Comparative Anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae.

III. On the Anatomy of the Gleicheniaceae¹.

BY

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With Plates XXXVIII and XXXIX.
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THE fullest account of the anatomy of the Gleicheniaceae previously published is that given by Poirault ('93), but although he enters into a careful description of the petiole and node in different species of *Gleichenia*, the structural characters of the Order have in some respects been less completely dealt with than was the case with the Hymenophyllaceae and Schizaeaceae, which formed the subject of two monographs by Prantl ('75 and '81).

The range of diversity in the structure of the rhizome is less in the Gleicheniaceae than in the Schizaeaceae. In the latter Order four main types of stelar structure were recognized, while in the Gleicheniaceae only three are found, as will be described below. No case of dialystely has so far been discovered. The homologies of the three types of structure which occur in the Gleicheniaceae is an interesting question, but, although it is as well to discuss it, there does not

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appear to be any immediate prospect of a definite solution to such morphological problems.

Two genera only are included in the Gleicheniaceae: *Platyzoma*, Br., and *Gleichenia*, Sm.; the species, on which *Stromatopteris*, Mett., was founded, being classed by Hooker and Baker ('74) as a species of *Gleichenia*. By both Christ ('97) and Diels ('00) *Platyzoma* is included in *Gleichenia*, and according to the latter author *Stromatopteris* ranks as a genus distinct from *Gleichenia*.

It is hoped to obtain further material of some of the species in which only small pieces of dried material were available, and to publish some additional observations together with those proposed in the case of the Schizaeaceae.

Of the two genera, *Gleichenia* will be taken first, and the description will be divided into sections in the same way as in the last part of this paper (p. 359 of this volume).

Below is a list of the species in which either rhizome, or petiole, or both were examined. This list is given here so that the specific names may be divested of their authors in other parts of the paper.

Platyzoma microphyllum, Br. In the subgenus *Eugleichenia*, *G. moniliformis*, Moore, *G. polypodioides*, Sm., *G. circinata*, Sw., *G. Boryi*, Kze., *G. dicarpa*, Br. In the subgenus *Mertensia*, *G. longissima*, Bl., *G. flabellata*, Br., *G. Cunninghami*, Hew., *G. pedalis*, Klfs., *G. cryptocarpa*, Hk., *G. revoluta*, H.B.K., *G. simplex*, Hk., *G. pubescens*, H.B.K., *G. flagellaris*, Spr., *G. vestita*, Bl., *G. pectinata*, Pr., *G. dichotoma*, Willd.

GLEICHENIA, habit.

The stem, except in *G. moniliformis*, is a creeping rhizome, bearing roots on its lower side and leaves on its upper side. The internodes are usually long, and the leaves, though sometimes apparently forming a single row, are in certain species tristichous, though with only a small divergence. The roots may be irregularly placed, or in rows (e. g. tristichous).

The leaf generally has a long petiole, and the first division is dichotomous, dividing the leaf into two primary pinnae,

but with a bud at the fork, which may continue to grow for a time as a main rachis, and then repeat the process of forking and production of a terminal bud. Thus many pairs of primary pinnae are formed, and their mode of growth may be identical with that of the main rachis. The pinnules are borne in a pinnate manner. Diagrams illustrating the leaf-form in the different sections of the subgenus *Mertensia* are given by Diels ('00, p. 353). The dichotomy of the primary pinnae, and the production (at the fork) of a bud, which afterwards develops as a secondary rachis, and the pinnate arrangement of the pinnules, are all characters which are also found in species of *Lygodium*. Further, in *G. pectinata* after the first dichotomy the rachis, which is perhaps a sympodium, bears pinnae singly, and as the latter are short and forked there is a close agreement with what is found in *Lygodium*. *G. moniliformis* and *G. simplex*, both of which appear to be reduced forms, have simple pinnatipartite leaves. Excluding these, dichotomy in the leaf is a character of the genus. It is a primitive character which is shared by species of *Lygodium*, *Schizaea* and *Gleichenia*. It may be pointed out as quite possible that the pinnate form of leaf, as found in *Anemia* and perhaps in some other groups of Ferns, may have originally been derived from a dichotomous form of leaf, like that of *Gleichenia*, the pairs of primary pinnae representing dichotomies, and the rachis representing the products of a series of buds formed in the successive forks. In other cases a pinnate leaf may occur in a dichotomous type, apparently by suppression of dichotomy, what would be the ultimate branches of the leaf being borne directly on the petiole.

Numerous forms of hairs and paleae occur on the rhizome and leaf.

GLEICHENIA, rhizome.

In the majority of the species of *Gleichenia* the rhizome has a uniform type of structure in the internode, namely, a centrally placed solid stele (protostele), consisting of a central mass of xylem, composed of tracheides and paren-

chyma, and surrounded by a continuous ring of phloem, pericycle and endodermis. There is thus a general resemblance to the structure of the rhizome of *Lygodium*, but a point of difference is that in *Gleichenia* the xylem is mesarch, and has several distinct groups of spiral protoxylem-elements.

The only other widely different type of structure found in the genus is the solenostelic, which has so far been observed only in *G. pectinata*. It will be convenient to describe the species, which possess a protostele, first, and to treat *G. pectinata* separately.

In each species the diameter of the rhizome is of course liable to variation according to the vigour of the specimen, but two examples will give an idea of the sizes met with. A rhizome of *G. polypodioides* measured about 1 mm. in diameter, while one of *G. pubescens* reached rather more than 3 mm. These, as compared with other species, may be taken as a small and a large rhizome respectively. The proportionate dimensions of stele and cortex in *G. flabellata* are shown in Fig. 1, Plate XXXVIII. In this diagram *a.* represents the epidermis and outer 2-3 layers of the cortex, whose cells have colourless and comparatively thin walls; *b.* and *c.* are the middle and inner zones respectively of the cortex, and consist of brown-walled sclerotic tissue, which is very thick-walled in proportion to the size of the lumen in *b.*, and less so in *c.* There is no very sharp line of demarcation between *b.* and *c.*, so the limit taken in the diagram is where the sclerenchyma begins to be appreciably thinner walled.

In most species the cortex consists chiefly of brown sclerotic tissue, of the kind so frequently found in the cortex of other Ferns. Thus the sclerotic tissue of the cortex of *G. dichotoma* is composed of long brown-walled fibrous elements with oblique end-walls, but divided into shorter elements by transverse septa. The walls of the fibres bear small oval pits. The length of the fibrous elements is however variable, as one piece of rhizome of the same species was found to have quite short sclerotic cells in place of the long fibres.

Several species resemble *G. flabellata* in having the epidermis

and the succeeding 1-2 or 3 layers of the cortex comparatively thin-walled, e.g. *G. vestita*. In *G. dichotoma* the epidermis and the next 1-2 layers contain mucilage, and are either sclerotic and brown-walled, or, especially on the lower side of the rhizome, they may have colourless and not very thick walls. In *G. pedalis* the epidermis and the whole of the cortex are brown-walled, the walls being of nearly uniform thickness throughout these tissues.

In the cortex of the rhizome in most species small intercellular spaces are found at the corners of the sclerotic cells; these spaces are, however, usually partly or nearly completely filled with a yellow, granular substance. It was not determined whether the intercellular space was first formed, by the splitting of the walls, and then partly filled by a granular deposit, or whether the space and the granules were produced simultaneously by the absorption of some of the constituents of the middle-lamella. The granular matter may perhaps consist of pectic substances, similar to the rodlets found between the parenchymatous cells of the petioles &c. of several Ferns (see Poirault, '93, p. 243), but infiltrated with the brown colouring matter (phlobaphene) found in the sclerotic membranes. In the rhizome of *G. moniliformis* intercellular spaces between the sclerotic cells appear to be absent.

Surrounding the stele there is a well-marked endodermis, which shows the usual characters in its radial walls. Its cells, in transverse section, often have a tangential diameter one-and-a-half times to twice the radial diameter (Figs. 3 and 6, e). The radial walls may become yellow in the mature rhizome. The endodermal cells usually abut directly on the sclerotic cortex (Fig. 3), but occasionally the outer tangential walls of the endodermis remain thin. In *G. dicarpa* and *G. circinata* the endodermal cells contain mucilage, and in *G. flabellata* they contain a colourless finely granular body, which is probably siliceous.

The pericycle is 2-5, generally 3-4 cells thick, its thickness varying according to the size of the stele. Its cells are

usually of about the same tangential diameter as the endodermal cells, but are more nearly isodiametric. In the mature stem they do not generally show definite radial seriation, but in a transverse section of the young rhizome of *G. dicarpa* the pericyclic cells at many points were neatly arranged in radial rows, which did not come to an end with the pericycle but were continued through the endodermis to the next two or three layers of the cortex. At other points the radial rows were disturbed by displacement of cell-walls, but this was so slight that their radial origin was still fairly clear. The pericycle therefore appears to be cortical in origin.

The protophloem forms a practically unbroken layer of small elements (sieve-tubes and phloem-parenchyma) similar to those in *Lygodium*, and taking a strong stain when treated with Kleinenberg's haematoxyline. The layer of protophloem may be recognized in the low-power photograph (Fig. 1, *pph.*), and is shown as it appears under the high-power in Fig. 3 (*pph.*). The metaphloem forms a continuous zone within the protophloem, and consists of large sieve-tubes and a certain amount of parenchyma. The walls of these sieve-tubes are seen to be of considerable thickness when the section is mounted in glycerine-jelly or in weak glycerine (*s.t.*, Fig. 3). Numerous refractive granules are often seen adhering to the walls as in other Ferns. As the sieve-tubes were not found to differ in any important point from those of *Lygodium*, as to the character of their sieve-plates, &c., there is no need to enter into detail, except as to the presence or absence of callus. Sections of the rhizome and petiole of two or three species of *Gleichenia* were tested with azoblue, but gave no evidence of the presence of callus. Subsequently the rhizome of *G. pectinata* was examined. In this case dried material was used, and a section was cut, and tested with azoblue, soon after the material had been softened by boiling in water. It was then found that a few of the sieve-tubes showed distinct callus-knobs on their sieve-plates, similar to those which occur in *Pteris aquilina* (Boodle, '01, p. 399). An

attempt to obtain similar preparations, after the material had been left in spirit for about two days, entirely failed. This indicates the possibility that in the other species of *Gleichenia* and in the Hymenophyllaceae and Schizaeaceae, where the azoblue-test failed, the callus-reaction might be obtained by means of some preliminary treatment, e. g. boiling for a short time; though this is unnecessary in the case of *Pteris* and many other Ferns. That is, either callus may be present, but masked by being infiltrated with some other substance, which prevents the appearance of the characteristic stain, or there may here be a body slightly differing from callus, but easily converted into it. Poirault ('93, p. 191), also working with dried material, mentions having found callus in the sieve-tubes of the Gleicheniaceae. Unstained preparations from dried material in two or three species showed bodies strongly resembling callus-rods and knobs.

A layer of parenchyma separates the metaphloem from the xylem (see Fig. 3). The xylem forms the central part of the stele. Its diameter varies roughly with that of the rhizome. In *G. polypodioides* it measures only about $\frac{1}{3}$ mm., while in *G. pubescens* it reaches $1\frac{1}{3}$ mm. In several species the xylem has an approximately circular outline in the internode (Fig. 1, *x.*), but becomes oval near the node (Fig. 2). *G. flabellata* and *G. pubescens* are two of the species, which have a circular xylem. In others it is distinctly lobed, and the lobes have a definite relation to the protoxylem-groups, e. g. in *G. dichotoma* (Fig. 14, *x.*), *G. dicarpa*, *G. circinata*. When the xylem is lobed the metaphloem forms a thicker layer, and is composed of larger sieve-tubes in the bays of the xylem than opposite the lobes. The structure of the xylem can be seen by comparing Figs. 2, 3, 4 and 5. The general low-power view of the xylem in Fig. 2 (*G. flabellata*) shows that the tracheides are arranged in chains and groups, separated by parenchyma as in *Lygodium*. The essential point of difference lies in the position and nature of the protoxylem. In *Gleichenia* there are several small groups of annular and spiral protoxylem-tracheides placed a short

distance below the periphery of the xylem, the remainder of the tracheides being scalariform. In Fig. 2 about fourteen protoxylems are present; some of these may be recognized as groups of small darkly stained elements (*px.*). Fig. 3 contains a peripheral piece of the xylem of *G. dichotoma*, showing the scalariform tracheides separated by xylem-parenchyma (*x.p.*). Fig. 4 represents one of the lobes of the xylem of *G. circinata*, and shows the mesarch position of the protoxylem (*px.*). Part of a young stele of *G. dichotoma* in Fig. 6 is at the stage in which the protoxylem (*px.*) is the only part of the xylem differentiated; young tracheides (*t., t.*), which have not yet begun to thicken their walls, are seen on the outer side of the protoxylem. Fig. 5 is a radial section of the outer part of the stele of *G. circinata* showing the protoxylem (*px.*) with one scalariform tracheide on the outer side; *pph.* is a protophloem element. Fig. 14 may be referred to for the relation of the protoxylem-groups to the lobes of the xylem in *G. dichotoma*. In species where the xylem is lobed, there is nearly always a protoxylem immersed in or below the xylem of each lobe, though there may sometimes be additional protoxylem-groups having no corresponding prominences.

In the internode of *G. dichotoma* the xylem generally shows six prominences with six protoxylems. The lobes are fairly symmetrically placed, so that the xylem may be described as roughly hexagonal, with rounded angles (Fig. 14). The three lobes on the lower half of the xylem serve for the attachment of roots, though a root is occasionally inserted on one of the upper lateral lobes, while the three protoxylems in the upper half are connected with leaf-traces. A rhizome of *G. dichotoma*, var. *nervosa*, which was larger than that of the type, had a xylem with 8-9 lobes. In *G. circinata* there are often six as in *G. dichotoma*.

In these species the xylem usually has a nearly symmetrical form, with protoxylem-groups equal in number to the lobes. In *G. dicarpa*, on the other hand, there are often 7-8 protoxylems, of which 2-3 on the upper side have no distinct

xylem-prominences connected with them, the outline of the xylem being rounded or nearly flat on this side, while the remainder of the protoxylems are found below well-marked lobes. This structure was seen, for instance, at a distance of about $\frac{3}{4}$ inch from a node.

A similar rounding or flattening of the upper side of the xylem occurs as one approaches the node in *G. dichotoma*, but in *G. dicarpa* and some other species it is found through most or the whole of the internode, so that the xylem only bears prominences below and at the sides.

G. dicarpa, var. *alpina*, has a much smaller rhizome than the type, and a rounded-quadrangular xylem, with a protoxylem embedded in each angle.

Once more comparing the structure of the rhizome of *Gleichenia* with that of *Lygodium*, and leaving the striking differences in the protoxylem out of the question, a few points of difference in detail may be mentioned. In *Gleichenia* there is usually a greater proportion of parenchyma in the xylem, and it more often occurs as 2-3-seriate chains of cells (instead of uniseriate); the tracheides are often broken up into shorter chains or groups, are often larger in proportion to the size of the stele, and frequently have a shorter common wall, where they are in contact with one another. Owing to the latter point and to the tracheides being in contact with a larger number of parenchyma-cells, the tracheides of *Gleichenia* in longitudinal section less frequently show the scalariform pits running right across the width of the elements than is the case in *Lygodium*. All the above small differences are probably liable to exception.

Having given a general description of the structure of the rhizome of *Gleichenia*, some peculiarities of certain protostelic species should be mentioned. In a section of the rhizome of *G. dicarpa* a few of the xylem-parenchyma-cells were seen to be thick-walled and lignified, and others showed traces of lignification at their corners in the middle-lamella, so it is quite likely that a general lignification of these cells may take place in quite old parts of the rhizome. Poirault ('93, p. 173)

mentions the rare occurrence of sclerotic cells among the scalariform tracheides in the rhizome of this species.

In *G. cryptocarpa* mucilage occurs in the xylem- and phloem-parenchyma, and in *G. dicarpa* it is found in the same cells as well as in the pericycle.

G. moniliformis is the most aberrant species in that no protoxylem-elements are distinguishable in the mature stem, and the tracheides all appear to be scalariform. The stele is small, the xylem measuring rather less than $\frac{1}{8}$ mm. in diameter. The absence of spiral protoxylem-elements is interesting, because this species is the only one of its genus with an upright stem. It was noted among the Hymenophyllaceae, where spiral protoxylems are general, that their absence in certain species of *Trichomanes* appeared to be correlated with an upright habit (*T. spicatum* and *T. Bancroftii*). Both *G. moniliformis* and the species of *Trichomanes* just mentioned have probably been derived from forms with a creeping rhizome, and the change to the upright stem has been accompanied with diminished length of the internodes and slower growth of the rhizome. This makes it easy to understand the disappearance of the spiral elements.

In the rhizome of *G. Cunninghami* the xylem in transverse section presented a curious appearance on account of the presence of a rather neat uniseriate peripheral band of large tracheides, which was continued about half way round the circumference, with only four of five inconspicuous interruptions by parenchymatous cells. This was probably a band of tracheides ready to form the chief part of a leaf-trace, though at some distance from a node.

The depth of the protoxylem-groups below the periphery of the xylem differs in the various species. *G. vestita* may be mentioned as a case in which they are deeply seated in proportion to the size of the xylem.

Lignified sieve-tubes were observed by Poirault ('93, p. 195) in the stem of *G. polypodioides*. Similar elements were not seen by the writer in the stem of this or any other species

of *Gleichenia*, but this may be due to the rhizomes examined not being sufficiently old.

When the rhizome branches, the stele divides in a simple manner as in *Lygodium*, but, in the cases observed, one stele is smaller than the other and passes off laterally. Both this character and the external appearance suggest monopodial branching, not dichotomy.

GLEICHENIA, petiole.

In most species of *Gleichenia* the cortex of the petiole bears a general resemblance to that of the stem. It consists largely of the usual brown-walled sclerotic tissue, which may be fairly uniform throughout, or may fall into two zones, one of which is formed of much thicker-walled elements than the other, or into three zones of which the middle is the thinnest-walled. The epidermis and sometimes one or two adjacent layers of the cortex may be comparatively thin-walled, as occurs in some rhizomes, or may be strongly sclerotic.

The structure of the petiole has been described by Poirault ('93, p. 176, &c.), and two detailed drawings (Figs. 17 and 18) are given by him of the petiolar bundles of *G. Speluncae*, Br., and *G. rupestris*, Br. Both of these belong to *Eugleichenia*. *G. Speluncae* is given by Hooker and Baker ('74, p. 11) as a synonym of *G. circinata*, and *G. rupestris* as a separate but very nearly allied species. *G. rupestris* has, however, been since reduced by Baker ('91, p. 183) to a variety of *G. circinata*.

The type of structure in the petiole is described by Poirault ('93, p. 189) as being very different in the two subgenera of *Gleichenia*, and the difference is illustrated by his diagrams of the separated leaf-traces (Figs. 13*c* and 14*d* for *Eugleichenia* and 16*d* for *Mertensia*). The distinguishing point is that the bundle is circular or subcordiform in *Eugleichenia*, but more or less shaped like a C in *Mertensia*. This distinction appears to hold good for the majority of species; however in *G. (Mertensia) pedalis* the indentation of the bundle is only slight, so that its form is about reniform, while

in *G. (Mertensia) dichotoma* the form of the bundle is as in *Eugleichenia*. In the latter species the internal structure of the bundle might be regarded as giving evidence of derivation from the usual type for *Mertensia*.

G. dicarpa may be taken to illustrate the type of petiolar structure found in *Eugleichenia*. Fig. 7 is a transverse section of the bundle. The xylem has the form of an arch with incurved ends, and possesses three protoxylem-groups. The position of the latter is indicated by the three cells marked *c.p.* in the drawing, which are elements resembling cavity-parenchyma. There is a protoxylem-group consisting of annular and spiral tracheides (some of which are often crushed) in contact with the outer side of each of these cells, i. e. radially external to them. It is thus seen that the xylem agrees with that of *Anemia Phyllitidis*, in that three protoxylems are present, and are internal to the xylem-arch, one being median, and the other two in the concavity of the hooked ends of the xylem. The phloem in *G. dicarpa* clothes the external surface of the xylem-arch, and bends inwards round its ends, following its outline, and continuing upwards towards the top of the arch, e.g. about three-quarters of the way. The phloem has the same constituent elements as in the stem, but has fibrous elements in addition. The proto-phloem, forming the boundary of the phloem towards the pericycle, can be recognized by its small elements (*pph'*). The latter are fairly thick-walled, but have not been represented so in the drawing, in order that the phloem-fibres might be distinguished by this character. The phloem-fibres are seen at *f.*, *f.*, and at the two corresponding points in the other half of the bundle. They have been formed by thickening and lignification of the walls of phloem-elements; both sieve-tubes as described by Poirault ('93, p. 195) for *G. circinata* and *G. dicarpa*, and also phloem-parenchyma, being thus transformed. A few similar fibres may occur in the phloem outside the top of the xylem-arch. The central region of the bundle probably represents pericycle, and consists partly of parenchyma and partly of sclerotic

elements (*sc.*), which have not the brown walls characteristic of the cortex. The pericycle on the outer side of the bundle is 3–4 cells thick, and bounds the drawing. In a section of another petiole of *G. dicarpa* each of the two lateral protoxylems was split into two slightly separated groups. The difference in structure at the base of the petiole in this species will be described in connexion with the node.

The other species of *Eugleichenia* have petioles of the same type as *G. dicarpa*; that is, the endodermis is not invaginated, the xylem forms an arch, and three similarly placed protoxylem-groups are present.

There are considerable differences in the size and proportion of parts in these other species, but the type of structure is practically the same. In *G. circinata* the structure is very similar to that of *G. dicarpa*. In *G. Boryi*, which has a much smaller petiole, no sclerotic cells are differentiated in the central tissue, and fibrous constituents of the phloem appear to be quite absent. In *G. moniliformis* also the bundle is small, the xylem-arch has more the form of a narrow U, in which the hooks are hardly represented, the phloem is only continued a short way up in the interior, and only about two sclerotic elements were found in the central parenchyma. In *G. polypodioides* the structure at first sight looks very different, as it shows an almost solid-looking mass of xylem, shaped something like an equilateral triangle with rounded angles. It may, however, be referred to the same type as the other species. The differences of detail are as follows:—in *G. polypodioides* the central mass of tissue (which in *G. dicarpa* includes the sclerotic tissue, *sc.*) is only represented by a narrow line of parenchyma, one to two cells thick¹; the hooks of the xylem have only narrow bays, containing parenchyma and fibrous phloem-elements, which are continuous with the phloem bending in through the small space

¹ In *G. circinata* a transverse section of a young petiole, with protophloem and protoxylems differentiated, showed an arrangement of the cells in the central mass of parenchyma, which gave evidence of comparatively late cell-division, apparently deriving the group from a single median row of cells.

between the tips of the hooks. The protoxylem groups have the usual positions. A few sclerotic elements are found in the phloem on the outer side of the xylem, chiefly opposite the lateral protoxylems.

Poirault ('93, p. 190) mentions as a distinguishing character, that all the species of *Eugleichenia* except *G. Boryi* possess strongly lignified, pitted or reticulate cells in the pericycle of the petiole, while in *Mertensia* such cells occur only isolated, or in the majority of species are completely absent. This cannot be held as a reliable distinction. Among species of *Eugleichenia*, *G. dicarpa* showed lignification and slight thickening of its pericyclic cells, and *G. dicarpa*, var. *alpina*, had a pericycle composed entirely of pitted and strongly sclerotic cells¹. *G. dicarpa*, var. *longipinnata*, also has a sclerotic pericycle. On the other hand, sclerotic pericyclic cells were not observed in *G. circinata*, though they were found by Poirault in *G. rupestris*, which is to be regarded as a variety of this species. Turning to *Mertensia*, *G. cryptocarpa* has its pericycle sclerotic throughout as in *G. dicarpa*, var. *alpina*, though not quite so thick-walled. As *G. cryptocarpa* and *G. dicarpa*, var. *alpina*, are both distinctly xerophytic, it appears probable that xerophytic habit may produce a strongly sclerotic pericycle in both subgenera, though *Eugleichenia* may have a more general tendency to form it than *Mertensia*.

We may now deal with the petiole of *Mertensia*. Some of the species have much larger petioles and petiolar bundles than are found in the other subgenus. The type of structure of the bundle may be said to be much the same as in *Eugleichenia*, with the exception that the endodermis is invaginated, so as to follow to some extent the outline of the xylem-arch, and so that the central region is occupied by sclerotic tissue continuous with the cortex, and apparently belonging to it, instead of to the pericycle as in *G. dicarpa*. Thus the bundle is arched, or in several species roughly C-

¹ Some of the more external of these had their walls slightly tinged with the brown colouring matter, which usually characterizes the cortical sclerenchyma.

shaped, as described by Poirault. The points of agreement with the *Eugleichenia*-type are best seen in the species of smaller stature, e. g. in *G. simplex*, where the petiolar bundle is rather smaller than that of *G. circinata*. The xylem here has the form of an arch with sharply hooked ends, has a median and two lateral protoxylems in the usual positions; the phloem is continued on the inner side of the xylem to about the same level as in *G. dicarpa*, and its elements are fibrous in the concavities of the xylem-hooks.

A point of difference from the other subgenus is seen in the incurving of the endodermis, which may be described as having been pushed into the arched bundle by a promontory of cortical sclerenchyma. Other points of difference from *Eugleichenia*, which would apply to a fair proportion of the species, are that in *Mertensia* the xylem-arch is composed of a continuous zone of tracheides of fairly uniform size, not interrupted by considerably smaller tracheides opposite the protoxylem-groups, and secondly that there is often a conspicuous group of small tracheides between the median protoxylem and the large tracheides forming the top of the xylem-arch.

In species of *Mertensia*, where the petiolar bundle is larger than in *G. simplex*, the protoxylem-groups become more and more numerous according to the size of the xylem-arch. Thus both the median and the two lateral protoxylems may each be represented by two groups, making six in all, or, to take an extreme case, in a large form of *G. longissima* about twenty groups were counted. The leaf-trace in the upper part of Fig. 27 shows the form of petiolar bundle found in some of the larger *Mertensias*.

The structure of the petiole of *G. dichotoma* differs from that of other species of *Mertensia* in that the bundle is bounded externally by an endodermis, which is not incurved, but in the central tissue of the bundle is found a mass of sclerotic tissue surrounded by a complete ring of endodermis¹

¹ Something similar to this is found in the basal part of the petiole of some *Eugleichenias*, to be described later, in dealing with the node.

(Fig. 8), or this mass may be broken up into three (Fig. 9). The difference between *G. dichotoma* and the *Egleichenia*-type can be seen by comparing Figs. 9 and 7. Some of the phloem in the hooks of the xylem is converted into fibrous elements in *G. dichotoma* just as in *G. dicarpa*, and similar cavity-parenchyma is found in connexion with the protoxylem-groups.

Cells which are evidently of the same nature as the cavity-parenchyma mentioned in the Schizaeaceae (Boodle, '01, p. 394) are found adjoining the protoxylems in the petiole of nearly all *Gleichenias*. They are cells which have evidently undergone extension towards the protoxylem-elements, either as the cause or effect of the crushing of the spiral tracheides, but in *Gleichenia* they generally have flattish walls, as seen in longitudinal section, and so do not present the character on which the name 'Lückenparenchym' was based. Fig. 10 shows three cells of this tissue (*c.p.*) in the petiole of *G. dichotoma*. One of them has undergone late division; and crushed protoxylem-elements are seen at *px'*. Throughout the genus it frequently occurs that a considerable number of the cavity-parenchyma-cells become rather thick-walled, pitted and lignified.

A small part of the petiolar bundle of *G. dichotoma* is shown as a high-power drawing in Fig. 11, where *sc.* is the left-hand end of the central sclerotic mass of Fig. 8. The sclerotic group is surrounded by an endodermis mostly torn (*i.e.*); *px'* is part of a crushed protoxylem-group; *ph'* and *pph'* are the meta- and protophloem of the incurved phloem, and the terminal part of it is replaced by fibres *f*. Two of these probably represent sieve-tubes, and the other two phloem-parenchyma. The sclerotic elements in Fig. 12 are some from the central mass in *G. dichotoma*, shown in longitudinal section. Many of the elements of this tissue are much longer, more pointed and thicker-walled (*i.e.* more fibrous) than those in the figure.

Before leaving the petiole, one or two peculiarities of structure in certain species of *Gleichenia* deserve notice. In *G. circinata* a granular body, apparently siliceous, was

observed in most of the endodermal cells of the petiole, both in the type and in the form originally separated as *G. rupestris*. These bodies, which are just like those in the endodermis of the stem of *G. flabellata*, were not seen in the petiole of any other species besides that mentioned.

In the bundle of *G. pedalis* the endodermis is only slightly incurved, so there is room for a mass of sclerotic pericycle, which is present here as in some *Eugleichenias*, between the endodermis and the cavity-parenchyma accompanying the median protoxylem. The cavity-parenchyma, as in several other *Mertensias*, forms a conspicuous group of lignified cells.

In the large form of *G. longissima* previously mentioned the fibres of the bundle are specially numerous. The bundle is of large size, and the fibres extend practically all the way round the inner face of the xylem. Opposite the terminal protoxylems they form a nearly continuous layer, and appear to belong to the phloem, elsewhere they are more scattered and perhaps represent pericycle.

The petiole of *G. cryptocarpa* is remarkable, as it contains three bundles instead of one. They are not widely separated, and if pushed into contact would form a typical C-shaped bundle with the usual orientation. There is one long slightly curved bundle, and two shorter sharply curved ones, representing the long side and the two hooked ends of the C respectively. As a single leaf-trace passes off from the stele to supply the leaf, and is continued into the base of the petiole as an arched bundle of the usual form for *Mertensia*, the peculiar structure described above is to be explained as due to a very early separation of the bundles for the first two pinnae¹. This division of the bundle generally takes place quite a short distance below the pinnae, but here it had already occurred at fourteen inches below the first pinnae.

In *G. flagellaris* and some other species each incurved end of the xylem-arch does not terminate in a hook, but in a knob, in the middle of which a protoxylem-group is placed. This feature may be more or less restricted to the upper part of

¹ The same thing appears to take place in *G. flagellaris* (Poirault, '93, p. 176).

the petiole, and may be described as being due to the folding back of the hook until the bay of parenchyma disappears. This may be illustrated in *G. dichotoma* by comparing Figs. 9 and 8.

GLEICHENIA, node.

Diagrams of series of sections through the node, illustrating the mode of separation of the leaf-trace, have been given by Poirault ('93, p. 172 et seq.) for two species of *Eugleichenia* and one of *Mertensia*. Poirault's description of these makes most of the features clear, but as the nodal structure is very interesting, and as one or two particulars appear to have escaped Poirault, two series of diagrams are given here (Figs. 14-25), viz. one series for *Mertensia* and one for *Eugleichenia*. In examining the separation of the leaf-trace in three or four nodes of *G. dichotoma*, it was found that several differences of detail occurred. Probably the same would be found to apply to other species also.

Fig. 14 represents the internodal structure of *G. (Mertensia) dichotoma*. Here we may speak of three upper and three lower protoxylem groups, or of two median and four lateral. Figs. 15-19 are diagrams of a series of sections through one particular node, which will now be described. On approaching this node¹, the upper median protoxylem travels towards, and then fuses with, one of the adjacent protoxylems, thus reducing the number of protoxylem-groups to five, which are placed as seen in Fig. 15. The protoxylem-group, A, is the one that has been formed by the fusion of two. In succeeding sections the protoxylem, B, multiplies its constituent tracheides, and then forks into two, the parenchyma adjacent to it having meanwhile increased in amount, so as to produce an island in the xylem, which may be called the 'nodal island,' as seen in Fig. 16, where *n.i.* is the nodal island, and *b., b.* are the protoxylems produced by the splitting of B. In the next stage (Fig. 17) the upper of these has travelled

¹ This and other nodes described are explained by beginning below and going in the acropetal direction.

upwards to b ., while the lower one has divided into b^1 . and b^2 ., and A has divided into a ., a . The lower a . and also b^2 . will remain in the stele, while the upper a ., b . and b^1 . will pass out as the three protoxylems of the leaf-trace. In the stage we are considering (Fig. 17) the nodal island (*n.i.*) has increased greatly in size, and other tissues besides parenchyma have become differentiated in it. There is a central mass of brown sclerotic tissue (*sc.*) surrounded by an endodermis, and on the lower side of the island are a few sieve-tubes, represented by short lines in the diagram. Detailed drawings of a similar nodal island are given by Poirault ('93, p. 175, Fig. 15) for *G. pubescens*, H. B. K., var. (under the syn. *G. furcata*). As described by Poirault, the first appearance of the sclerotic group, as one goes towards the node, is one fibre sheathed by endodermis; then more and more fibres are added until the group, still surrounded by an endodermis, attains considerable size. Passing on from Fig. 17, the thickness of the parenchyma increases on the inner side of the sclerotic group, the phloem in the nodal island increases in amount, and splits into two bands, which become separated by a bar or bridge of xylem appearing between them, as seen in Fig. 18, Pl. XXXIX. In the next stage (Fig. 19), the xylem of the leaf-trace has become separated from that of the stele by the splitting of this bar of xylem. Consequently part of the original nodal island passes off inside the leaf-trace, and contains the sclerotic tissue and a band of phloem; while part of the nodal island remains enclosed in the xylem of the stele (*n.i.*). It still contains a few sieve-tubes, but these soon disappear, and the parenchymatous island shrinks in size, until it is reduced to a few cells accompanying the protoxylem b^2 . in the internode. A new upper median protoxylem is supplied by the division of a ., and the typical internodal structure is restored.

In a second node of *G. dichotoma*, the xylem of the leaf-trace again passes off closed; the only difference of detail is that, in the stage a little later than Fig. 17, three or four sclerotic elements, apparently surrounded by an endodermis, branch away from the main mass at the same time that the

phloem-band splits, and pass into the stelar part of the nodal island, but die out upwards almost at once, i. e. at the level of the first appearance of the xylem-bridge.

In a third node, when the leaf-trace separates, its xylem is closed, as in the previous cases, but becomes open while the leaf-trace is still in the cortex of the stem.

In the fourth node examined, the bar of xylem which usually appears in the nodal island, cutting it into two, is not formed, and the leaf-trace consequently passes off from the stele with an open xylem-arch, leaving the inner part of the original nodal island as simply a bay in the exterior of the xylem. In this case the phloem in the nodal island and the internal phloem of the leaf-trace both have a connexion with the external phloem of the stele, though this was of course not the case in the other three nodes.

In the last two nodes mentioned, the leaf-trace passes off in the median plane of the stele, i. e. from a point on the opposite side from the lower median lobe, not obliquely as in Fig. 18. It is no doubt in connexion with this that the behaviour of the protoxylems is much simpler than in the first node described. In the last two nodes, the upper median protoxylem of the internode passes out as the median protoxylem of the leaf-trace, whose two lateral protoxylem-groups are supplied by forking of the two upper lateral protoxylems of the internode. Thus the behaviour of the protoxylems and the position of the leaf-trace as it leaves the stele show that the leaf-arrangement should be regarded as tristichous, median and slightly lateral leaf-traces being produced.

The petiole, belonging to the second node described, was $14\frac{1}{2}$ cm. in length, and was sectioned at close intervals. The results need not be given in detail, but one or two changes in structure should be referred to. The central sclerotic mass with its investment of endodermis divides into three, and then fuses again (as in Figs. 9 and 8). It appears to remain permanently enclosed in the bundle, having no connexion with the cortex or the outer endodermis. The xylem of the bundle in this petiole remains closed until a height of 4–5 cm. is

reached, when it opens, and allows continuity first between the inner and outer phloem (Fig. 9), and then between inner and outer pericycle (as in Fig. 8). Near the top of the petiole the reverse changes are gone through, so that the xylem becomes closed again just before the separation of the pinnae.

G. dichotoma has been described at length, because its petiole being of an exceptional type, the nodal structures differ in several points from Poirault's description of the node of *Mertensia*, and because the completely enclosed sclerotic tissue with its endodermis is an interesting feature.

The node of *G. flabellata* may probably be taken as fairly typical for *Mertensia*, and agrees in most points with the diagrams given by Poirault ('93, Fig. 16, p. 177) for that subgenus. The structure is as follows:—A nodal island appears in the stele, a few sieve-tubes appear near the middle of the island (*i. ph.* in Fig. 2); the sieve-tubes increase in number, and shift their position, so as to lie near the periphery of the island, forming an arc on the inner side and a scattered series on the outer; in the mass of parenchyma within this ring of sieve-tubes a sclerotic group, surrounded by an endodermis, appears; the arched xylem of the leaf-trace separates from the xylem of the stele at one end first, and, through the gap formed, the external phloem becomes continuous with the internal in the manner seen in *G. dicarpa* (Fig. 21, to be described later); then a stage, resembling that shown for *G. dicarpa* in Fig. 22, is reached, though in *G. flabellata* the bending in of the external endodermis round the sclerotic group takes place when the xylem and phloem of the other end of the petiolar bundle have become separated from the corresponding tissues of the stele. This point is connected with the bundle not swinging round so far as it does in *G. dicarpa* before becoming free. The type of structure now attained, viz. an arched bundle with an intrusion of endodermis and cortical sclerenchyma in its concavity, is continued in the petiole.

For *Eugleichenia* Poirault gives diagrams (Figs. 13 and 14) of the nodes of *G. Boryi* and *G. dicarpa* (under syn. *G. hecistophylla*). In *G. Boryi* one may summarize his description

thus:—A nodal island consisting of parenchyma and a ring of sieve-tubes appears in the xylem, but contains no sclerotic tissue or endodermis; the arch of xylem outside this with three protoxylems separates for the leaf-trace, while the phloem of the nodal island becomes continuous with the outer phloem of the stele, part of it then apparently passing out as the internal phloem of the leaf-trace, and part remaining to repair the gap in the phloem of the stele. Apart from the absence of sclerotic tissue and endodermis here, the structure is not very different from what was found in one of the nodes of *G. dichotoma* (the fourth node described).

As a node of *G. dicarpa* showed some points of difference from Poirault's description ('93, p. 173), diagrams of the node of this species are given here. Figs. 20 and 21 show two stages, in which the xylem of the leaf-trace is preparing to separate. In Fig. 20 the phloem (*ph.*¹) has curved into the bay of the xylem. In Fig. 21 the phloem forms a wide loop in the xylem-arch, and a group of brown sclerotic tissue (*sc.*), surrounded by an endodermis, has appeared in the pericycle. In Fig. 22 the sclerotic group holds a transitory connexion with the sclerotic cortex, its endodermis becoming continuous with the outer endodermis¹. The sclerotic group then becomes shut in as it was before, and the leaf-trace becomes nipped off from the stele in the usual way, so that in Fig. 23 one sees the leaf-trace separate, and with a sclerotic group (*sc.*, which is bounded by an endodermis) in its central parenchyma (pericycle). The type of structure is identical with what is found in certain parts of the petiole of *G. dichotoma*. The group of sclerenchyma, however, is only continued for a short distance upwards in the base of the petiole, its elements becoming reduced in number till none are left, but surrounded to the last by an endodermis. Fig. 13 shows the group reduced to two fibres, which are separated by an endodermis from the surrounding, sclerotic elements of the pericycle.

¹ Neither the presence of the endodermis surrounding the sclerotic group nor the connexion of the latter with the cortex appears to have been observed by Poirault.

In the lower part of the petiole of *G. circinata* a small sclerotic group, surrounded by an endodermis¹, is found in the central pericycle, just as in the leaf-trace and petiole of *G. dicarpa* (Figs. 23 and 13). In the case examined, however, it nowhere included more than three fibres. It dies out upwards in the petiole as in the other species just quoted. A node of *G. circinata* was examined with the expectation that the sclerotic group would behave as in *G. dicarpa*, but it was found to be restricted to the base of the petiole, and to have no connexion with the cortical sclerenchyma. In the node examined, the leaf-trace separated with a closed xylem surrounding very little central parenchyma. As the leaf-trace passed through the cortex, its central parenchyma increased to a triangular sclerotic group, and within this there appeared a brown sclerenchyma-fibre, surrounded by an endodermis, just about when the petiole became free. The single fibre was soon replaced by two and then three, and these were reduced to one again, which soon disappeared. The fibres thus had no connexion with the cortical sclerenchyma, but formed a thin spindle-shaped group sheathed with endodermis and isolated in the central pericycle of the petiolar bundle. As the group is so small, and occurs within other sclerotic tissue, it is probably a reduced structure, derived from one like that found in *G. dicarpa*. Poirault gives a figure of the petiole of a variety of *G. circinata* (*G. Speluncae*), showing a central sclerotic group of thirteen elements, surrounded by an endodermis, so in this form the sclerotic tissue is better developed, and might be continued down into the node as in *G. dicarpa*, or still further into an enclosed nodal island as in Poirault's diagram of *G. hecistophylla*, and in *G. dichotoma*.

The characters of the node of *Gleichenia* may be summarized shortly: in several species a parenchymatous nodal island is formed in the xylem of the stele, and contains phloem and a group of sclerenchyma (surrounded by endodermis); the sclerenchyma is continued for a short distance

¹ This endodermis contains granular (probably siliceous) bodies exactly similar to those occurring in the external endodermis of the bundle in this species.

upwards inside the bundle of the petiole (*G. dicarpa*), or to the top of the petiole (*G. dichotoma*); it has no connexion with the cortex (*G. dichotoma*), or a transitory connexion with the cortex just before the separation of the leaf-trace (*G. dicarpa*), or becomes continuous with the cortex when the leaf-trace separates, and is not afterwards continued inside the leaf-trace (*G. flabellata*, &c.); but in this case it may perhaps be represented by the sclerotic tissue filling the concavity of the bundle, but external to the endodermis of the latter.

Poirault's comparison of the nodal structure of *Gleichenia* with that of the young seedling stem of *Trichomanes* appears to be based on a misapprehension with regard to the structure of *Trichomanes*, as pointed out under the Hymenophyllaceae (Boodle, '00, p. 493).

GLEICHENIA, rachis and pinnules.

In the primary and secondary pinnae at their bases and for some distance upwards, and also in the primary rachis, the vascular bundle has the same type of structure as in the petiole of the same plant, though it is of smaller size.

In *G. dicarpa*, var. *longipinnata*, the separation of the bundles for the first two primary pinnae takes place in a simple manner. The C-shaped band of xylem becomes buckled in at two points so as to form three contiguous arches (standing on the same plane), which then separate and diverge each invested by the other usual constituents of the bundle, so that three separate and nearly similar bundles are produced. The two outer ones pass out to the first pair of pinnae, while the middle one is continued straight on into the main rachis. This division of the petiolar bundle into three takes place close below the point of insertion of the pinnae.

G. cryptocarpa has been mentioned before for the exceptional feature it presents in the division of the bundle into three close to the base of the petiole. Here also the mode of separation appears to be simple. The whole bundle, as well as the

xylem, is C-shaped, and divides into three separate arched bundles, probably without much previous buckling.

In *G. flabellata* there is greater complexity. The behaviour of the xylem could not well be made clear without the aid of diagrams, so the description will be restricted to the bundle, as limited by the endodermis. Near the top of the petiole the bundle becomes elongated at right angles to its median plane, so as to form a low arch with the ends turned in like a compressed C. The ends approach until they meet, when the endodermis becomes fused, so that the bundle now has a complete inner and outer ring of endodermis. The form of the bundle is now a long hollow ellipse. Two bridges of bundle-tissue are now formed across the central cavity, and the bundle becomes a chain of three loops. By splitting of the bundle through the two bridges, three closed annular bundles are produced, of which the middle one, belonging to the rachis, has an annular xylem. Before long all three bundles open and return to the typical arched form. In *G. dichotoma* the division of the bundle takes place in a somewhat similar manner.

There is the same transition to collateral structure that is found in the leaf of many other Ferns. In *G. flabellata* one of the secondary pinnae not very far from its tip had a bundle with an oval endodermis (not invaginated) and an arched xylem with three protoxylems. The form of the xylem is very similar to that found by Gwynne-Vaughan ('01, Pl. III, Fig. 8) near the tip of the rachis in *Loxsonia*. The phloem curves round the hooked ends of the xylem, so as nearly to meet; the bundle is therefore practically concentric. In the pinnules, however, the bundle of the midrib is reduced to collateral structure. The small bundle, which is circular in outline, is bounded by an endodermis, has a roughly semi-circular group of xylem, with a layer of phloem on its curved lower side, and one protoxylem-group at the middle point of its flat upper side. This again corresponds with what is found in the principal vein of the leaf-segment of *Loxsonia* (Gwynne-Vaughan, '01, Pl. III, Fig. 7, e.).

In the species examined the stomata were restricted to the lower surface of the pinnules. One interesting arrangement in the xerophytic form, *G. dicarpa*, var. *alpina*, is worth mentioning. Each pinnule was, in a sense, revolute. As seen in transverse section the right and left half of the lamina formed two semicircles springing from the midrib, and the lower surface of the midrib bore flat scales, which were spread out horizontally and reached the margins of the lamina. Consequently the lower surface of the latter, which bore the stomata, formed the lining of a chamber, to which the scales acted like a lid. The mesophyll in this variety was more lacunar than in species, which appeared less or scarcely xerophytic. The upper epidermis was also thicker-walled.

GLEICHENIA PECTINATA.

This species differs from all those described above in possessing solenostelic structure. Figs. 24-27 illustrate the internodal and nodal structure of *G. pectinata*. Only dried material was obtainable, which accounts for the collapsed condition of most of the soft tissues. Fig. 24 is a photograph of a transverse section of the stele in the internode. The position of the protoxylems, inner and outer phloem, &c., is shown in the diagram of the same section (Fig. 25). The phloem on both sides of the xylem is mostly crushed, but here and there patches of it were in fairly good condition, and when examined under the high-power showed elements, which in the characters of their refractive walls, sieve-plates, &c., were typical Fern-sieve-tubes. It was in the internal phloem of this species that callus-knobs were recognized by using the azo-blue test. The central space in Fig. 24 was due to the inner endodermis having become torn, and the central sclerenchyma having dropped out. The xylem contains very large scalariform tracheides, and these are separated from one another by chains and groups of parenchymatous cells. The xylem is mesarch with, at this point, 8-9 groups of spiral protoxylem-elements. The structure is essentially the same as in other species of *Gleichenia* possessing a lobed xylem,

but with the remarkable difference, that here the more central part of the xylem is replaced by a mass of sclerenchyma surrounded by a ring of endodermis (Fig. 25, *i.e.*), pericycle, phloem (*i.ph.*) and conjunctive parenchyma. The upper part of the xylem has a rounded surface; in the lower part the lobes correspond with the protoxylem-groups. One of the groups, however, appeared to have split into two, probably as a stage preliminary to the production of a root. A point to which we shall return is the occurrence of a few fibres in connexion with one or more of the protoxylems. The stele of *G. pectinata* is larger than that of any other species examined, the diameter of its xylem being $1\frac{2}{3}$ mm., while that of *G. pubescens* is $1\frac{1}{3}$ mm. The larger forms of *G. longissima* could not be examined, but they would probably have a stele at any rate as large as that of *G. pectinata*, and might possibly also show solenostelic structure.

A section through the nodal region is seen in Fig. 26. The lower part of the stele remains as in the internode; the central sclerotic tissue is *in situ*, and has a two-armed upward extension, which fills the concavity of the band of tissue preparing to separate as a leaf-trace. At this point the whole mass of sclerenchyma has a form resembling a T, or perhaps still more like a longitudinal section of a mushroom. In Fig. 27 the leaf-trace has become free, and is on its way out through the cortex. The stele is left open by a leaf-gap, so that both its central sclerenchyma and that of the leaf-trace are continuous with the cortical sclerenchyma.

The petiolar bundle resembles the leaf-trace, but has a nearly circular external outline, broken of course at the point where the T-shaped promontory of cortical sclerenchyma passes into its interior. The xylem has the usual arched form, has one protoxylem in each of the two hooks of the xylem, and about ten other groups. Fibres are found in the slight bays of the hooks, and are scattered at intervals on the inner side of the xylem-arch. The fibres represent phloem-elements in the lower part, but may perhaps be pericyclic elsewhere. The petiolar bundle is thus like that

of other *Mertensias*, e.g. the form of *G. longissima* described above, though smaller than in the latter.

To return to Fig. 26 for some details connected with the separation of the leaf-trace, there is a protoxylem-group in the xylem just below the tip of each arm of the sclerenchyma. Phloem is of course found surrounding the whole of the xylem, and, on the inner side of the latter, it is found as a continuous layer, interrupted only below the middle region of the arch of xylem destined for the leaf-trace. Of the phloem-elements present within the lower parts of the xylem-arch a few are transformed into fibres, and the latter are also found in the phloem between the tip of each arm of the sclerenchyma and the adjacent protoxylem-group, already mentioned. This protoxylem forks into two, of which one group goes to supply the future hook of the leaf-trace, while the other one remains in the stele, still with the phloem containing fibres between it and the sclerenchyma. Then a bar of xylem is formed cutting across the arm of sclerenchyma near its tip; the latter having become previously elongated as on the right-hand side in Fig. 26. In this way a piece of brown sclerotic tissue (apparently surrounded by an endodermis) comes to be enclosed in an island in the xylem, in which also phloem is found, though chiefly represented by pale-walled fibrous elements, and this island is adjacent to a protoxylem-group. Next the bar of xylem splits, so that the xylem of the leaf-trace is separate from that of the stele, then phloem, endodermis, &c., appear in the gap so that the end of the leaf-trace becomes free from the end of the solenostele. The above stages do not take place simultaneously at the two ends of the leaf-trace, as it swings round slightly so as to pass off obliquely. In Fig. 27 two dark patches are seen immersed in the xylem of the open solenostele near its two ends. These are the two islands, whose formation has just been explained. They contain brown sclerenchyma, parenchyma, and phloem-fibres. The brown fibres in the two islands are not continued above the node for any great distance after the separation of the

leaf-trace, but the phloem-fibres are found after the solenostele has become closed. In this node moreover a few phloem-fibres occurred in connexion with the two protoxylem-groups next below those concerned with the leaf-trace, but the protoxylems in the lowest pair of xylem-lobes (in Figs. 26 and 27) were not accompanied by any such fibres. From this it appears that the phloem-fibres may be continued (as in this specimen) from one node to the next, and that the two lowest lobes of the xylem serve for the attachment of roots only, while all the other protoxylems are connected with leaf-traces, which are therefore probably tristichously arranged, the node described being one that bears a median leaf. Fig. 28 represents a scalariform tracheide of this species, and shows a peculiarity in the arrangement of the pits, which is rather common here.

GLEICHENIA, root.

The roots of *Gleichenia* are commonly tetrarch, and rootlets of *G. circinata*, var. *longipinnata*, were found to be diarch and triarch. Russow ('72, p. 97) describes the roots of *G. polypodioides* and *G. glauca* (= *G. polypodioides*, Sm., or perhaps *G. longissima*, Bl.) as being triarch and pentarch respectively. The stele of the root of *G. circinata*, var. *microphylla*, is represented in Fig. 29. The four protoxylem-groups are seen in contact with the pericycle, which varies from one to two cells in thickness. Only one of the four phloem-groups is shown in the drawing; its protophloem is at *pph*. Two of the large scalariform tracheides are incompletely differentiated (*y.t.*). A root of *G. dicarpa* had a structure, which at first sight appeared to be normally triarch, but, although there were only three groups of phloem, one of the protoxylems was split into two groups of small peripheral tracheides, which were separated by two parenchyma-cells. This structure probably signified that the root was tetrarch in one region and triarch in another.

At any rate in certain cultivated specimens, arrested roots

occur rather frequently. A root-stele passes through the cortex of the stem, and enters a short spine-like projection, which is the free part of the root. As the external tissues at its tip become sclerotic, it appears to be incapable of further growth. The stele in this spine and the root-trace in the cortex of the rhizome were found to be tetrarch in *G. dichotoma* and *G. dicarpa*, but differed from the normal roots of these species in having a tendency to form a pith. Thus in an arrested root of *G. dicarpa* the four xylem-groups did not meet at the centre but abutted on a small pith. A section through the trace of this root in the cortex of the rhizome showed a similar structure, except that one of the pith-cells near the centre was replaced by a tracheide, while two or three others appeared to have begun to thicken their walls and then to have undergone partial mucilaginous degeneration. Probably, when the arresting cause affected the organ, no further tracheides were differentiated, and consequently in the free part of the root the elements in the central part of the stele, which normally would have developed as tracheides, remained parenchymatous to form a pith. In an arrested root of *G. dichotoma* most of the central tracheides had been formed, both in the root-trace and in the spine.

These points are mentioned partly as an analogy illustrating what may perhaps have taken place in the stem of certain Ferns, and led to the production of a pith. In this connexion it is as well to refer to the occasional occurrence of half-thickened and partly collapsed or even scarcely thickened elements, evidently representing tracheides. They were found sometimes as a group of two or three in the xylem of otherwise typical roots, and also near the centre of the xylem in the rhizome in specimens of three or four species. They sometimes also occur in petiolar bundles, and are apparently quite unconnected with any external mechanical injury. They may perhaps be due to the plant having grown, whether in the open or in cultivation, under conditions differing from those of the normal habitat of the species.

In species with a lobed xylem-mass in the rhizome, the

roots are inserted on the lower and lateral lobes. If one follows one of these lobes in the acropetal direction towards the insertion of a root, one finds that it becomes more and more prominent (Fig. 14, *r.*), and finally the outer part of the lobe separates as the root-stele. The latter passes out slowly, making a very acute angle with the stele until it has passed through the pericycle, but as it enters the cortex, it usually curves more sharply and soon turns outwards horizontally, i. e. radially in a transverse plane.

In *G. dichotoma* an attempt was made to determine the origin of the protoxylems of the root. Though the point was not established with certainty, it appeared that two protoxylems of the root-trace were supplied from the protoxylem of the xylem-lobe, and that the remaining two originated independently, during the passage of the root-trace through the cortex.

GLEICHENIA, seedling.

A series of microtome-sections was made of a seedling of *G. circinata*, var. *microphylla*. Although the soft tissues became rather shrunk in the process of embedding, the structure could be fairly well determined.

The primary root has diarch structure. In the region of the foot, the root-stele curves towards the prothallus, becoming horizontal, and then vertical again. It then still has diarch structure, but in passing upwards the protoxylems become less evident, and the xylem-plate gradually becomes broader. The first leaf-trace, containing only a few tracheides, is given off from one of the ends of the xylem, corresponding in position to one of the root-protoxylems. The xylem by this time has a narrow elliptical outline, but rapidly approaches oval form, while one or two parenchymatous cells appear amongst the tracheides, soon after the first leaf-trace has become free. The first root-trace is attached somewhat laterally to the xylem, and shortly afterwards the second root-trace is inserted about opposite the first one. The parenchyma-cells in the xylem have increased in number,

and some have arranged themselves in chains, the external cells being in contact with the conjunctive parenchyma bounding the xylem. They become more scattered again, the second leaf-trace is given off about opposite the first one, and a little higher up the third root is attached. The xylem of the stem is now roughly circular in outline, and consists of tracheides of fairly uniform size (probably all scalariform) and a few xylem-parenchyma-cells amongst them. Thus, except for the absence of protoxylem-groups, the type of structure of the mature stem is already attained. Where the third leaf-trace was given off, the stele was incompletely differentiated, and, at a short distance above, became procambial. It is a pity that no older seedling was obtainable, but as a structure practically resembling that of the mature stem of *Gleichenia* was arrived at without any more complicated stage being passed through, it seems probable that such complication (e. g. solenostely) would not be found higher up. Thus, as far as the data go, the seedling-structure gives no evidence of the protostely of *Gleichenia* being due to reduction. The petiolar bundle of the third leaf has a small band of about seven tracheides, and apparently has phloem on the outer side only, i. e. it is collateral.

PLATYZOMA, habit.

The stem of *Platyzoma microphyllum*, which is the only species of its genus, is a creeping rhizome, with roots on its lower side. It differs from the rhizome of *Gleichenia* in bearing densely crowded leaves, which are not restricted to the upper side of the stem, but have polystichous arrangement. The leaves are 12 in. or less in length, and are simply pinnate. The pinnae are very small (about 2 mm. in length), ovate-orbicular in outline, and have their margins revolute as in *Erica hiemalis*, so that the stomata, which are restricted to the lower side, are placed in a nearly closed cavity. The plant is evidently strongly xerophytic, and the leaf has no doubt become simply pinnate by reduction. As mentioned

by Bower ('99, p. 32), the leaf is occasionally forked, which points to its having been reduced from a dichotomous type, such as is found in *Gleichenia*.

PLATYZOMA, structure.

In *Platyzoma microphyllum*, as the leaves are crowded, numerous leaf-traces are seen in the cortex of the rhizome in any transverse section. The leaf-traces show spiral seriation, as is seen in Fig. 30. This was drawn from a section, which included rather less than half the cortex—the part with bundles on the right; the dotted outline of the remainder of the cortex is added to complete the diagram. Fig. 31 is a diagram of the stele, giving the position of the outer endodermis, phloem, xylem and inner endodermis. Fig. 32 is a photograph of about half the stele. On the outside of the figure are the pericycle (3–4 cells thick) and the phloem (*ph.*) (seen in places as a dark line), each forming a continuous zone. Within these is the xylem, which resembles that of *Gleichenia* in being composed of scalariform tracheides together with chains and groups of parenchymatous cells, but differs from the xylem of all the species of *Gleichenia* except *G. moniliformis* in having no definite protoxylem-groups. The smallest tracheides occur in the outer region of the xylem, as seen in Fig. 32, so one may assume that the protoxylem-elements are distributed at or near the periphery. They are scalariform, and both in this respect and in being scattered at the periphery they resemble the corresponding elements in *Lygodium*. On the other hand the structure of the stem resembles what is found in *G. pectinata*, in that the xylem forms a ring, and that within it there is an inner endodermis enclosing a central mass of sclerenchyma. Of course it differs from that species in the absence of internal phloem, and of definite groups of spiral protoxylem-elements. The inner endodermis has its radial walls ruptured at most points in the photograph (Fig. 32, *i. e.*), and the central sclerotic tissue comes out as a dark mass. Its walls were not

very strongly thickened in this specimen, but were brown, and its elements contained a mucilaginous substance, which was stained deeply with haematoxyline. The phloem contains typical Fern-sieve-tubes.

Figs. 33 and 34 illustrate the mode of separation of the leaf-trace. A small peripheral tangential band of tracheides becomes marked out by the appearance of a group of parenchyma in the xylem below it (Fig. 33). In this section the group of parenchyma is unusually large, and happens to fit on to a chain of xylem-parenchyma (*p.r.*), which is radially placed. The band of xylem mentioned above becomes free as the xylem of the leaf-trace. It may pass off straight, or may swing round slightly before separating. In Fig. 34 the same leaf-trace (*l. t.*) has reached the outer limit of the pericycle. It consists of the band of xylem and an arc of phloem, detached from that of the stele, which has already repaired the gap. After the leaf-trace passes the endodermis of the stele, it is invested with a complete endodermis. As it passes through the cortex of the stem, it remains collateral, its xylem becomes crescent-shaped, and acquires two protoxylem groups on its inner side, not far from its ends. No median protoxylem-group could be recognized. No leaf-gap affecting the endodermis is present, and frequently the exit of the leaf-trace scarcely affects the xylem of the stele, beyond leaving a small external pit like that seen in Fig. 32. Figs. 33 and 34 were drawn to show the nearest approach to a true leaf-gap met with. Longitudinal sections through the insertion of a leaf-trace did not show any passage of leaf-trace-parenchyma towards the centre of the stele.

A diagram of the petiolar bundle is given in Fig. 35. It has an arched xylem with protoxylems on the inner face at the two sharp bends. The tissue within the arch appears to consist chiefly of phloem.

In the rachis the xylem-arch is converted into a nearly straight band with a protoxylem immersed in it near each end. A little phloem is still found on the upper side, besides the arc of it on the lower. There is still no median protoxylem.

In the pinnae, which probably represent the pinnules of species of *Gleichenia*, the upper epidermis is thick-walled, and the mesophyll lacunar. The form &c. of the pinnae has been described in the section on the habit.

The roots are diarch.

CONCLUSIONS.

Owing to lack of space, general considerations on the structure of the Gleicheniaceae must be treated very shortly in the present paper.

Two possibilities must be kept in view: (1) That the protostelic condition of most *Gleichenias* is primitive and that the solenostelic type of *G. pectinata* has been derived from it; or, (2) that the protostelic *Gleichenias* owe their structure to reduction from solenostely. Taking the second assumption, the nodal islands of the protostelic *Gleichenias* might be regarded as ancestral remnants of a previous solenostelic structure. On the first supposition, on the other hand, the nodal islands might be looked upon as local complications of the stele, directly connected with the insertion of the leaf-trace. The further theory may be added, that the solenostelic structure of *G. pectinata* may have originated through the formation of a more bulky nodal island (containing phloem, sclerenchyma, &c.) and the continuation of the structure found in it through the internode. This is practically similar to the explanation given by Poirault ('93, p. 182) of the origin of the structure in *Platyzoma*. The node is often regarded as being prone to show ancestral characters. This may be true in certain cases, and the reverse in others. The importance of the effect of the leaf in moulding the structure of the stem has been pointed out by Jeffrey ('00) and by Gwynne-Vaughan ('01, p. 87). The requirements to be fulfilled in conduction and mechanical support would be somewhat more complicated at the node than in the internode, and might well lead to greater complexity in structure at the node, so that new types of structure would be liable to appear there. If the

new structure were suitable for the internode, it might spread through that region, by what might be called transformation of the tissues there. On the other hand, if reduction should take place in the structure of the internode owing to change in habit or other causes, a vestige of the previous structure might be retained at the node, as being more suitable to the slightly different requirements of the latter. The nodal island in *Gleichenia* may therefore be looked upon as either a remnant of previous solenostelic structure, or as a local modification in the stele, which finally led to solenostely in *G. pectinata*. The latter view on the whole appears the more probable. It is favoured by the two facts that the seedling-stem up to the third leaf shows protostelic structure, and that the leaf of *G. pectinata* does not carry dichotomy so far in the ramification of its frond as the other species, dichotomy in the leaf being taken as a primitive character. Much weight must not be laid on either of these features, but they are of some value, as nothing important has been noticed pointing in the other direction. In this connexion it is very interesting to note that the sorus of *G. pectinata* has unusual characters, which it shares with *G. dichotoma*, and in which these two species differ from the others of the genus, as described by Bower ('99, p. 33), namely, that it consists of more numerous sporangia. The latter are multiseriate in the sorus, and in this respect approach other Leptosporangiate Ferns (Bower, '99, p. 34). Though, considering the direction of specialization in the Leptosporangiate Ferns, the change to multiseriate sori may be taken as an advance, the uniseriate sorus might in certain cases be due to reduction, so the evidence of the sorus does not materially help in solving the present question.

It will be seen from what has been said above that the following suggestions must be put forward in a quite tentative manner. The protostelic structure of *Gleichenia* may be regarded as primitive, and the solenostelic type of *G. pectinata* as derived from it, the nodal islands of the protostelic forms representing an intermediate step. *Platyzoma* appears to be a xerophytically reduced form, in which the leaf-traces have

become small and crowded; it is perhaps probable that it may have been derived from a solenostelic form, by obliteration of the leaf-gaps, and disappearance of the internal phloem of the stele. This view is, I believe, held by Dr. E. C. Jeffrey. It is possible on the other hand that *Platyzoma* may have been derived from a protostelic *Gleichenia*, and its structure might then be due to the formation of a pith and internal endodermis. Although the nodal island in *Gleichenia* is here held not to be a remnant of solenostelic structure, some forms, e.g. *G. circinata*, seem to show reduction of the nodal island.

The two small nodal islands of *G. pectinata* further complicate the question. Assuming that they do not represent the nodal island of other *Gleichenias* split into two, but that the solenostelic structure is due to extension of the original nodal island, a similar extension (accompanied by fusion) of the small nodal islands of *G. pectinata*, so as to assume tubular form, would produce a double vascular ring like that described by Seward ('99) in his interesting paper on *Matonia pectinata*. This plant is perhaps not so very far removed from the Gleicheniaceae in its affinities.

Shortening of internodes and decrease of rate of growth of the stem are probably two factors, which both tend to abolition of spiral protoxylem elements. This is illustrated by *Platyzoma* and *G. moniliformis*, where spiral elements are absent, and both factors are likely to have been brought into play by the strongly xerophytic conditions, of which the habit and habitat of the two plants give evidence. The shortening of the internodes is not so manifest in *G. moniliformis*, but the change to its upright stem from the elongated rhizome of other species would probably greatly favour it.

One or two structural characters in the Order have a bearing on stelar theories. The sclerotic tissue with its endodermis in the nodal island and in the leaf-bundle is no doubt a homologous structure in the different species. Yet it may be connected with the cortex in some species, and not in

others, so that continuity of tissue is of no value in this case for determining its morphological nature. Again, it seems probable that the phloem-fibres which accompany certain protoxylem-groups through the internode in *G. pectinata* have been formed by transformation of some of the parenchyma usually found in that position, and the same might apply to the island of sclerenchyma, which is, however, only continued for a short distance above the node.

The morphology of stelar structures must remain at present doubtful, but the Gleicheniaceae have afforded no evidence disproving the general position taken in the section on the stele in the paper on Schizaeaceae (Boodle, '01, p. 403). In that paper the author is sorry to find that he misquoted Mr. Gwynne-Vaughan, by stating ('01, p. 405) that he had applied the term phloeoterma to the endodermis, and takes this opportunity of offering him an apology.

While not laying too much weight on the importance of structural differences, it may be said that the anatomy supports several points in Hooker and Baker's classification of the Gleicheniaceae, e.g. the inclusion of *G. moniliformis* in *Gleichenia*, perhaps the separation of *Platyroma microphyllum*, and the raising of *G. pectinata* to a distinct section of the genus.

A discussion of the relation of the Gleicheniaceae to the Hymenophyllaceae and Schizaeaceae must be deferred, but it may be said here that anatomical characters rather point to *Lygodium* as being the most primitive type found within these three Orders, to the Gleicheniaceae standing higher and having been derived from some form resembling *Lygodium*, while the Hymenophyllaceae may well have been derived by specialization from some stock not far removed anatomically from the Gleicheniaceae. This agrees well with the positions assigned to these Orders on other grounds by Bower ('99, p. 129).

SUMMARY.

1. Two chief types of stem-structure are found in the genus *Gleichenia*: (a) protostelic, (b) solenostelic. The latter has only been met with in one species, *G. pectinata*. The genus *Platyzoma* exhibits a third type: (c) medullate stele, with annular xylem and internal endodermis.

2. The xylem is mesarch with distinct groups of spiral protoxylem except in *G. moniliformis* and in *Platyzoma*. No spiral protoxylem was recognized in either of these, but in *Platyzoma* some of the smaller, sub-peripheral, or peripheral scalariform tracheides quite possibly represent scattered protoxylem.

3. As pointed out by Poirault, the bundle of the petiole is rounded in *Eugleichenia*, and nearly always arched in *Mertensia*, but *G. dichotoma* forms an exception. General sclerosis of the pericycle in the petiole may occur in both subgenera.

4. In all cases a single leaf-trace enters the petiole, and usually divides into three, close below the first pinnae; in one species this division takes place near the base of the petiole.

5. The xylem in the petiole has usually the form of an arch with incurved ends. Where the bundle is small, there are one median and two lateral protoxylems on the upper side of the xylem. In larger bundles the protoxylems are more numerous.

6. In several species, at any rate, a nodal island is found in the xylem of the stele, as described by Poirault. It contains phloem and sclerenchyma; the latter being surrounded by an endodermis. When the leaf-trace becomes free, the sclerotic tissue in the nodal island may fuse permanently with the cortex, or it may have a transitory connexion with it, and then be continued for some distance upwards (surrounded by its endodermis) inside the petiolar bundle; or it may have no connexion with the cortex, although continued to the top of the petiole inside the bundle (*G. dichotoma*). The phloem in the nodal island is connected

with the phloem on the inner or upper side of the leaf-trace, but may also be continued upwards in the xylem of the stem for a short distance after the separation of the leaf-trace. In *G. pectinata* two nodal islands are found, but some of their constituent elements may be continued as far as the next node.

7. *Platyzoma* has a collateral leaf-trace but apparently a concentric petiolar bundle. The median protoxylem is absent. There is no true leaf-gap. The group of parenchyma below the separating leaf-trace contains no phloem or sclerenchyma.

8. The bundle in the midrib of the pinnules shows collateral structure.

9. The roots are mostly tetrarch. Rootlets may be diarch or triarch. The roots of *Platyzoma* are diarch.

10. The seedling stem of *Gleichenia*, except for the absence of definite protoxylem-groups, attains the typical stem-structure of the genus below the insertion of the third leaf, and by that time has given no evidence of reduction from a more complicated type.

The most important structural point met with in examining the anatomy of this Order, not previously described, is the solenostelic structure of one of the species of *Gleichenia*. Our knowledge of this type may throw considerable light on the comparative anatomy of the group.

I wish once again to express my indebtedness and thanks to Dr. D. H. Scott, F.R.S., for many valuable suggestions. I have also to thank Mr. J. G. Baker, F.R.S., Mr. C. B. Clarke, F.R.S., and Mr. C. H. Wright, A.L.S., for giving me their kind assistance in one or two points. The material used for this investigation was from plants in cultivation in the Royal Botanic Gardens, Kew, in the case of several species of *Gleichenia*; in other species and in *Platyzoma* only dried material was available. Seedling plants of *Gleichenia* appear to be difficult to raise. The one examined was grown at Kew.

REFERENCE TO LITERATURE.

Among the earlier references to Gleicheniaceae is one by Von Mohl ('45, p. 115), who mentions that in many thin elongated stems, e.g. *Gleichenia*, the vessels are all united into a central bundle. He also points to *Platyzoma*, previously described structurally by Robert Brown ('38-'52, p. 2), as a connecting link between the above type and that of the hollow reticulate cylinder of other Ferns. Presl ('47, p. 2) refers to the presence of only a single circular or semicircular vascular bundle in the petiole of the Gleicheniaceae, and gives diagrams (Pl. VI) of the petioles of *Platyzoma* and of seven species of *Gleichenia*, but in each case the bundle is simply represented by a circular outline.

Russow ('72, p. 96) states that the rhizome of *G. polypodioides* agrees in structure with that of *Trichomanes radicans*. He also describes the petiolar bundle in three species of *Gleichenia*—*G. polypodioides*, *G. dichotoma*, and *G. dicarpa*, var. *alpina* (under syn. *G. vulcanica*), and gives a fairly accurate diagram (Taf. X, Fig. 10) of the last-named variety. The only point of difference from his figure, shown by a petiole of this plant examined, was the restriction of the phloem inside the xylem-arch to the region of the hooks. The sclerotic pericycle is correctly described, and also the fibres adjoining the hooks of the xylem. Phloem-fibres are also described as being found on the outer side of the xylem at the top of the arch in this species and in *G. dichotoma*. They certainly sometimes occur in this position in both these species, but are late in differentiation and not always found. Russow makes no mention of the internal endodermis in the petiolar bundle of *G. dichotoma*.

Potonié ('83, p. 39) examined the rhizome of *G. Mendelii* (= *G. circinata*, var.), and found the typical *Gleichenia*-structure, and notes that the xylem-parenchyma (amylom of the hadrom) is a strongly developed tissue.

Thomae ('86, p. 144) remarks on the fact that in the Gleicheniaceae only a single vascular bundle passes into

the petiole, and mentions the occurrence of phloem-fibres and of the central sclerenchyma in the petiolar bundle of *G. dichotoma* and *G. rigida*. He gives a diagram (Pl. VII, Fig. 1 a.) of a transverse section of the petiolar bundle of *G. dichotoma*, showing the form of the xylem-arch, and three diagrams (Fig. 1, b., c., and d.) illustrating the mode of constitution of the xylem-masses of the first two pinnae and the rachis. If one bears in mind that in these diagrams it is only the xylem that is shown, and that in his description (p. 155) 'Bündel' represents 'xylem-mass,' the stages he gives may be taken as fairly accurate.

Van Tieghem ('91, p. 1376) describes the intermittent growth of the leaf in *Gleichenia*, due to the production of the dormant bud in the fork of the pinnae, and its subsequent growth as a rachis, and mentions the solid stele of the rhizome.

Poirault's work ('93) has been frequently referred to above, as he deals rather fully with the node and petiole of *Gleichenia*. In describing the rhizome of *G. Boryi* (p. 171) he speaks of the protoxylem-elements as narrow tracheides with very wide pits, so it seems that he must have missed the true protoxylem elements, which are spiral in that species, and probably in all except *G. moniliformis*. Poirault refers to the structure of *Platyzoma*, and, as mentioned above, gives an explanation of the manner in which its structure may have been derived from that of *Gleichenia*.

LIST OF WORKS REFERRED TO.

- BAKER, '91: A summary of new Ferns. *Annals of Botany*, vol. v.
 BOODLE, '00: Anatomy of the Hymenophyllaceae. *Annals of Botany*, vol. xiv,
 p. 455.
 ——— '01: Anatomy of the Schizaeaceae. *Annals of Botany*, vol. xv, p. 359.
 BOWER, '99: Studies in the Morphology of Spore-producing Members, iv. The
 Leptosporangiate Ferns. *Phil. Trans., B.*, vol. cxcii, p. 29.
 BROWN, ROBERT, in BENNETT ('38-'52): *Plantae javanicae rariores*.
 CHRIST, '97: *Die Farnkräuter der Erde*.
 DIELS, '00: Gleicheniaceae; in Engler and Prantl: *Die natürlichen Pflanzenfam.*,
 i. Teil, iv. Abteil., p. 350.
 GWYNNE-VAUGHAN, '01: Observations on the Anatomy of Solenostelic Ferns.
 I. *Loxsonia*, *Annals of Botany*, vol. xv, p. 71.
 HOOKER and BAKER, '74: *Synopsis Filicum*.
 JEFFREY, '00: The Morphology of the Central Cylinder. Reprint from *Trans.*
Canadian Inst.
 MOHL, VON, '45: Ueber den Bau des Stammes der Baumfarne. *Vermischte*
Schriften, p. 108.
 POIRAUT, '93: Recherches sur les Cryptogames Vasculaires. *Ann. des Sci. Nat.*,
Bot., 7^e sér., tom. xviii, p. 113.
 POTONIE, '83: Zusammensetzung der Leitbündel. *Jahrb. d. k. bot. Gart.*
Berlin, ii.
 PRANTL, '75: *Unters. z. Morph. d. Gefässkryptogamen*. I. Hymenophyllaceen.
 ——— '81: *Unters.* II. Schizaeaceen.
 PRESL, '47: Die Gefässbündel im Stipes der Farne. *Abh. d. k. Böhm. Ges.*, v, 5.
 RUSSOW, '72: Vergleich. *Unters. d. Leitbündel-Kryptogamen*. *Mém. de l'Acad.*
des Sci. de St.-Petersbourg, xix.
 SEWARD, '99: Structure and Affinities of *Matonia pectinata*. *Phil. Trans., B.*
 vol. cxci, p. 171.
 THOMAE, '86: Die Blattstiele der Farne. *Jahrb. f. wiss. Bot.*, xvii.
 TIEGHEM, VAN, '91: *Traité de Botanique*.

EXPLANATION OF THE FIGURES IN PLATES
XXXVIII AND XXXIX.

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

The broken lines in the diagrams represent protophloem. The following lettering is used in several of the illustrations: *e.*, endodermis; *i.e.*, inner endodermis; *x.*, xylem; *px.*, protoxylem; *ph.*, phloem; *pph.*, protophloem; *i.ph.*, inner phloem. Where *x'*, *px'*, *ph'*, *pph'* are used, they refer to the xylem, protoxylem, phloem and protophloem respectively of a leaf-trace or petiolar bundle; *sc.*, sclerotic tissue. Fig. 2 is from a photograph by Dr. E. C. Bousfield; Figs. 24, 26, 27, and 32 are also from photographs.

Fig. 1. *Gleichenia flabellata*, rhizome. Diagram of transverse section. *a.*, epidermis and outer cortex; *b.* and *c.*, middle and inner zones of the cortex respectively. $\times 9$.

Fig. 2. *Gleichenia flabellata*, rhizome. Transverse section of the stele. $\times 50$.

Fig. 3. *Gleichenia dichotoma*, rhizome. Transverse section of outer part of stele. *sc.*, innermost layer of sclerotic cortex; *s.t.*, sieve-tube; *x.p.*, xylem-parenchyma. $\times 390$.

Fig. 4. *Gleichenia circinata*, rhizome. One lobe of xylem in transverse section, showing position of protoxylem (*px.*). $\times 390$.

Fig. 5. *Gleichenia circinata* (var. *rupestris*), rhizome. Radial section of outer part of stele. *sc.*, scalariform tracheide; *x.p.*, xylem-parenchyma. $\times 390$.

Fig. 6. *Gleichenia dichotoma*, young rhizome. Transverse section of outer part of stele. *t.t.*, undifferentiated tracheides. $\times 390$.

Fig. 7. *Gleichenia dicarpa*, petiolar bundle. Transverse section. *c.p.*, cavity-parenchyma; *f.*, phloem-fibres. $\times 145$.

Fig. 8. *Gleichenia dichotoma*, petiole. Diagram of transverse section. $\times 45$.

Fig. 9. *Gleichenia dichotoma*, petiole. Diagram of transverse section of vascular bundle. $\times 45$.

Fig. 10. *Gleichenia dichotoma*, petiole. Transverse section of part of bundle, showing cavity-parenchyma (*c.p.*) and adjacent tissues. $\times 390$.

Fig. 11. *Gleichenia dichotoma*, petiole. End of central strand of sclerenchyma and adjacent tissues in transverse section. $\times 390$.

Fig. 12. *Gleichenia dichotoma*, petiole. Elements of central sclerotic strand in longitudinal section. $\times 260$.

Fig. 13. *Gleichenia dicarpa*, petiole. Two brown-walled fibres separated by an endodermis from the surrounding sclerotic pericycle. $\times 390$.

Fig. 14. *Gleichenia dichotoma*, rhizome. Diagram of transverse section of the stele in the internode. *r.*, a lobe of the xylem preparing for the separation of a root-stele. $\times 45$.

Figs. 15-19. *Gleichenia dichotoma*, rhizome. Diagrams of the stele in a series of sections through the node. *n.i.*, nodal island. The broken lines surrounding the stele show the position of the protophloem, while those in the nodal island represent all the phloem that is present there. All $\times 45$.

Figs. 20–23. *Gleichenia dicarpa*, rhizome. Diagrams of the stele in a series of sections through the node. All $\times 30$.

Fig. 24. *Gleichenia pectinata*, rhizome. Transverse section of stele. The central sclerenchyma has dropped out. $\times$ about 18.

Fig. 25. *Gleichenia pectinata*, rhizome. Diagram of transverse section of stele. $\times 30$.

Fig. 26. *Gleichenia pectinata*, rhizome. Transverse section of stele at the node. Leaf-trace preparing to separate. $\times 15$.

Fig. 27. *Gleichenia pectinata*, rhizome. Transverse section of node. The leaf-trace has become free. $\times$ about 6.

Fig. 28. *Gleichenia pectinata*. Part of a scalariform tracheide from the rhizome. $\times 390$.

Fig. 29. *Gleichenia circinata*, var. *microphylla*, root. Transverse section. Only one of the four phloem-groups is shown. *y.t.*, incompletely differentiated tracheides. $\times 390$.

Fig. 30. *Platyzoma microphyllum*. Diagram of transverse section of rhizome. Phloem not represented. Leaf-traces shown in the right-hand part of the cortex only. $\times 7$.

Fig. 31. *Platyzoma microphyllum*, rhizome. Diagram of transverse section of stele. $\times 30$.

Fig. 32. *Platyzoma microphyllum*, rhizome. Transverse section of about half the stele. $\times 45$.

Fig. 33. *Platyzoma microphyllum*, rhizome. Transverse section, showing leaf-trace separating from stele. *p.r.*, parenchymatous ray. $\times 145$.

Fig. 34. *Platyzoma microphyllum*, rhizome. Transverse section, showing leaf-trace free. $\times 145$.

Fig. 35. *Platyzoma microphyllum*. Diagram of transverse section of petiolar bundle. $\times 90$.

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University Press, Oxford

Boodle, Leonard Alfred. 1901. "Comparative anatomy of the Hymenophyllaceae, Schizaeaceae and Gleicheniaceae III. On the anatomy of the Gleicheniaceae." *Annals of botany* 15, 703–747.

<https://doi.org/10.1093/oxfordjournals.aob.a088846>.

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