inner than on the outer side.

The xylem occupies the centre and has nearly the same form as the whole strand. In this region it consists entirely of scalariform tracheides and parenchyma; spiral elements being absent. As seen in Fig. 40 the smaller tracheides are at or towards the outside (on the right in the figure), the largest ones being at the inner side. At the two ends of the xylem-strand there are rather numerous small tracheides taking up the greater part of the thickness of the xylem. Some of the small tracheides scattered along the outside of the xylem-band together with some at the ends, and one or two immersed in the xylem, are the first to differentiate. So the strand has rather irregular development, but a tendency to the exarch type¹. Root-steles are attached to the ends of the stele, where the numerous small tracheides are present; a root may fuse with one end of the strand, just before the attachment of a leaf-trace to that end.

The scalariform tracheides are of a common type, with the pits often running the whole width of the wall. The sieve-tubes have inclined end-walls, and the sieve-plates are crowded on the longitudinal walls of the larger elements so as to give them a reticulate appearance. The strips of wall between the sieve-plates are narrow, but sometimes thickened to a remarkable extent, and the thickenings on the two sides of a longitudinal wall may together have a dumb-bell-shape in section, so that the sieve-plates are in these cases actually bordered. Granules are seen on some of the sieve-plates. In Fig. 40 some of the small tracheides are detached from the rest of the xylem, so as to be in contact with the sieve-tubes. This is rather exceptional.

In the majority of species of *Anemia* (viz. excepting Prantl's subgenus *Aneimiorrhiza*) the structure of the stem appears

¹ That is, exarch with regard to the centre of the stem.

from Prantl's statements (p. 22) to be of the same type as in *A. Phyllitidis*. The stem of *A. Dregeana*, Kze., was examined, and found to be dialystelic, and differed only in unimportant details from *A. Phyllitidis*.

ANEMIA, petiole and 'node.'

The petiolar bundle of *Anemia Phyllitidis* is well figured and described by Prantl (Fig. 30), but an illustration is given here for the sake of completeness (Fig. 17). The xylem consists of a band of tracheides shaped like a flat-topped arch with divergent supports, which have hooked ends turned inwards. The tracheides are mostly scalariform, but three protoxylem-groups of annular and spiral elements are found on the inner surface of the xylem:—one at the median point, and one at a short distance from each hook. The hooks are formed of small scalariform tracheides. The phloem, which is usually separated from the xylem by a layer of conjunctive parenchyma, forms a layer covering the outer surface of the xylem-arch, and is continued on the inner surface about half way up each arm. It consists of sieve-tubes and parenchymatous cells scattered among them, and distinguished from them by their dense contents and larger size. The phloem is thickest on the outer and inner sides of the arms. Several of the sieve-tubes become converted into thick-walled lignified fibres, one of which is shown in Fig. 19. This element was already lignified, but its walls had not attained their full thickness, and the structure of the oblique end-wall, and also the presence of numerous refractive granules on it, are suggestive of what is found in a functional sieve-tube. These fibrous elements form a thin continuous layer along the flat top of the xylem-arch and on the convex surface of both the xylem-hooks. In these regions the phloem is thin, and practically all the sieve-tubes are replaced by fibres. Fibres also form a fairly compact mass filling the concavity of the hooks, and some occur scattered along the inner and outer face of the xylem for some little distance upward from the hooks. In all these cases the fibres are usually separated from the xylem by

a layer of conjunctive parenchyma, but several fibres may also be in contact with the xylem. The pericycle forms a continuous layer of rather large cells, and is 2-4 cells thick, but reduced to a single row of cells on the flat top of the arch and at the ends of the arms. In these regions its cells have dense contents. The endodermis is very distinct, and roughly follows the outline of the xylem. Cavity-parenchyma¹, which belongs to the conjunctive parenchyma adjoining the xylem, occurs in connexion with the three protoxylem-groups, but is most marked in the case of the median group, where two enlarged cells of this tissue may be recognized in Fig. 17. A cell belonging to the cavity-parenchyma is shown in longitudinal section in Fig. 18. It contains a nucleus and protoplasm, and has formed two large protrusions, which have grown into the space originally occupied by an annular tracheide of the protoxylem. Some of the rings of this element are seen crushed together at *r*.

The epidermis and the succeeding five or six layers of the cortex are sclerotic, and there is a gradation from the small-celled epidermis to the large-celled inner layer of this zone. The rest of the cortex or ground-tissue is thin-walled. In cells of this tissue not far outside the endodermis a few silica-nodules were met with. They were usually solid-looking, and roundish or irregular in form. Fig. 20 is one of them, and is double, with a cavity in each half.

In the basal region of the petiole the fibres become reduced in number until none are left. The top of the xylem-arch becomes more rounded, and the hooks become less incurved, until nearly absent. There are still three protoxylem-groups in the same positions as before, but, close to the base of the petiole, the median protoxylem appears to be the only one which possesses spiral tracheides, and is formed a little earlier than the other two. The ground tissue becomes fairly thick-walled, and the part of it filling up the concavity of the arched bundle becomes specially thick-walled.

The leaf-trace in the cortex of the stem resembles the

¹ This tissue will be referred to again below.

bundle in the base of the petiole in structure; no fibres are present; the pericycle forms a layer of nearly uniform thickness; the phloem is continuous round the ends of the bundle, and three protoxylem-groups are present. As it passes inwards through the cortex the phloem on the inner side of the xylem spreads from both ends towards the median point, where it ultimately meets. When the leaf-trace reaches the vascular cylinder a rounded stele fuses with one end of it, producing a knob at that end; soon afterwards a long flat stele approaches the other end and fuses with it, thus producing a long stele curved towards one end. The lower stele in Fig. 16 is an example of this. The knob is seen at the right-hand end; the curved part is the leaf-trace, and the straight part on the left is the long flat stele just referred to. The little projection on the lower side is connected with a root, which is attached to the stele just as it fuses with the leaf-trace. Part of this flat stele remains as a knob on the left-hand end of the leaf-trace, and the remainder of the stele branches away again as a rounded stele ready to fuse with the next leaf-trace. The leaf-trace that we have been following has by this time a slightly curved form with a knob at each end, the phloem is interrupted at its ends, and the median protoxylem-group, which was present and contained spiral elements while the fusions were going on, now or a little lower down becomes lost. In passing downwards this strand becomes straightened out, and the enlargements at its ends less pronounced, while its protoxylem becomes scattered and largely external, as mentioned above when describing the stem; that is, it gradually loses its leaf-trace characters. If one reverses the order of this series, one may say that, in following a stele upwards in the stem, it divides into three parts, of which the middle one, changing slightly in structure, becomes the leaf-trace.

The petiolar bundle of *A. Dregeana* is not very different in type from that of *A. Phyllitidis*, except that, as Prantl (p. 25) observed, fibres are absent. The xylem forms a considerably flattened arch, with slightly hooked ends. The phloem has

about the same distribution as in *A. Phyllitidis*; it is continuous over the top of the arch, and continuous or slightly interrupted at the ends of the two arms. There is a median protoxylem-group with cavity-parenchyma, and two other protoxylem-groups on the inner side of the xylem-arms; they start just above the hooks, and are spread out about one-third of the way towards the median group. On account of the flatness of the xylem-arch the endodermis only dips in slightly on the upper side of the bundle.

ANEMIA, root.

In the root of *Anemia Phyllitidis* the cortex is twelve or more cells in thickness. The outer three or four layers are comparatively thin-walled and graduate into the sclerotic inner cortex. The endodermis and pericycle are both many-celled, and the pericycle is usually one cell thick. The stele has a typical diarch structure, often with two very large tracheides in the metaxylem. The protoxylem-elements and adjacent tracheides are not spread out tangentially to the same extent as in *Lygodium*. The base of the root stele in the cortex of the stem is diarch, but the middle region of the xylem-plate is occupied by numerous irregularly placed tracheides, and the structure may be slightly asymmetrical.

ANEMIA MEXICANA, ETC.

The following species are included by Prantl in the subgenus *Aneimiorrhiza*:—*A. aurita*, Sw., *A. coriacea*, Gris., *A. mexicana*, Klotzsch., *A. cicutaria*, Kze., *A. Wrightii*, Baker, *A. cuneata*, Kze., *A. adiantifolia*, Sw. These are characterized among other things by their creeping rhizome and distichous dorsal leaves. This appears to be correct at any rate for some of these species, but certain specimens may perhaps have polystichous leaves.

A transverse section of an internode of *A. mexicana* shows a structure which differs from that of *Anemia Phyllitidis* in having a closed ring of vascular tissue instead of an interrupted

one. The structure resembles the *solenostelic* type¹ as defined by Gwynne-Vaughan ('01, p. 73), while *Anemia Phyllitidis* is dialystelic. The cortex of *A. mexicana* consists of brown elements, which are slightly sclerotic in the outer half, and strongly sclerotic in the inner half. Fig. 38 represents the stelar ring of this species, which is bounded by an outer and inner endodermis. Owing to the rupture of the radial walls of inner and outer endodermis, the cortex and central ground-tissue which is sclerotic have broken away, and only the stelar ring is shown in the figure. It is about 1 mm. in diameter, and its structure is as follows:—the pericycle forms a layer 2-4 cells thick on the inner and outer side; there is an inner and outer layer of phloem, each consisting of a practically continuous layer of sieve-tubes, mostly one element thick. The sieve-tubes are rather thick-walled, and stain deeply with haematoxyline. A layer of conjunctive parenchyma separates the phloem on both sides from the xylem. The xylem-ring is about five tracheides in thickness. The tracheides are scalariform, and the larger ones are on the inner side, the smallest tracheides being at or near the outer side. This is seen in the small piece of the stelar ring shown in Fig. 39. A comparison of this figure with Fig. 40 shows that there is a close agreement in structure between the solenostelic ring of *Anemia mexicana* and the separate 'steles' of the stem of *A. Phyllitidis*. In *A. mexicana* a spiral protoxylem-group which comes in with the leaf-trace is continued a short way down in the stem. The tracheides elsewhere in the stelar tube appear to be all scalariform. In this and other species of the same subgenus which were examined, only small pieces of dried material were obtainable, so the structure was not as fully investigated as was desirable. The petiole in this and the next species was not examined.

A. adiantifolia has in its rhizome practically the same structure as *A. mexicana*.

In *A. coriacea*, Griseb.², the solenostele is less than $\frac{1}{2}$ mm.

¹ Leaving the behaviour of the endodermis at the node out of the question.

² In Hooker and Baker's *Synopsis Filicum* (p. 433) the authors were inclined

in diameter; it is thus much smaller than in *A. mexicana*, but has similar structural details. Fig. 41 is a diagram of the structure found just below the node. The inner and outer phloem are each represented by a ring of dots; *e.* and *i. e.* are the outer and inner endodermis, separated in each case from the phloem by a wide layer of pericycle. The xylem-ring is bulged out on the right, preparatory to the separation of a leaf-trace, and *e'* is a group of three or four endodermal cells differentiated in the pericycle in this region. The shaded mass within the inner endodermis (*i. e.*) is a group of sclerotic tissue. The structure found a little higher up in the nodal region is seen in Fig. 42. The xylem of the leaf-trace has become separate, but the phloem is still attached at one end. The little group of endodermal cells (*e'*) was not well preserved, but appears to form a ring as shown in the diagram. Higher up, this ring becomes broader, until it meets and fuses with the outer endodermis, which bends inwards on either side between the leaf-trace and stele. The endodermis then splits so that the stele and the leaf-trace are each surrounded by an endodermis. In this way the continuity of the endodermal sheath is not broken. Fig. 43 shows the leaf-trace (*l. t.*) on its way out through the cortex. It has a slightly arched xylem with a protoxylem-group at the median point on the inner side. The phloem is nearly continuous, or perhaps interrupted for a short distance near the middle of the inner side. For the petiole see p. 421.

The stele of *A. cuneata* has the same type of structure as *A. mexicana* and *A. coriacea*, and is intermediate between them in size.

In *A. aurita* an unexpected structure was found in the rhizome. The stele is about $\frac{1}{2}$ mm. in diameter, which is slightly larger than in *A. coriacea*. The xylem forms a nearly solid mass of circular outline, and consists of tracheides, with a few rows of parenchyma-cells among them. The large tracheides are towards the centre, and the smaller ones at

to refer *A. coriacea*, Griseb., to *A. hirsuta*; but Mr. J. G. Baker has since seen specimens of *A. coriacea* and is of opinion that it is distinct from *A. hirsuta*.

the periphery. This structure might be taken for that of a small species of *Lygodium*, if it were not for the presence of a quite small excentrically placed group of parenchyma or other soft-walled tissue. Unfortunately this was partly disorganized and its nature could not be determined. In the petiole of this species the bundle is like that of *Anemia Phyllitidis* on a small scale, but differs as to endodermis and one or two other points. The xylem forms a V-shaped arch, the ends of which are slightly incurved, hardly hooked. There is a median protoxylem placed just as in *A. Phyllitidis*, and two other groups in much the same position as in that species. The phloem is slightly interrupted at the ends of the xylem-arch, but forms a layer covering the rest of the outside of it, and on the inner side of it reaches about a third of the way up towards the median protoxylem. Several fibres, apparently formed from sieve-tubes, occur in the phloem; a few above the top of the arch and more numerous ones near the ends of the xylem. There is a thick pericycle, and the endodermis does not dip into the concavity of the arch, but has a rounded outline.

The structure of *Anemia aurita* was not examined by Prantl, but he investigated some of the other species included by him in *Aneimiorrhiza*, and described the tubular stele as occurring in them. Robert Brown ('38-'52, p. 2) mentions having observed a complete circle of scalariform tracheides in the stem of some species of *Anemia*.

The occurrence of a solenostele-like stelar tube in one group of species, and of the dialystelic structure in the remainder, is, as Prantl states, connected with the fact that the leaves are distichous and not crowded in the first case, but polystichous and crowded in the second case.

ANEMIA, seedling.

Several series of microtome sections were made of seedlings of *Anemia Phyllitidis*, but on account of the difficulty of penetrating the sclerotic tissue with paraffin and of cutting it, most of these were incomplete. However, by comparing one

series with another, the structure of the transitional region was ascertained. By soaking one of the seedlings for nearly twenty-four hours in Eau de Javelle before embedding, a series was obtained, which was satisfactory through the greater part of its length. Figs. 21-31 (excluding Fig. 23) are sections of the axis in ascending order. Fig. 21 shows the structure of the primary root. It is of the typical diarch type, but is not quite mature. One point, however, in which the majority of Ferns would perhaps show a difference, is that here the first-formed phloem-elements (*pph.*) are adjacent to the protoxylems, so that there are four protophloems. The same mode of development is also found in the lateral roots of the young plant. The root stele bends in towards the prothallus in the region of the foot, and becomes vertical again, just as in *Lygodium*. It may then or soon afterwards be called the stem-stele, as it has lost the characteristic root-structure, and its xylem consists of a solid mass of tracheides of fairly uniform size. The first leaf-trace is then given off (Fig. 22), and the xylem of this leaf-trace (*x'*.) consists of only about six tracheides. One or two small ones which were crushed are not shown in the drawing. Fig. 23 is the xylem of the same leaf-trace on its way out through the cortex. Soon after the separation of the first leaf-trace, a parenchyma-cell appears inside the xylem (Fig. 24). It may be connected by one or more obliquely placed cells with the conjunctive parenchyma surrounding the xylem at a lower level, and not with the leaf-trace; e.g. the parenchyma-cell seen in Fig. 24 had a downward connexion of this kind on the side away from the leaf-trace. The second leaf-trace is given off leaving the stele much as in Fig. 24. Then two or three more soft-walled elements appear adjoining the first parenchyma-cell in the xylem, and of these one or two are probably sieve-tubes. These immersed elements change their position slightly, so that the xylem becomes open, and one of them comes into contact with the external conjunctive parenchyma. A stage of this kind is shown in Fig. 25, where the two elements embedded deepest in the xylem are probably sieve-tubes,

and the cells marked with crosses are endodermal cells. The first lateral root-trace joins the stele, and the central parenchyma and sieve-tubes keep changing their position slightly so as to be again connected with the outer parenchyma and again shut in. The third leaf-trace passes out, the parenchyma remains enclosed, and the second root-trace joins the stele. The central soft-walled tissue increases and the xylem opens. Fig. 26 illustrates this stage. The four elements marked with crosses are almost certainly sieve-tubes, the other elements immersed in the xylem being parenchyma. Thus the central tissue at this stage is to be regarded as phloem. The fourth leaf-trace is then given off, leaving the xylem open, and the third root-trace is attached. The parenchyma then tends to form a more rounded mass with the sieve-tubes in the middle of it, and they here have a connexion with the external sieve-tubes. After the exit of the sixth or seventh leaf-trace the xylem closes and a parenchyma-cell appears in the middle of the central group of sieve-tubes. Then several other parenchyma-cells are formed adjacent to it, so that the stage shown in Fig. 27 is reached. This is where the eighth or ninth leaf-trace is preparing to pass out, and in this figure *x'*. and *ph'*. are the xylem and inner phloem which will pass out in the leaf-trace. After this one or two endodermal cells appear in the central parenchyma, and a little higher up are connected (the xylem being now open) by a single row of endodermal cells with the outer endodermis. This is shown diagrammatically in Fig. 28. The connexion is almost at once broken again; one or two endodermal cells remain in the central parenchyma, increase in number, and a parenchyma cell is formed in the middle of the endodermal group. Fig. 29 is a diagram of this stage, and Fig. 30 is a drawing of part of the section showing the ring of endodermis and the adjacent tissues. This endodermal ring or group, at a later leaf-gap, becomes connected with the outer endodermis by a double row of endodermal cells so that the horseshoe-shaped stele of Fig. 31 is formed. The incurved part of the endodermis (*e.*) surrounds a projection of parenchymatous tissue resembling

the ground tissue outside. When the next leaf-trace passes off the horseshoe-shaped stele becomes broken in its arched region so that two sausage-shaped or reniform 'steles' are formed, each surrounded by an endodermis. These may be repaired again to form a horseshoe-stele once more, but at the next leaf-trace the two separate steles are re-formed, and subsequent leaf-gaps cause further division of them, and they become more distant from one another so as to form a broken ring round a fairly large mass of central ground-tissue. The mature stem-structure is then attained. Differences occur in different seedlings as to the size of the xylem, the number of central phloem elements, and the stage reached at the level of a certain leaf-trace, but the above description may be taken as recording the successive changes in the arrangement of the tissues. The main facts as to the continuity of the tissues up to the horseshoe-stage of the stele agree with what is found in another dialystelic Fern, *Pteris aquilina*, as described by Leclerc du Sablon ('90, p. 3) and Jeffrey ('00, p. 9).

The transitional region of the seedling having been described, a few remarks may be made on other structural points in the seedling. It could not be clearly made out whether the first one or two leaves had a collateral or a concentric petiolar bundle, but the bundle in the petiole of an early leaf (Fig. 32) shows the phloem (*ph'*) surrounding the xylem. There is probably only one protoxylem group, the median one (*px'*), and the xylem forms a very slightly arched band. A few fibres (*f.*) are found in the phloem. Fig. 33 shows the petiolar bundle of a later leaf in an early stage of development. The median protoxylem-group (*px'*) and two protophloems (*pph'*) are differentiated. The incompletely differentiated phloem elsewhere is small-celled, and it can be seen that it is interrupted in the median region of the morphologically upper side, as in the leaves of the mature plant. Fig. 34 is a young stage of one of the steles in the dialystelic region of the stem in the seedling. The first formed tracheides are scattered. The first three or four leaves of the seedling are simple, with

a nearly orbicular, or ovate cordate lamina. The next leaf is tripartite.

MOHRIA, habit.

The stem of *Mohria caffrorum*, Desv., is an ascending or nearly horizontal rhizome, and bears polystichous leaves which appear to have a $2/5$ phyllotaxy, as in *Anemia Phyllitidis*. The leaves are bipinnate, that is, in the lower region of the pinnae. The genus includes about three species. Christ ('97, p. 352) describes it as 'vielleicht der auffallendste aller Farne, indem er die Fructification einer so weit entlegenen Gruppe mit der Organisation einer Pteridee vereinigt.' In anatomy, however, *Mohria* shows close relation to the type of structure of species of *Anemia*.

MOHRIA, stem.

Prantl ('81, p. 26) states that *Mohria* agrees completely in the structure of its strands with the majority of *Anemias*, only the fibres are absent. This is the case, as the points of structural differences between it and the dialystelic *Anemias* lie chiefly in unimportant details such as the distribution of sclerenchyma in the stem and petiole, and the outline of the bundles.

In the mature stem of *Mohria caffrorum* the epidermis is thin-walled and contains mucilage. The outer cortex or ground-tissue is fairly thin-walled, and is followed by a zone of brown sclerotic tissue which surrounds the vascular cylinder, but has an irregular form, as it curves outside the incoming leaf-traces. The central tissue within the vascular cylinder also consists of brown sclerotic elements. Fig. 35 shows the arrangement of the vascular tissue in a transverse section. This is drawn from a young stem in which the tissues were not mature, so the sclerotic ground tissue is not yet differentiated. In this figure, *sc.* is a group of sclerotic tissue filling the concavity of a leaf-trace. In the mature stem one such group, which is continuous with a similar one in the petiole, accompanies each leaf-trace through the cortex, and

finally abuts on the mass of sclerotic tissue occupying the centre of the stem. No axillary pockets are present. The leaf-trace on entering the stem has the form of a low curved arch, then becomes U-shaped as it passes inwards, and fuses at its ends with two adjacent steles in much the same way as in *Anemia Phyllitidis*. *a, a* are two steles, which will fuse with the leaf-trace opposite them; the larger one corresponds with the long-flat stele described in *Anemia*. After fusion the bundle has a conspicuous knob at each end (Fig. 35, *b.*), as in *Anemia*, and soon becomes less curved, and finally the whole has an oval outline. The changes with regard to the phloem and protoxylems are nearly the same as in *Anemia Phyllitidis*, but the leaf-trace in passing through the cortex often has five protoxylem-groups, one median one, which includes spiral elements, and is a little earlier than the others, two close to the ends of the xylem-arch, and one about halfway up each arm of the xylem. This, however, sometimes occurs in *Anemia*. The steles are smaller than in *Anemia Phyllitidis*, but have a similar structure. The tracheides are scalariform, and the sieve-tubes sometimes have very prominent thickenings between the sieve-plates. Fig. 37 is a longitudinal section of a stele in the young rhizome, at a level where hardly more than protoxylem was differentiated. It shows two sieve-tubes (*ph.*) separated from one of the early tracheides by conjunctive parenchyma.

MOHRIA, petiole.

The petiolar bundle of *Mohria caffrorum* with the adjacent group of sclerotic tissue (*sc.*) is shown diagrammatically in Fig. 36. The distribution of the phloem is shown by the shading. The xylem forms an arch with hooked ends, and there are three protoxylem-groups: one median, and one just above each hook. They are on the inner surface of the arch, and each is accompanied by cavity-parenchyma. Excluding the sclerotic tissue, which does not belong to the bundle, the structure is almost indistinguishable from that of

Anemia Dregeana, except for the fact that in the latter species the lateral protoxylem-groups are spread out, while in *Mohria* they are small. Fibres are absent in both.

MOHRIA, root.

The root of *Mohria caffrorum* agrees with that of *Anemia Phyllitidis* in the structure of its cortex, endodermis and pericycle, the chief point of difference being in the stele, which in the roots examined did not have two specially large tracheides in the middle of the metaxylem, but the xylem-band showed more gradation from the small elements at its ends to the larger tracheides in the middle, which were fairly numerous and irregularly placed. This distinction is however not very important, as the *Mohria* type of structure is sometimes found in species of certain Polypodiaceae, which usually have two large tracheides in the metaxylem, as in *Anemia*. The root of *Mohria* resembles somewhat the basal region of the root in *Anemia*.

CAVITY-PARENCHYMA.

This tissue, which is well developed in *Anemia Phyllitidis*, has been described in that plant by Prantl ('81, p. 24). A similar tissue was found by Gwynne-Vaughan ('01, p. 87) in *Loxsoma*, and his term (cavity-parenchyma), which is an equivalent for Russow's Lückenparenchym, has been adopted here. Reference to other authors who have described a similar tissue are given by Prantl and Gwynne-Vaughan. It is found in a large number of Ferns belonging to different Natural Orders, e. g. besides the two genera just mentioned, in *Helminthostachys*, *Matonia*, *Osmunda*, *Angiopteris*, *Cyathea*, *Pteris*. The character of this tissue, as described by different authors, lies in the fact that the cells composing it become enlarged and produce thylosis-like swellings or branches. As mentioned by Gwynne-Vaughan, they grow into the space caused by the disintegration of the protoxylem-elements. They may perhaps have a mechanical function. In *Tricho-*

manes Pricurii the cavity-parenchyma becomes lignified, and one element of this tissue was noticed, which was much elongated, fibrous, and pitted like other fibres in the bundle, but with one or two protrusions on the side on which it was in contact with an annular tracheide.

SIEVE-TUBES.

In examining the sieve-tubes of the Schizaeaceae aniline blue and corallin-soda were at first used for the purpose of determining whether callus was present. These stains were however discarded¹ in favour of azo-blue, which was found to be preferable for several reasons. It may be stated at once that no callus was found in any of the Schizaeaceae examined, but, as it was found by experimenting with other plants, that azo-blue is an excellent stain for differentiating callus, it will be as well to describe the method of using it. Poirault ('93, p. 139) recommends the use of azo-violet as a specially good stain for callus. Its action appears to be similar to that of azo-blue, for Mangin ('90, p. 120) classes the two together with other dyes, and states that they are generally precipitated by acids, but stain cellulose and callus in a neutral or slightly alkaline solution.

To prepare the stain, a little of the solid (Grübler's azo-blue) is stirred up in water. It is practically insoluble, but in suspension has somewhat the appearance of a violet solution. A little caustic-soda or potash-solution is added until the colour becomes reddish, the solution is then shaken up and filtered, and a fairly dark red solution is obtained, which is the reagent for staining callus. This solution when exposed to the air gradually loses its alkalinity owing to carbonation of the potash, and finally turns violet, the stain being then precipitated. One can judge of the relative alkalinity of the red solution by the length of time a little of it in a watch-glass requires before assuming a violet tinge at the periphery. The dye gives the best results in a fairly strong but only

¹ Staining deep enough to colour very small masses of callus was found to incur a danger of staining proteid granules as well.

slightly alkaline solution. When testing for callus it is advisable always to work with a section of *Cucurbita* used as a control, to be stained in the same watch-glass with the other sections. This shows at once whether the dye is working properly. If the staining solution is strongly alkaline, it will stain all parts of the section, but if rightly used it produces remarkable differentiation, when any callus is present. Sections may be left for ten minutes or more in the stain, according to its strength. They are then transferred to a slide, the stain is drained off, and a few drops of water are added until the sections change from red to lilac or bluish or nearly colourless, as the case may be. They are then examined at once, and the callus if present is found to be crimson, while cellulose walls are generally lilac or blue, but proteid and also lignified walls are entirely uncoloured. In time the callus turns violet and its colour finally fades, but when first mounted as above, the callus is the only red-stained substance in the section, and is deeply stained. The staining should be done in a watch-glass, which is covered up, so that the solution may not turn violet throughout during the operation.

The following were the examples tested with azo-blue in the Schizaeaceae:—

Lygodium japonicum, petiole; *L. dichotomum*, petiole; *Schizaea digitata*, rhizome; *Anemia Phyllitidis*, petiole; *Mohria caffrorum*, petiole. No callus was found in any of the specimens examined. A similar negative result was obtained in the Hymenophyllaceae. In this family the sieve-tubes were tested with azo-blue in:—*Trichomanes radicans*, rhizome and petiole; *Trichomanes Prieurii*, petiole; *Hymenophyllum demissum*, var. *nitens*, rhizome.

The results obtained with azo-blue in other Ferns may as well be mentioned. Well-marked callus occurs on the sieve-plates of the end-walls and vertical walls of the sieve-tubes in both rhizome and petiole of *Pteris aquilina*. Equally distinct callus was also found in the petiole of *Thyrsopteris elegans*, and in the rachis of *Onoclea germanica*. A small amount was

seen on some sieve-plates in the root of *Dicksonia antarctica*, and in the rhizome of *Davallia elegans* and *Nephrodium Thelypteris*. In *Angiopteris evecta* however the root and petiole showed no callus in the sieve-tubes; but in an old petiole lumps of a substance staining rather like callus occurred in many parenchymatous cells of the ground-tissue. In the petiole of *Todea barbara* no normal callus appeared to be present, but irregular masses of a substance like callus were present in some sieve-tubes and other elements. In appearance it suggested a degeneration product of the cell-wall.

It must be pointed out that where a negative result was obtained with azo-blue, the sieve-tubes of the plant may perhaps exceptionally or at some seasons produce callus. But from the nature of the results, it seems probable that callus is absent or only rarely formed in the Schizaeaceae and Hymenophyllaceae, but that its formation is general in the Polypodiaceae. No general deduction will be drawn as to the Cyatheaceae, Marattiaceae, and Osmundaceae, as only one example of each was examined.

As the sieve-tubes of the Hymenophyllaceae were only shortly described in the previous part of this paper (Boodle, '00, p. 457), a few details may be added here. In Schulze's solution the walls of the sieve-tubes of *Trichomanes radicans* stain slightly blue (distinctly bluer than the walls of the pericyclic cells), while the sieve-plates on the vertical walls are seen in surface-view as nearly colourless areas which often have several yellow-stained granules (probably of proteid) on them. The granules appear to be sometimes scattered indiscriminately in a sieve-tube, but are often distinctly grouped on the sieve-plates, and much less numerous on the parts of the wall destitute of sieve-plates. Nuclei are perhaps occasionally retained in some sieve-tubes, but are usually evidently absent, while they are constantly present in the adjacent parenchymatous cells. Fig. 47 represents two sieve-tubes and one adjacent pericyclic cell from the rhizome of *Trichomanes radicans*. Sieve-plates with granules are seen in the sieve-tubes, and there is a much elongated nucleus (*n.*) in

the pericyclic cell. Sieve-plates in section in the longitudinal walls of the sieve-tubes may be best seen when the walls are slightly swelled with Schulze's solution, as in the case of Fig. 47. After long-continued immersion in this reagent the walls become too much swelled and indistinct. Sieve-plates in section are not well seen in preparations stained with haematoxyline and mounted in canada-balsam, because the walls then become comparatively thin through dehydration, as is seen in Fig. 48. The sieve-tubes are elongated elements with very long inclined end-walls (Fig. 48, *e.*).

The conclusion to be derived from additional observations made since the publication of the first part of this paper is that the sieve-tubes of the Hymenophyllaceae agree in structure with those of other Ferns.

In examining the sieve-tubes the question of the perforation of the sieve-plates¹ was not attacked, but the observations on callus may be compared with some of the previous investigations on the sieve-tubes of Ferns.

De Bary ('77, p. 181) stated that the sieve-plates were not callous, and that he had seen the granules of contiguous sieve-tubes connected by thin filamentous processes which traverse the transverse pores in longitudinal sections of *Pteris aquilina*. Janczewski ('82, p. 89) describes callus blocking the pores of the sieve-plate in *Pteris aquilina*, but regards it as quite exceptional for the Vascular Cryptogams. Russow ('82, p. 208) states that he has met with callus generally in the Vascular Cryptogams, but only traces of it in the Marattiaceae and Ophioglosseae. He mentions that the callus often takes the form of little rods traversing the membrane of the sieve-plate, and that there are usually small brilliant granules at the extremities of the callus-rods. In *Pteris aquilina* Terletzki ('84, p. 487) describes refractive granules as aggregated on the pores of the sieve-plates, and quoting De Bary's statement with regard to the filamentous connexions between the refractive granules, remarks that the granules are not connected,

¹ Poirault ('93, p. 139) finds the sieve-plates perforated in Ophioglosseae and Marattiaceae.

but that the whole protoplasm of the sieve-tubes is connected, and represents it so, e. g. in his Fig. 26. Poirault ('93, p. 138) found callus blocking the pores of the sieve-plates generally in the Ferns, though absent in Ophioglosseae and Marattiaceae. He points out (p. 139) that Terletzki had confused under the same name ('very refractive bodies adhering strongly to the wall') the proteid granules and the callus stoppers. Poirault found that azo-violet left the former uncoloured, but stained the latter bright pink.

The results obtained with azo-blue correspond on the whole with those of Poirault, in that callus was found in *Thyrsopteris*, in *Dicksonia* and in several of the Polypodiaceae, but not in *Ophioglossum* nor in Marattiaceae. However, callus was not found in Schizaeaceae nor in Hymenophyllaceae, though these Orders are not cited by Poirault as exceptions to his generalization.

In *Pteris* and in *Thyrsopteris*, where the callus was specially well developed, it took the form of a small rod running through the pore, and often e. g. on the vertical walls expanded into a round knob at each end. The knob was frequently surrounded by a perfectly neat ring of refractive granules. This structure corresponds with Russow's description, but De Bary ('77, p. 181 and accompanying figure) did not distinguish between the refractive granules and the callus-knobs, and evidently saw the callus-rods but apparently took them for protoplasmic connexions, as Terletzki also seems to have done. Callus-rods are also found in the pits connecting sieve-tubes with phloem-parenchyma-cells.

Poirault ('93, p. 138) states that callus is formed very early on the pores of the sieve-plates, and the callus, when formed, appears to completely fill the pores; so it seems that in *Pteris aquilina* and many other Ferns the sieve-tubes have no protoplasmic connexions through the sieve-plates, except perhaps at an early stage. But there is the possibility that there may be a delicate protoplasmic thread running through the callus-rod and only recognizable by more refined methods.

FIBRES.

Fibrous elements, as described above, occur in the petiolar bundle of certain species of *Lygodium*, *Anemia*, and *Schizaea*, but are absent in *Mohria*. In all three genera they appear to represent thickened and lignified sieve-tubes. In Gwynne-Vaughan's interesting paper on *Loxsoma* ('01, p. 83, &c.) similar fibres are carefully described in that genus, and their nature in that and other cases discussed. The conclusion he arrives at is that in *Loxsoma* the fibres represent elements of the phloem originally designed for sieve-tubes, and he extends the same explanation to the fibres of *Lygodium*, *Schizaea*, and *Anemia*. The position and structure of the fibres in these three Schizaeaceous genera entirely support this view, and further in *Lygodium lanceolatum* and in *Anemia Phyllitidis* some of the fibrous elements may have even functioned as sieve-tubes prior to their sclerosis. This is suggested by the presence of granules on the end-wall of Fig. 19, and by the late sclerosis of some of the large sieve-tubes in the species of *Lygodium* just mentioned. In the case of *Trichomanes Prieurii*, as pointed out by Gwynne-Vaughan ('01, p. 86), all the sclerotic elements cannot be regarded as derived from sieve-tubes, as the end-walls of some of them do not at all resemble sieve-plates. Others however, judged by their structure, might represent sieve-tubes, as in the element shown in Fig. 46. No granules were observed on such end-walls, and it must be remarked that structures almost identical with the example figured may be met with in other sclerotic tissues, for instance in the epidermis of a rather old petiole of *Mohria caffrorum*. Hence it is necessary to depend more on the position of these elements in *T. Prieurii* for an explanation of their nature. This was chiefly relied on in the paper on the Hymenophyllaceae (Boodle, '00, p. 475), where the fibres were regarded as being derived from parenchyma. This still appears extremely probable for the bulk of the fibres, but it must be left doubtful whether some of them may have been derived from sieve-tubes. Some of the fibres lie

embedded in the xylem, and these no doubt are derived from xylem-parenchyma; some are found just outside the xylem, and a few of these are in contact with the phloem, and may perhaps represent sieve-tubes; and again among the large central mass of sclerotic elements, a few of the fibres adjacent to the incurved ends of the phloem-zone may be lignified sieve-tubes, but the majority of the internal fibres are larger elements than the sieve-tubes, and in the median upper region they correspond closely in size with the adjacent parenchyma, which lies between them and the endodermis. Gwynne-Vaughan ('01, p. 86) suggests that perhaps both sieve-tubes and parenchyma are implicated in the sclerosis. As stated above this may be the case, but, as far as present data go, the fibres may on the other hand all be parenchymatous. In that case they would be of a different nature from those of the Schizaeaceae. Outside the Schizaeaceae, Hymenophyllaceae, and Gleicheniaceae, fibres in the bundle-tissue appear to be rare among Ferns. The example given by Thomae ('86, p. 129) is that of *Adiantum trapeziforme*. Fig. 45 is a drawing of a small piece of one of the petiolar bundles. The fibres (*f.*) occur both in the xylem among the tracheides, and on the inner and outer side of the xylem band; those at the top right-hand corner of the figure being on the inner side. It is no doubt, as Gwynne-Vaughan suggests, a case of sclerosis of xylem-parenchyma. Probably few if any of the outer fibres represent sieve-tubes, so most at any rate of these sclerotic elements belong to a different category from the fibres of the Schizaeaceae. Fig. 44, which represents half the petiolar bundle of *Nephrodium Thelypteris*, is included here to illustrate the occurrence of thick-walled, unligified elements, apparently sieve-tubes, in a member of the Polypodiaceae. They occur within the hook of the xylem. Similar elements are mentioned by Gwynne-Vaughan ('01, p. 85) in *Davallia*, &c.

SILICEOUS DEPOSITS.

The silica-nodules in *Lygodium dichotomum* described above are the most conspicuous deposits of silica to be found in the Schizaeaceae. They appear to be very similar bodies to those described by Poirault ('93) in epidermal cells of the Marattiaceae. Besides these, the only other cases of free silica-concretions within the cell hitherto recorded among the Ferns are those found in the 'Deckzellen' of Hymenophyllaceae, and according to a statement of Mettenius ('64, p. 426), in epidermal 'Deckzellen' of the leaf of *Aspidium deltoideum*. The siliceous bodies in *Lygodium* agree with those of the Marattiaceae, but differ from those of the Hymenophyllaceae in having an indefinite form, and they differ from those of both these Orders in occurring in deep-seated tissues, e. g. in the stele.

Among the Angiosperms intracellular silica-concretions are found in the xylem-parenchyma and other tissues of *Moquilea* (Kohl, '89, p. 248), but a closer agreement with *Lygodium* as to the form of the silica-nodules is found in the Podostemaceae.

According to Kohl, Ferns are mostly poor in silica (e. g. about 5 per cent. of the ash), but *Blechnum Spicant* and *Pteris aquilina* are cited as having a large amount (about 53 and 45 per cent. respectively). The silica in these cases is possibly an infiltration of the cell-walls of certain specialized epidermal cells, as described by Kohl in *Antrophyum*, &c.

A few silica-nodules similar to those of *Lygodium* were found in the ground-tissue of *Anemia*, but none in *Schizaea* or *Mohria*.

In *Schizaea digitata* and in *Anemia Phyllitidis* the outer wall of the epidermis of the petiole has small warts arranged in longitudinal rows. Each is due to a refractive, probably siliceous body embedded in the wall. They have been described by Prantl, and figured by him ('81, p. 33, and Taf. 4, Fig. 50), in *S. pennula*, Sw., and by Britton and Taylor ('01, Pl. 6, Fig. 93) in *S. pusilla*, Pursh.

HAIRS.

The hair-structures of the Schizaeaceae need not be fully described here, as details are given by Prantl ('81, p. 35). Two kinds of hairs are found, namely stout or long hairs, each consisting of a single row of cells, which may or may not bear a glandular cell at the top, and short glandular hairs, consisting of either one or two cells, and usually adpressed. The glandular cell of these short hairs is therefore either seated on the epidermis or on a single stalk-cell. It is oval, and has a distinct nucleus. The larger kind of hairs, in this case blackish and not glandular, are found for instance densely covering the stem apex and leaf-rudiments of *Lygodium dichotomum*. On the young petiole of *Anemia Phyllitidis* there are both long filiform brown hairs (e.g. 3 mm. in length), and small unicellular glandular hairs. Both kinds of hairs of similar proportions were found by Britton and Taylor ('01, p. 13) in *Schizaea pusilla*.

Mohria caffrorum is exceptional in possessing paleae, resembling those of the Polypodiaceae, but it is interesting to find that in *Lygodium dichotomum* longitudinal divisions occasionally take place in the long hairs, so that the basal part is converted into a flat plate of cells, i.e. a small palea. Prantl does not appear to have seen any such cases, but he regarded the long uniseriate hairs as homologous with the paleae of other Ferns ('81, p. 37). The rhizome of *Mohria* bears paleae, long rhizoid-like hairs, and also very numerous unicellular glandular hairs, identical with those of *Anemia*.

THE STELE.

An important paper dealing with the stele has recently been published by Jeffrey ('00). In this paper the structure of the stem in seedling plants belonging to several groups has been carefully described, and the manner in which the mature structure is attained has been followed, the changes in the disposition of the vascular elements and the behaviour of the endodermis being worked out in relation to the leaf-gaps. Further, wide generalizations as to the morphology

of stelar structures are arrived at. One of these is that Van Tieghem's three types of central cylinder are modifications of the siphonostelic type, i.e. a vascular tube with leaf-gaps. Basing one's terminology on the position of the endodermis, this is evidently the case for the examples investigated, and is probably generally true for the polystelic type. But it must be recognized that the homology of different types of stelar structure is a difficult question, and is not at once disposed of by merely tracing the continuity of the various tissues. Perhaps in the present state of our knowledge it does not admit of any certain solution.

One would be inclined to describe Fig. 31 as a horseshoe-shaped stele with a projection of ground-tissue in its concavity, and to regard the endodermis as limiting the ground-tissue towards the stele. This is no doubt a convenient description, but there is no proof that it is anything more than a physiological use of terms, which does not necessarily agree with the morphology of the parts. The central 'ground-tissue' is certainly continuous with, and similar to, the external ground-tissue, but one must regard it as possible that in this case the stele may really have a roundish outline, and that part of its tissue has been differentiated as parenchyma with the characters of ground-tissue, and limited by a piece of endodermis formed from stelar tissue so as to join the external endodermis, which is interrupted opposite the stelar parenchyma. The endodermis is usually formed from the innermost layer of the cortex¹, but that the endodermis is not dependable as a morphological limit in certain other cases is sufficiently shown by the species of *Equisetum*² as pointed

¹ In several Ferns at any rate the pericycle is formed by subdivision of the same layer, as described by Van Tieghem ('88, p. 404) for the stem of *Hymenophyllum* and the stolon of *Nephrolepis*, and the same is probably the case in *Lygodium*. Other cases are quoted by Strasburger ('91, p. 446), but these being polystelic involve other questions.

² The parenchyma-rays between the bundles would have a different morphological value in nearly allied species (gamodesmic and dialydesmic), if the endodermis were regarded as always limiting stelar tissue. Jeffrey ('99, p. 157) regards Strasburger's conclusions as invalidated by the structural facts cited by Van Tieghem ('90), but the case just mentioned appears to weigh heavily against the morphological value of the endodermis.

out by Strasburger ('91, p. 441). On account of his view of the different morphological nature of the endodermis in different cases, Strasburger used the term 'endodermis' in the physiological sense, for the layer bearing cuticularized bands, and introduced the term 'phloeoterma' to designate the innermost layer of the cortex ('91, p. 435); but he used the term phloeoterma in a way that may be called in question in the case of polystelic Ferns. As the morphological value of the endodermis cannot be said to have been definitely established in the case of 'polystelic' plants, it would be preferable to call the cutinized layer in them an endodermis, and not to apply the term phloeoterma to it, as Jeffrey and Gwynne-Vaughan have done, until it has been if possible proved that this layer *is* the innermost layer of the cortex. In Jeffrey's work the endodermis is regarded as revealing the position of the limit of the cortex, and is called phloeoterma; and the continuity of tissues in the seedling is relied on for determining their morphological nature.

The latter point is shown by the following statement regarding *Ranunculus*:—'In the young axis the stelar system possesses an internal phloeoterma, which is continuous with the external phloeoterma through the foliar gaps, and is therefore of the same morphological value.' This conclusion cannot be said to carry conviction. It is not wished in any way to imply the impossibility of such interpretations being correct, but simply to point out that proof is required as to the morphological nature of the endodermis, and as to the value of the continuity of tissues.

In relation to the questions involved it will be as well to attempt to regard some of the structures from a physiological standpoint. The function of the endodermis appears to be to form a closed layer of cells shutting off vascular tissue from tissues which contain intercellular spaces (Strasburger, '91, p. 611), and thus to prevent air from penetrating to the tracheae. The mechanical firmness which enables the endodermis to escape rupture of its cells is attained by the network formed by the tangential suberized bands (Haberlandt, '84,

p. 245). In the stems of many Monocotyledons a function similar to that of the endodermis is probably performed by the sclerotic sheaths of the bundles, which would prevent accidental ruptures in the ground-tissue from continuing the intercellular spaces right up to the tracheae. In Dicotyledons, where intercellular spaces occur in the pith, the perimedullary zone may perhaps have a similar function. But the spoiling of a few tracheides would be comparatively unimportant in plants which form new ones by secondary thickening. In the Ferns, on the other hand, the endodermis seems to be an important layer, though often assisted in its function in the mature plant by adjacent sclerotic tissue. The vascular tissue is therefore normally completely enclosed by an endodermis, especially towards any loose parenchyma. In solenostelic forms the connexion of inner and outer endodermis at the leaf-gap is of course necessary from this point of view, if a leaf-gap is to be formed. We will now assume the hypothesis mentioned previously, that the horseshoe-shaped 'stele' is morphologically only part of a circular or oval stele, and further that in the polystelic (or dialystelic) type the limit of the stele is also circular and includes the separate 'steles' and the central ground-tissue. The following might then be a physiological description of what has taken place. The primitive solid stele has become much enlarged by increased cell-division in the cylinder of cells which were set apart to produce it. This increase in diameter may be connected with the attachment of the tangentially broad leaf-traces of large leaves¹, especially if they are polystichous. A *solid* mass of tracheides of the increased diameter is not necessary for the water-supply, and consequently the central cells do not attain to tracheide-formation, but remain parenchymatous or become sclerotic as the case may be. At this stage one would have a ring of xylem surrounded by phloem, and enclosing a central pith. This is found in *Schizaea*. In *S. digitata* the pith is

¹ Jeffrey ('00, p. 38) connects the siphonostelic type of structure with mechanical strengthening of the axis to enable it to bear large leaves; this may be one factor, but sclerotic tissue is the *chief* supporting tissue in Ferns.

sclerotic, in *S. fistulosa* it is parenchymatous (or collenchymatous). There is no internal endodermis in these species; which is perhaps connected with the fact that there are no intercellular spaces in the pith. In the next stage in complication, internal phloem is present, differentiated from tissue near the inner limit of the xylem. This would be formed for the attachment of the inner phloem of a concentric or bicollateral petiolar bundle. *Schizaea* having collateral petiolar bundles has no internal phloem in the stem. The type with internal phloem is not necessarily derived from the medullated type with none. If the petiole was already concentric at the time when the solid type of stele was departed from, internal phloem might be formed as soon as there was any centrally placed soft tissue. The one or the other structure might appear first in different phyla. No mature Fern appears to be known with internal phloem, and at the same time no inner endodermis, but this condition is met with in the seedling stem of *Anemia*. This is where there is not much tissue within the phloem; but, when a large mass of parenchyma with intercellular spaces is present, an inner endodermis becomes necessary. This is the solenostelic stage. This central tissue is not required by the stele, and for it to be of use, e.g. in storing up starch, it must be in free connexion with the outer ground-tissue; hence (as all the walls of endodermal cells frequently become suberized) the necessity for leaf-gaps as found in the solenostele. Continuity being established between the central and outer ground-tissue, they may have the same functions and resemble one another structurally. Nothing further need be said as to the dialystelic type, which only differs from the solenostelic in its more crowded leaf-gaps.

The preceding is a purely theoretical discussion, and of course proves nothing as to the correctness of the hypothesis with which we started. One may now see whether anything can be done towards solving the morphological problem. The structure of the seedling is accepted as giving some clue to the course of phylogenetic changes. In describing the seedling of *Pteris aquilina*, Jeffrey ('00, p. 9) points out

that there is no evidence for the repeated bifurcation of the young central cylinder, described by Van Tieghem as characteristic of his polystelic type. The structure of the seedling of *Anemia* bears this out; the stele as a whole does not appear to branch. In *Anemia*, internal phloem appears, when there are only a few soft elements inside the xylem. This may mean that a medullated stage was not passed through in this particular phylum, or it may be a case of the early appearance of an acquired structural character. Again, in the seedling solenostelic structure precedes dialystelic, which may have phylogenetic significance. But these facts do not elucidate the morphological difficulties. Neither does investigation of the apex greatly help the matter. Gwynne-Vaughan ('97, p. 323) found in species of *Primula*, with several steles arranged in a slightly interrupted ring, that these were represented in the apex by a similar ring of desmogen-strands, which could be followed up as far as any differentiation could be distinguished in the meristem. This practically describes what was found in the apical region of an oldish seedling of *Anemia Phyllitidis*. This was to be expected. When differentiation begins in a meristem, the form and mode of division of its elements is intimately connected with the form and arrangement of the tissue-elements to be produced, so one is not likely to learn much from these characters in the meristem, that cannot be seen in the mature structure. The relation of the meristematic tissues to the divisions of the segments of the apical cell could not be made out. If this could be determined, it would carry some morphological weight, especially in nearly allied forms. If, for instance, it could be shown that the steles of *Anemia Phyllitidis* together with the central ground-tissue were formed from similar divisions of the apical cell-segments to those from which the solid stele of *Lygodium* is formed, a presumption of morphological identity would be established. The arrangement of cell-walls in the apical region of *Anemia* did not suggest what might be called an *intrusion* of cortex into the stelar ring.

An important method of investigation is a comparison of the structure in nearly allied species. A thorough examination of several species of *Anemia* would be most interesting from this point of view, but sufficient material has so far not been obtainable. One or two points that have some bearing on the endodermis and stele, however, must be mentioned. *A. mexicana* is solenostelic with a central mass of sclerotic tissue inside the inner endodermis. This is homologous with the central ground-tissue of *Anemia Phyllitidis*. Such tissue may become sclerotic in polystelic forms, as seen in *Mohria*. The formation of abundant sclerotic tissue is rather a character of xerophytic forms, and its function, besides being mechanical, is possibly connected with the storage of water in its walls and cavities. *A. mexicana* is distinctly xerophytic in appearance, which would be expected, as it is described as growing on rocks. In this species at the node a group of sclerotic tissue appears to become detached from the central sclerotic ground-tissue and to pass out behind the leaf-trace so as to join the external sclerotic ground-tissue, as in *Mohria*; there is thus a leaf-gap in the endodermis. In the node of *A. coriacea*, which is probably nearly related to *A. mexicana*, no sclerotic tissue passes out, and the endodermis is not interrupted, hence, judged by the node examined, this species is not properly solenostelic. If this character were constant for all the nodes of *A. coriacea*, its central ground-tissue, judged by continuity, would have a totally different morphological nature from that in *A. mexicana*; which is extremely improbable. This matter must be left for future investigation, but it may be pointed out, that from the physiological point of view the connexion at the nodes between the inner and outer ground-tissue, when they become sclerotic, is comparatively unimportant, except perhaps that an occasional connexion might be necessary, either as a tie between two mechanical systems, or for the slow transference of water from one to the other.

Another point suggested by these species is that, assuming them to have been derived from polystichous forms by

suppression of the leaves on the lower side of the creeping rhizome, which at any rate appears probable, the parenchymatous tissue representing the original leaf-gaps on the lower side appears to have been converted into vascular tissue, and the leaf-gaps thus repaired. This would agree with the view that the leaf-gap-parenchyma is really stelar tissue in the phylogenetic sense. Again, *A. aurita*, if its structure were better known, would form an interesting type for comparison with *A. mexicana*.

What has been said above may at any rate show that a fuller investigation of species of *Anemia* would probably throw a great deal of light on questions connected with the morphology of the stele.

A few more remarks must be made with regard to the seedling. There is probably a tendency for plants to show acquired structural characters at earlier and earlier stages in their ontogeny. The strip of endodermis (*e.*) seen in Fig. 28 is apparently useless, and may represent an attempt to form a loop of endodermis such as is found at a later leaf-gap (Fig. 31), and for which in the small stele there is not sufficient room. The early connexion between inner and outer phloem and between other tissues in the seedling suggests a possibility, though this is very hypothetical, that when a new kind of tissue is to be formed, e. g. internal phloem from stelar parenchyma, contact with similar tissue, in this case phloem, may be necessary. That is to say, protoplasmic continuity between different elements when young may in some way help in leading to the formation of corresponding mature elements; or one might say a 'contagion' for forming a special kind of element is handed on.

To conclude the subject, the homologies of different types of stelar structure at present appear doubtful, but the writer inclines to the view that the medullated, solenostelic, and dialystelic types have been derived from the solid stele by the transformation of its central tissues into parenchyma in the first case, and into parenchyma together with a certain amount of phloem and endodermis in the second and third cases.

The time for the application of rigorous terminology does

not seem to have arrived, but 'dialystelic' and 'solenostelic' are convenient words for describing structures like those of *Anemia Phyllitidis* and *A. mexicana*, whether they are really based on the disposition of the whole stelar tissue, or of the part of the stele which shows typical stelar characters. The separate parts of the dialystelic type have here been usually spoken of as 'steles'; but 'meristeles' or 'dialysteles' would be perhaps a preferable term, if one regards them as being only circumscribed parts of a stele.

COMPARISON OF STRUCTURE.

Some points of agreement and difference between the structure of the genera of Schizaeaceae should now be referred to.

A *single* leaf-trace passes off to supply each leaf, and is continued as the petiolar bundle which remains undivided. In the bundle of the petiole (of three of the genera) a median protoxylem-group is present on the upper side of the xylem. Two other protoxylem-groups, which are also on the upper side of the xylem, may also be present (e.g. *Anemia*). In *Lygodium*, on the other hand, two approximated groups of protoxylem separated by the median plane are present on the *lower* side of the xylem. These, however, tend to fuse into one median group towards the base of the petiole, and in *L. palmatum* one median group is found in the petiole. In all the species of *Lygodium*, besides the protoxylems mentioned, two lateral external groups are also present. The two nearly median protoxylem-groups have probably been produced by the splitting of a median single group, as found near the base of the petiole, for that is probably a less modified region. Therefore *L. palmatum*, with its undivided median protoxylem, shows a less modified structure than the other species, and it is noteworthy that in this species the median group is not peripheral but embedded in the xylem. A possible explanation of the great difference in type between the bundle of *Lygodium* (Fig. 4) and that of *Anemia* (Fig. 17), is that in *Lygodium* there has been a large addition of xylem

elements in the region corresponding with the concavity of the xylem-arch in *Anemia*, and a suppression of the xylem external to the three protoxylem-groups, except in the case of the median group in *L. palmatum*, together with a splitting of the median group except in *L. palmatum*. In both *Anemia* and *Lygodium* the median group (or pair of groups) differentiates before the others. In *Schizaea* only the median endarch group appears to be present. Possibly one median endarch protoxylem-group is primitive for the Order, and the lateral groups have been added in connexion with increase in size of the bundle. The protoxylem-groups in the petioles of all the genera contain spiral or annular elements, but in *Lygodium* and *Schizaea* spiral elements are absent in the basal region of the petiole; but in *Lygodium* at any rate small early-formed scalariform tracheides occur in a nearly identical position to that occupied by the spiral elements higher up. The term 'protoxylem' appears applicable to these. In the Schizaeaceae the stem-protoxylem does not occur in definite groups, but is represented by scattered tracheides which are scalariform. No spiral tracheides are present in the stem except in *Anemia* and *Mohria*, where a spiral protoxylem of the leaf-trace is continued a short distance down in the stem. Gwynne-Vaughan ('01, p. 87) has laid stress on the distinction between stem- and leaf-protoxylem in *Loxsonia*; and it certainly appears probable that the differentiation of stem-protoxylems in close relation to leaf-trace-protoxylems may be a comparatively late character. Where the xylem is of considerable thickness the protoxylem-elements of the stem are at or near the periphery.

Sclerosed sieve-tubes, forming fibres in the petiolar bundle, occur in certain species of *Lygodium*, *Schizaea*, and *Anemia*, but not in *Mohria*.

Fibres of this kind are uncommon among Ferns. Their presence here, and the occurrence of 1-2-celled glandular hairs on the stem and petiole, and of silica-deposits, within the cell-cavity (in *Lygodium*), or in the form of knobs in the outer walls of epidermal cells (in *Schizaea* and *Anemia*) may

be pointed out as rather characteristic features in the Schizaeaceae.

Four types of stele are represented among the Schizaeaceae:—the solid stele in *Lygodium*, the medullated stele in *Schizaea*, solenostely in some species of *Anemia*, and dialystely in other species of *Anemia* and in *Mohria*. With regard to *Schizaea*, as the transitional region of seedlings has not yet been specially examined, it cannot be said whether any different type of structure occurs at an early stage in the ontogeny, as seen by Jeffrey in some Angiosperms. De Bary ('77, p. 344) agrees with Russow's view that the central tissue within the xylem of *Schizaea* is not to be regarded as a pith, but as parenchyma belonging to the stele. But as pith is not a sharply characterized term there is no harm in applying it to this tissue, especially if one inclines to the view that phylogenetically pith is stelar tissue. A structure is found in *Anemia coriacea*, which though resembling solenostely may differ in the behaviour of the endodermis at the node.

The petiole-bundle is concentric in *Lygodium*, collateral in *Schizaea*, and roughly speaking bicollateral in *Anemia* and *Mohria*.

The structure of *Anemia* and *Mohria* must be compared, as Christ ('97, p. 352) regards the external characters of the latter as so anomalous for the Order. *Mohria* resembles *Anemia Phyllitidis* completely in the type of its stelar system, and agrees roughly with other species of *Anemia*, as to the dimensions of the parts. The petiolar bundle in *Mohria* is of the type found in *Anemia*. There are no fibres in the bundle of *Mohria*, but that is also true for certain species of *Anemia*, e.g. *A. Dregeana*. *Mohria* possesses glandular hairs exactly similar to those of *Anemia*, but differs in possessing paleae. An approach to palea-formation occurs however in *Lygodium*, therefore this character is not of great importance. Again, the sclerotic group accompanying the petiole-bundle of *Mohria* is suggested by the thick-walled elements which occur in a corresponding position with regard to the bundle at the base of the petiole of *Anemia Phyllitidis*.

Finally the sclerotic central ground-tissue in the stem of *Mohria* finds its counterpart in the solenostelic *A. mexicana*. The structure of *Mohria* thus suggests that the genus is probably quite nearly allied to *Anemia*, but it shows some characters which suggest greater tendency to xerophytism, than is found in *A. Phyllitidis*.

Judged structurally, *Anemia* and *Mohria* are less primitive than *Lygodium* and *Schizaea*; and of these *Lygodium*, having a solid stele, should be the more primitive. The petiolar bundle of *Lygodium*, however, is concentric, which is probably not a primitive character. It must be remembered that the well-developed leaves of this genus are specialized for twining, and it is probably because of this, that the bundle forms a rounded cylinder instead of conforming more to the type found in the other genera. The form of the petiole-bundle may in its turn have determined the retention of the primitive type of stele, because a solid cylindrical stele would be suitable for the attachment of a similarly shaped leaf-trace. Hence the structure of the stem alone should perhaps not be taken as pointing to the genus being necessarily more primitive than *Schizaea*. It is interesting, however, to observe that Bower ('99, p. 44) found that among the Schizaeaceae *Lygodium* showed the largest sporangia and the largest output of spores, and that these characters generally indicate primitive nature.

A comparison of the structure of the Schizaeaceae with that of the Hymenophyllaceae and of other Ferns will be reserved for the concluding part of this paper, on the Gleicheniaceae, but one comparison may be made here.

The structure of some species of *Anemia* shows considerable resemblance to *Loxsonia*. Gwynne-Vaughan ('01, p. 94) regards these resemblances as insufficient to constitute a close relationship, and this appears to be the case; but perhaps a closer relationship to the Schizaeaceae than to the Hymenophyllaceae is suggested. The facts may be stated thus:—the solenostele of *Loxsonia* resembles that of *A. mexicana* in the elements of the stem-protostele being scalariform and scattered, and also approximately in their position. The

possession of sclerosed sieve-tubes is common to both genera, and there is a single petiolar bundle in both, of a somewhat similar form, and it is endarch. On the other hand, *Loxsoma* has more numerous protoxylem-groups, and there is no median group. At the top of the petiole, however, there are only four groups, two in the hooks of the xylem, about as in *Anemia*, and two at the ends of the top of the arch. These two may have originally been produced by splitting of a median group, as has been supposed in the case of *Lygodium*. The distribution of the fibres in *Loxsoma* is different from what occurs in *Anemia*; they extend nearly all round the xylem. Another point of difference is that in *Anemia* the spiral elements of the leaf-trace are continued a short way down the stem. Further, the only solenostelic forms in *Anemia* are probably to be regarded as reduced from dialystelic forms; and these latter would show less resemblance to *Loxsoma* in stem-structure, than the species chosen for comparison; though this is perhaps less important.

REFERENCE TO LITERATURE.

A few further allusions to Prantl's work on the Schizaeaceae and to that of one or two other authors ought to be made. A full description of the form and veining of the leaves, and of the fructifications, is given by him. He also gives a detailed account of the vegetative structure, which is to a great extent correct. He recognized that the distinction between the solenostelic and dialystelic species of *Anemia* is one of degree, and is related to the phyllotaxy (p. 22). Only a few special points in his account of the anatomy need be referred to. In *Schizaea elegans* some large reticulate tracheides on the median lower side of the petiole-bundle are described as being the first to differentiate (p. 24). If this is correct, it is different from *S. digitata*. The petiole of *Anemia Phyllitidis* is well described and figured. In the petiole of *A. coriacea* a curious bundle-structure is described, in which the xylem is separated into two bands. In the stem of *Lygodium* the protoxylem is stated to be 'regellos über

den Strangquerschnitt zerstreut,' but this is not correct. The protoxylem elements of the stem were recognized by Prantl as scalariform in *Schizaea*, but for the other genera he describes them as reticulate, which has not been confirmed. Prantl records the agreement of *Mohria* with most *Anemias* in the structure of its bundles.

Bauke ('78, p. 642) shows that *Anemia* and *Mohria* exhibit a special type of development in their prothalli, distinct from that of the Polypodiaceae, and points out that this resemblance is of importance, as these two genera are unlike in habit. This indication of affinity fits in well with the anatomy.

Russow ('72) gives a short account of the anatomy of the Schizaeaceae (p. 97). In the stem of *Lygodium* he refers to the irregular order of development of the tracheides. He also describes the fibres in the petioles of *Schizaea* and *Anemia*. The petiole-bundle of *Anemia* is fairly correctly represented in his diagram (Pl. X, Fig. 9), except that the protophloem is drawn as continuous. In *Schizaea pectinata* also (Pl. X, Fig. 7), the protophloem is made to surround the xylem.

Thomae ('86, p. 155) quotes several of Prantl's statements with regard to the Schizaeaceae and does not add many new observations.

Britton and Taylor have given an account of the life-history of *Schizaea pusilla*¹. The structure of stem and petiole as described by these authors agrees in type with *S. digitata*.

SUMMARY OF SOME OF THE RESULTS.

1. The sieve-tubes of the Schizaeaceae and Hymenophyllaceae do not appear to form callus, but in other respects (perhaps excepting *Schizaea*) agree structurally with the sieve-tubes of other Ferns.

2. Silica-nodules occur in the cavities of parenchyma-cells in some species of *Lygodium* and *Anemia*.

3. The fibres in the petiolar bundle of some species of

¹ I am indebted to Mrs. Britton for material of this species, but have not yet made any preparations of it.

Lygodium, *Schizaea*, and *Anemia* are to be regarded as modified sieve-tubes. The fibres in *Trichomanes Prieurii* appear to be formed, either all from parenchyma, or some from parenchyma and some from sieve-tubes.

4. The species of *Lygodium* are very uniform in structure, and possess a solid stele; *Schizaea* has a medullated stele, while dialystelic structure is found in *Mohria* and some species of *Anemia*, solenostelic structure in others.

5. The seedling of *Lygodium* does not suggest reduction from a more complicated type.

6. In the seedling of *Anemia* the solid stele is converted into a dialystelic one, by gradations similar in type to those found in *Pteris* for instance; but no very definite *morphological* conclusions should be drawn from this fact.

7. The protoxylem belonging to the stem in the Schizaeaceae is scattered, does not include spiral elements, and is differentiated mostly with no relation to the leaf-traces.

8. The petiole possesses a single bundle.

9. The roots appear to be diarch throughout.

In conclusion it may be said that anatomically the Schizaeaceae form a most interesting group, and that further examination of some of the forms may give useful data, on which to base conclusions with regard to the homologies of the different types of stelar structure found in the Order.

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EXPLANATION OF FIGURES IN PLATES XIX, XX, AND XXI.

Illustrating Mr. Boodle's paper on the Anatomy of the Schizaeaceae.

The following lettering is used in several of the illustrations: *e.*, endodermis; *x.*, xylem; *px.*, protoxylem; *ph.*, phloem; *pph.*, protophloem. Where *x'*, *px'*, *ph'*, *pph'* are used, they refer to the xylem, protoxylem, phloem, and protophloem respectively of a petiole or leaf-trace. *i. e.*, inner endodermis; *i. ph.*, inner phloem. Figs. 1, 4, and 17 are reproduced from photographs by Dr. E. C. Bousfield; Figs. 11, 38, and 44 are also from photographs.

Fig. 1. Transverse section of rhizome of *Lygodium dichotomum*. The different layers may be easily recognized by comparison with Fig. 2. × 50.

Fig. 2. Part of transverse section of rhizome of *Lygodium dichotomum*. *s. l.*, layer of suberized cells; *x. p.*, one of the xylem-parenchyma-cells; *si.*, silica-nodule in a xylem-parenchyma-cell. × 390.

Fig. 3. Part of transverse section of young rhizome of *Lygodium dichotomum*. × 390.

Fig. 4. Transverse section of petiole of *Lygodium japonicum*. × 75.

Fig. 5. Silica-nodule from xylem-parenchyma of rhizome of *Lygodium dichotomum*. × 900.

Fig. 6. Tracheide isolated by maceration from node of *Lygodium dichotomum*. × 90.

Fig. 7. Part of a small sieve-tube in the rhizome of *Lygodium dichotomum*, showing sieve-plates and granules. × 900.

Fig. 8. Section of seedling of *Lygodium japonicum*. *f.*, foot; *p.*, prothallus; *x.*, diarch xylem of primary root. × 45.

Fig. 9. Transverse section of seedling-stem of *Lygodium japonicum*, below first leaf. *p.*, one of the xylem-parenchyma-cells. × 390.

Fig. 10. *Lygodium japonicum*. First leaf-trace of the seedling, separating from the stele. × 390.

Fig. 11. *Schizaea dichotoma*. Transverse section through a node. × about 30.

Fig. 12. *Schizaea digitata*. Transverse section of young stem at node. *a.*, *b.*, examples of outer and inner tracheide respectively developing first; *m.*, pith. × 90.

Fig. 13. *Schizaea digitata*. Transverse section of petiole near base. *f.*, fibre. × 260.

420 *Boodle.—Anatomy of the Schizaeaceae.*

- Fig. 14. *Schizaea digitata*. Transverse section of young petiole. $\times 260$.
 Fig. 15. *Schizaea dichotoma*. Diagram of transverse section of node. $\times 30$.
 Fig. 16. *Anemia Phyllitidis*. Diagram of transverse section of stem. *l. t.*, leaf-trace; *r.*, roots. $\times 7\frac{1}{2}$.
 Fig. 17. *Anemia Phyllitidis*. Transverse section of petiole. $\times 75$.
 Fig. 18. *Anemia Phyllitidis*. 'Cavity-parenchyma' connected with the median protoxylem-group of the petiole. *r.*, rings of an annular tracheide. $\times 390$.
 Fig. 19. *Anemia Phyllitidis*. Fibre representing a lignified sieve-tube, from the petiole. $\times 900$.
 Fig. 20. *Anemia Phyllitidis*. Silica-nodule from the ground-tissue close outside the endodermis of the petiole. $\times 900$.
 Fig. 21. *Anemia Phyllitidis*. Transverse section of primary root of seedling. $\times 390$.
 Figs. 22 and 24-31, represent transverse sections of the seedling-stem at successively higher levels.
 Fig. 22. *Anemia Phyllitidis*. Transverse section of stem of seedling. *x'*, xylem of first leaf-trace. $\times 390$.
 Fig. 23. *Anemia Phyllitidis*, seedling. Xylem of first leaf-trace in cortex of stem. $\times 900$.
 Fig. 24. *Anemia Phyllitidis*. Xylem of stele after departure of first leaf-trace. One parenchyma-cell is seen inside the xylem-mass. $\times 390$.
 Fig. 25. *Anemia Phyllitidis*, seedling. The endodermal cells are marked with crosses. $\times 390$.
 Fig. 26. *Anemia Phyllitidis*, seedling. The four elements in the centre marked with crosses are sieve-tubes. $\times 390$.
 Fig. 27. *Anemia Phyllitidis*, seedling. *ph.*, internal phloem. $\times 390$.
 Fig. 28. *Anemia Phyllitidis*, seedling. Diagram showing a row of endodermal cells (*e.*) connected with the outer endodermis. $\times 90$.
 Fig. 29. *Anemia Phyllitidis*, seedling. Diagram showing a ring of inner endodermal cells (*e.*) enclosing one parenchymatous cell. $\times 90$.
 Fig. 30. Drawing of the same. *e.*, inner endodermis; *ph.*, inner phloem. $\times 390$.
 Fig. 31. *Anemia Phyllitidis*, seedling. Diagram showing both xylem and endodermis horseshoe-shaped. $\times 90$.
 Fig. 32. *Anemia Phyllitidis*, seedling. Transverse section of petiolar bundle of early leaf. *f.*, probably fibres. $\times 390$.
 Fig. 33. *Anemia Phyllitidis*, seedling. Transverse section of young petiolar bundle of later leaf. $\times 390$.
 Fig. 34. *Anemia Phyllitidis*, seedling. Transverse section of one of the steles in the stem; early stage with only a few tracheides differentiated. $\times 390$.
 Fig. 35. *Mohria caffrorum*. Diagram of transverse section of stem. *r.*, roots; *a.*, 'stem-steles'; *b.*, leaf-trace; *sc.*, sclerenchyma-group accompanying leaf-trace. $\times 7\frac{1}{2}$.
 Fig. 36. *Mohria caffrorum*. Diagram of transverse section of petiolar bundle. *sc.*, sclerotic cells; the phloem is shaded. $\times 45$.
 Fig. 37. *Mohria caffrorum*. Part of longitudinal section of young stem, showing two sieve-tubes (*ph.*) and one protoxylem element. $\times 390$.
 Fig. 38. *Anemia mexicana*. Transverse section of the stele in the rhizome. $\times 40$.

Fig. 39. *Anemia mexicana*. Part of transverse section of stele. *i. ph.*, inner phloem. $\times 140$.

Fig. 40. *Anemia Phyllitidis*. Part of transverse section of one of the steles in the stem. *i. e.*, inner endodermis; *i. ph.*, inner phloem. $\times 140$.

Fig. 41. *Anemia coriacea*. Diagram of stele of rhizome, just below node. *e'*, group of endodermal cells. $\times 90$.

Fig. 42. *Anemia coriacea*. Diagram of stele at node. $\times 90$.

Fig. 43. *Anemia coriacea*. Diagram of node. *l. t.*, leaf-trace. $\times$ about 75.

Fig. 44. *Nephrodium Thelypteris*. Half petiolar bundle, showing thick-walled sieve-tubes. $\times 40$.

Fig. 45. *Adiantum trapeziforme*. Part of petiolar bundle. *f.*, fibres. $\times 390$.

Fig. 46. *Trichomanes Prieurii*. Fibre in bundle of petiole. $\times 390$.

Fig. 47. *Trichomanes radicans*. Two sieve-tubes and one pericyclic cell from rhizome. *s.*, sieve-plates; *n.*, nucleus of parenchyma-cell. $\times 390$.

Fig. 48. *Trichomanes radicans*. Three sieve-tubes from rhizome. *s.*, sieve-plate; *e.*, end-wall. $\times 390$.

POSTSCRIPT.

In the lower part of the petiole of *Anemia coriacea* the bundle is of the type found in other species of *Anemia*, e.g. *A. aurita*, but in the upper part of the petiole it divides into two, one bundle having a V-shaped xylem, and the other, which is smaller, having a straight band of xylem. Prantl's description ('81, p. 26) of the petiole of this species probably refers to the region where the division of the bundle is incomplete. The division of the petiolar bundle appears to be an unusually early separation of a bundle for one of the first pinnae of the leaf.

Two papers not cited in the list of Literature must be mentioned here, viz.:—

SCOTT, '94: Recent work on the Morphology of tissues in the Higher Plants. Science Progress, vol. i, and

TANSLEY, '96: The Stellar Theory. Science Progress, vol. v.

In these papers several views are discussed or brought forward, which have been adopted in the present paper (see the section on the Stele, p. 403).

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