On some points in the Anatomy of the Ophioglosseae[1].

BY

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With Plate XX.

THE present paper is the result of an examination of *Ophioglossum vulgatum*, *Botrychium Lunaria*, &c., which was undertaken in the first instance for comparison with 'seedling' plants of *Botrychium virginianum*[2]. It seemed probable that such a comparison might throw some light on the meaning of the monarch roots of *Ophioglossum*, or on some other peculiarity in one or other of the two genera.

Some further investigation of the development of the root-stele in *Ophioglossum vulgatum* also appeared desirable, to determine whether the xylem or phloem showed any trace of diarch structure.

The accounts previously given of the structure, development, &c., of these plants will be referred to later on, after the present observations have been described. Those relating

[1] From the Jodrell Laboratory, Royal Gardens, Kew.

[2] Material of prothalli and seedling-plants of this species was kindly presented to Kew by Mr. E. C. Jeffrey of Toronto University.

to the structure of the root will be taken first. Then indications of secondary thickening in the root and stem of *Ophioglossum* will be described, and the concluding part will contain a summary of previous work on the points dealt with.

1. Structure of the Root.

The roots of *Ophioglossum vulgatum* run horizontally in the soil, so one may conveniently speak of the upper and lower sides of the root. The xylem-mass of the mature stele is roughly semicircular in outline [1] and occupies the lower half of the stele, the upper half being occupied by the phloem and conjunctive parenchyma (see Fig. 9).

The differentiation of the xylem from the procambial strand, as seen near the apex of the root, begins with the formation of a single tracheide on the lower side. It is shown at *px* in Fig. 1, where it is placed rather to one side of the middle point of the arc of cells, which afterwards forms the lower limit of the primary xylem. This is the usual position of the first protoxylem-element, though it is sometimes found at the middle point of this arc.

Comparison with sections further from the apex showed that in this root the second tracheide is developed in the position of the cell marked *a* in Fig. 1, and that the third tracheide is formed between the first and second but nearer to *a*. The second tracheide is sometimes placed as given for this root, but it may occur immediately adjoining the first, or in other positions.

To generalize from several series of sections cut through root-tips, one may say that the differentiation of the primary xylem always begins with the formation of a single tracheide at the periphery of the procambial strand, and then other tracheides are formed, in the same peripheral arc, but in no definite order, until it is complete, when the further develop-

[1] The shape of the xylem mass is variable.

ment takes place in a centripetal direction (i. e. towards the phloem). The xylem is therefore monarch.

For comparison with the transverse sections, a root-tip was prepared in the following way:—Some of the cortex was sliced off on two opposite sides; the remaining part, which contained the stele intact, was then boiled in potash, washed, and mounted in strong glycerine. The stele was thus rendered transparent. It is represented in Fig. 2, where *px* is the first protoxylem element. Two of the tracheides are shown more highly magnified in Fig. 3, where it is seen that the thickenings in these early protoxylem-elements are annular, with an approach to reticulate thickening in places.

The first protoxylem-element is marked *px* at about the same point in Figs. 2 and 3.

To return to the transverse section; the phloem is seen at the upper limit of the procambial strand. It consists of an arc of sieve-tubes (*s.t.* Fig. 1), (which are in contact with the endodermis, *e*), together with a certain amount of the parenchyma lying between the sieve-tubes and the xylem. The walls of the sieve-tubes are, at this stage, already thickened, and stain strongly with haematoxylin; the paucity of contents also serves to distinguish these elements. A few sieve-tubes are still undifferentiated, viz. the inner ones opposite the middle region of the arc. Thus, when differentiation is complete, the row of sieve-tubes is usually one element thick at the ends, and often two elements thick in the middle. When mature the sieve-tubes show the characteristic granules in contact with the walls.

A section at an earlier stage, before the differentiation of any xylem, showed the arc of sieve-tubes easily recognizable, and with one or two sieve-tubes near each end slightly thicker-walled than the rest. This suggests the presence of two protophloems. Their position, determined by comparison with younger stages, is shown at *pp.* in Fig. 1.

It will be seen from Fig. 9 that in the mature root there is a considerable zone of parenchyma between the sieve-tubes (*ph*) and the xylem. The outer part of this parenchyma, about two or three cells thick, bordering on the sieve-tubes, is differentiated and should be regarded as belonging to the phloem. In roots collected in December, this zone of cells differed from the parenchyma below it in having very little or no starch, and in the dense granular proteid contents of many of the cells. The rest of the parenchyma may be called conjunctive[1].

The roots of several other species of *Ophioglossum* are also monarch. Prantl[2] gives monarch roots as a character common to the whole section *Euophioglossum*, which includes twenty-seven species in his monograph[3]. Poirault[4], however, states that this does not hold good, and that *O. ellipticum* is an exception. The two remaining species, in Prantl's classification, are *O. pendulum* and *O. palmatum*. The former he describes as having triarch and tetrarch roots, and the latter diarch. *O. pendulum* has sometimes diarch roots, and an interesting fact (for comparison with *O. vulgatum*, &c.) is that monarch structure may occur as a modification in these roots. This was seen in the basal region of a rootlet[5]. The diarch rootlet is shown in transverse section in Fig. 5, and its monarch base in Fig. 4, which represents the stele of this rootlet where it passes through the cortex of the parent root. A comparison of Figs. 4 and 5 makes it pretty clear that the xylem-group in Fig. 4 represents the right-hand one in Fig. 5, and that the

[1] In Fig. 9 the distinctions between sieve-tubes and parenchyma are not clearly represented. The rather large elements, one to two cells thick, touching the endodermis, and marked *ph*, are sieve-tubes. The next two or three layers, including some rather small cells, are phloem-parenchyma; the rest of the tissue down to the xylem is conjunctive parenchyma (*p*).

[2] Prantl, Beiträge zur Systematik der Ophioglosseen, in Jahrb. d. k. bot. Gartens zu Berlin, Bd. iii, p. 297.

[3] Many of these rank as synonyms in Hooker and Baker's Synopsis Filicum, where only six species are given under the section *Euophioglossum*.

[4] Poirault, Sur l'*Ophioglossum vulgatum*, Journ. de Botanique, t. vi, p. 71.

[5] This was clearly a true rootlet, not a case of dichotomy of the root as described by Rostowzew and Poirault for *O. vulgatum*. It is curious that dichotomous and monopodial branching should occur in roots of the same genus. Possibly the dichotomy may be restricted to the monarch roots; cf. Van Tieghem (Symétrie, &c., p. 108). In speaking of the root of *O. vulgatum* he says: 'Si elle vient à se diviser, nous savons à l'avance que ce sera par dichotomie.'

left-hand group of the diarch plate of Fig. 5 is absent in the part shown in Fig. 4, which is consequently monarch [1].

Several series of sections were cut through the bases of diarch rootlets in *Botrychium Lunaria*. They also have a monarch region, as seen in Fig. 6. Here the phloem is interrupted opposite the protoxylem (*px*), but continuous at the other side of the stele. A little further out in the same rootlet the structure becomes diarch (Fig. 7) [2]. The two protoxylems are marked *px*, and the phloem is interrupted opposite both [3]. As arranged in the figures, the lower xylem-mass of Fig. 7 is the only one present in Fig. 6, while the upper one in Fig. 7 has just appeared, and is only represented by two tracheides. A comparison of these two sections is much more conclusive than the example of *Ophioglossum pendulum* figured.

It is interesting to notice that these sections (Figs. 6 and 7) closely resemble, in the distribution of their xylem, two roots of *Ophioglossum Bergianum* figured by Bower [4], and described by him as monarch and diarch respectively.

The above facts lead to the conclusion that the rootlet-base has in these cases probably become monarch by reduction from diarch structure; one xylem-group being abortive and the two phloems joined on the other side where the missing xylem-group would be. The monarch structure of the roots of *Ophioglossum vulgatum* may admit of a similar explanation, the reduction extending throughout the roots.

The possibility of these monarch structures being primitive must be acknowledged, but what evidence there is points rather to reduction. Thus, though the bases of diarch

[1] This cannot be said with absolute certainty until the development in this region has been observed. Unfortunately the material obtainable, both in this species and in *Botrychium Lunaria*, did not include any rootlet at the right stage for determining the matter developmentally.

[2] Figs. 6 and 7 both represent sections of the *free* rootlet near its base.

[3] A few of the sieve-tubes in these two sections are difficult to determine, and a little doubtful, but the sieve-tubes are at any rate approximately as shown.

[4] Bower, Studies in the Morphology of Spore-producing Members: II, Ophioglossaceae, Figs. 114 and 113.

rootlets in *Botrychium Lunaria* are monarch, the bases of the *roots* bearing them are diarch; and the base of the root is more likely to show primitive structure than that of the rootlet. For the roots of *Ophioglossum vulgatum*, the presence of two protophloems favours the hypothesis of reduction from diarch structure by suppression of one of the xylem-groups.

Van Tieghem and Bower have both studied the passage of the root-stele through the cortex of the stem. The former described the stele as twisting through 90° on its way out [1], while the latter was unable to observe this rotation [2].

Series of sections were made transverse to the root-stele on its way through the cortex of the stem, and these showed a distinct change in orientation. Starting from the outside, on entering the cortex the xylem is directed downwards and the phloem upwards; but in passing inwards a twisting takes place which amounts, at any rate in some cases, to nearly 90°, so that the xylem and phloem become lateral to an approximately vertical plane before fusing with the stem-bundle. This is illustrated in Fig. 8, where the sieve-tube on the right is about parallel with the axis of the stem, and thus shows the orientation of the xylem of the root. Perhaps the root-stele may sometimes pass in without any twisting, as described by Bower, but the twisting appeared to be the rule in the plants examined.

Holle [3], from sections and from an examination of the vascular skeleton, comes to the conclusion that each leaf-trace bundle, after passing down the stem for a certain distance and fusing with commissural bundles, bends out again as a root-bundle, there being one root to each leaf.

This would give a simple explanation of the monarch structure of the root. Its vascular bundle would then be a continuation of the leaf-trace bundle, which, after passing down the stem, bends outwards without any twisting, and with no change in structure, the monarch bundle being

[1] Van Tieghem, Traité, p. 1394.

[2] Bower, l. c., p. 73.

[3] Holle, Bot. Zeit., 1875, p. 251.

practically identical with a collateral bundle. This relation between leaf-trace and root is not, however, without exception[1], and the structure seen in several sections has much more the appearance of a root-bundle abutting on a stem-bundle at or near the part forming the downward prolongation of the leaf-trace. It is certainly difficult to follow the tracheides of a leaf-trace down as far as the insertion of the corresponding root; but in one series of transverse sections the root-stele (as also happened in several other cases) was attached quite to the lateral edge of a stem-bundle, and here appeared to be connected with commissural elements rather than with leaf-trace tracheides.

On Holle's interpretation, the twisting of the bundle, described above, would also seem purposeless, and would amount to this:—the leaf-trace, instead of simply bending outwards without any twisting, when it would obtain the correct orientation for the root, bends sharply through about 90°, and then bends back again through the same angle in passing through the cortex.

Series of sections were also cut through the root-stele in the cortex of the stem of *Botrychium Lunaria*. When the orientation could be clearly made out, the xylem-plate, in the case of diarch roots, appeared to be horizontal[2] just before joining the stem-bundles; that is, there was a protoxylem-group on each side of the vertical plane. If the protoxylem on one side of the vertical plane were abortive, and the two phloem-masses were to fuse on the other side (a kind of

[1] Bower, l. c., p. 67. 'This regularity, however, does not hold for the lowest leaf of a shoot, nor is the regularity always maintained.' Holle (l. c., p. 314) also mentions that the first two leaves have no roots belonging to them. Rostowzew (Recherches sur l'*Ophioglossum vulgatum*, in Oversigt Videnskab. Selskabs, 1891 (No. 2, p. 72), states that very rarely there are two roots to a leaf; and Prantl (*Helminthostachys zeylanica*, u. ihre Beziehungen zu *Ophioglossum* u. *Botrychium*, Ber. deutsch. bot. Gesellschaft, i, 1883, p. 156) also calls in question the relation between leaves and roots as described by Holle.

[2] This agrees with Holle's observations on this and two other species of the genus, l. c., p. 268; and with those of Van Tieghem on *Botrychium Lunaria* (Symétrie de structure des plantes; Annales des Sciences Nat., Bot., v. sér., t. xiii, p. 105).

reduction, which takes place in rootlet-bases of *Botrychium Lunaria*), one would obtain the structure of the monarch root of *Ophioglossum vulgatum* and with the orientation that it has at its junction with the stem-bundle.

The first root of seedlings of *Botrychium virginianum* is of typical diarch or triarch structure[1], and this point may be regarded as slight evidence that the monarch structure in roots of *Ophioglossum* and rootlet-bases of *Botrychium* is a case of reduction. If monarch structure were primitive for the group, and retained in some species, one would expect to find it in the first root of the seedling in others.

If the monarch structure in *Ophioglossum vulgatum* is to be regarded as reduced from the diarch type, there should be some physiological peculiarity with which this reduction is connected.

The horizontal position of the roots is no doubt connected with the production of adventitious buds, the roots keeping at a convenient distance below the surface of the soil. Monarch structure, of the type and orientation found in *Ophioglossum vulgatum*, may have arisen from the diarch form as a means of favouring the development of numerous adventitious buds. Thus, to suppose a phylogenetic series, the *diarch* root would probably produce an adventitious bud about opposite one of the protoxylems. If the two phloem-groups now become approximated at this side of the stele (which we may call the upper), and abortive towards the other side, the development of the bud will be favoured, because most of the phloem will convey nourishment to the adventitious bud, and there will be only a little phloem towards the lower side of the stele to carry nourishment *direct* to the root-apex. Further modification in the same direction would result in the fusion of the two phloems on the upper side of the stele, where the adventitious bud is. This would lead to the abortion of the protoxylem on that side,

[1] Jeffrey, The Gametophyte of *Botrychium virginianum*; Transactions of the Canadian Institute, vol. v, 1896–7, p. 283. Specimens obtained from him showed diarch structure in the first root.

as its absorption from the cortex would be interfered with by the phloem outside it. Further, this would be compensated for by the spreading out of the other protoxylem into a long, peripheral arc, such as is found in this plant.

Adventitious buds occur on roots of *Ophioglossum pendulum* and other species. Prantl[1] has observed them in *O. lusitanicum*, *O. coriaceum*, *O. capense*, *O. Luersseni*, *O. ellipticum*, *O. japonicum*, *O. pedunculosum*, *O. reticulatum*. They may possibly occur in most of the species, but Welwitsch[2] notifies their absence in *O. fibrosum*.

The theory suggested above is purely tentative, owing to want of material and of sufficient data. It may be stated thus:—The monarch structure in *Ophioglossum* is an adaptation for favouring the growth of numerous adventitious buds on the roots, in the case of comparatively small and slow-growing species, where the supply of nourishment from the parent plant is limited. Owing to the monarch structure, the assimilated food has to reach the root-tip viâ the adventitious bud, so that the latter may be able to divert all that is necessary for its growth. To test this theory it would be necessary to observe whether many or few adventitious buds were produced in proportion to the size of the assimilating surface of the plant; this is not possible at present, but one or two cases may be mentioned.

O. pendulum produces adventitious buds, but has a large assimilating surface, more than ten times that of any species in the section *Euophioglossum*, judging from data of leaf-measurements given by Prantl. There is thus presumably plenty of material for producing buds in this species without putting any restriction on the further growth of the roots which form them. And this plant has diarch, triarch, and tetrarch roots.

O. palmatum is also a large-leaved species, having diarch roots.

O. fibrosum would be an exception, as, assuming the observa-

[1] Prantl, l. c., p. 308.

[2] Welwitsch, quoted by Prantl, l. c., p. 308.

tions of Welwitsch and Prantl[1] to be correct, it produces no adventitious buds but has monarch roots. Such cases might arise in the event of a species giving up the production of buds but retaining monarch structure.

O. ellipticum is another exception as it produces adventitious buds, but has not monarch roots, according to Poirault. However, one cannot really test the probability of the theory without knowing the number of buds produced in proportion to leaf-area, &c.

O. Bergianum has a small leaf-area, and produces adventitious buds[2], and has both diarch and monarch roots[3]. It would be interesting to know whether the *monarch* roots are those that produce the buds.

2. Secondary Thickening.

In sections of mature roots of *Ophioglossum vulgatum* one sometimes finds developing tracheides at the periphery of the xylem-mass. By staining transverse and longitudinal sections with methyl-green and eosin this is clearly shown. If the double staining is carried out so as to give the right balance to the two colours, the mature xylem is bright blue (or bluish green) and the phloem and parenchyma are pink; while any half-lignified tracheides present take up both stains and become purple, so that they are made very conspicuous[4].

Fig. 9 is a transverse section of a root in which are five developing tracheides (*t*). Fig. 10 is more highly magnified, and shows one developing tracheide (*t*) with its protoplasmic contents. Fig. 11 is a longitudinal section showing part of the xylem with one developing tracheide on the left, containing protoplasm and nucleus (*n*). In the preparation from

[1] Prantl, l. c.

[2] Poirault, Journal de Botanique, vi, p. 73.

[3] Bower, l. c.

[4] The stain used was watery solution of methyl-green, followed by alcoholic solution of eosin. It unfortunately fades.

which the drawing was made, this tracheide was well differentiated from the others by the staining of its walls.

These developing tracheides must, it seems, be regarded as secondary, as the addition of such elements takes place in roots several years old. Thus the part of the root shown in Fig. 9 was cut close to the attachment of an adventitious plant, on the side towards the parent plant; and, judging from the number of young leaves on the adventitious plant, this part of the root must have been four or five years old. The secondary tracheides are only formed in small numbers; and, as they are added one here and one there, there is no definite cambial layer, though a newly divided cell may occasionally be seen with its thin division-wall, as in a cell bordering on the xylem in Fig. 10.

The greatest addition of secondary elements was seen in the region of the root near the base of an adventitious plant. Now and then the outermost tracheides show radial arrangement; in many cases no doubt these elements are secondary, but their arrangement does not give a safe criterion, as occasionally the xylem may have a roughly radial disposition from the first.

The root-material examined was collected in June and December. As one would expect, no good cases of developing tracheides were found in the December material.

The stem also was examined for secondary thickening, with the result that it showed an exactly similar addition of tracheides, though this was more difficult to observe on account of the oblique course of the bundles. The tracheides here appeared to be added on the outer side of the wood only, while in the root they may be added on all sides. Fig. 13 shows part of a stem-bundle in which there are five developing tracheides on the outer side of the xylem. This bundle must have been differentiated four or five years; and developing tracheides were seen in one or two still older bundles.

Sections of the young stem show that the leaf-trace bundles arise as distinct procambial strands, and that the first-formed xylem-elements are at the inner limit of the strands; that is, the bundles are endarch. This is an important character, because, as Professor Farmer informs me, the vascular ring in the rhizome of *Helminthostachys* is distinctly mesarch. An examination of some material of the mature rhizome of *Helminthostachys* [1] led me to the same conclusion.

There is a considerable amount of secondary thickening at the bases of many of the roots of *Botrychium Lunaria*, where they are immersed in the cortex of the stem. This sometimes makes it impossible to tell the position or number of protoxylem-groups, as one sees in the case of Fig. 14. For this reason some of the series of sections cut to determine the orientation of the root-stele at its junction with the stem-bundle were useless.

The well-known secondary thickening in the stem of *Botrychium Lunaria* makes it not surprising to find a trace of it in the stem of *Ophioglossum vulgatum*, but secondary thickening was hitherto unknown in the root of any recent Pteridophyte.

In the petioles of unfolded leaves of *Ophioglossum vulgatum* the vascular bundles sometimes show developing tracheides (as in Fig. 12), but it seems uncertain whether these should be regarded as secondary or not.

Conclusion.

Some of the works on *Ophioglossum* have been referred to above, but it remains to quote the results of some authors more in order and detail.

The main facts as to the structure and development of the root of *Ophioglossum vulgatum* were described and figured by Stenzel [2] as early as 1858. His Fig. 4 (Tab. 58) is a very good representation of the early stage of the stele, in which

[1] Kindly sent by Mr. A. C. Seward, F.R.S.

[2] Stenzel, Unters. über Bau u. Wachsthum der Farne, I. Stamm u. Wurzel v. Ophioglossum vulgatum, Nov. Act. Acad. Leopold.-Carolin. Nat. Cur., xxvi (1858).

the first two tracheides have been differentiated, and in this case they are close together (one cell apart). Later stages are also given; the production of the adventitious buds is described, and the conclusion arrived at that they are formed on true roots, not stolons.

Russow[1] gives a short description and a diagram of the root. He describes the root as monarch, the protophloem as being in contact with the endodermis, and as appearing some time before the protoxylem, and describes the formation of a peripheral arc of xylem, followed by centripetal development of the remainder; but his description and figure would give the impression that the first-formed protoxylem-element was practically at one end of the arc, and that the development proceeded regularly towards the other end of the arc. He also, curiously enough, states that the xylem occupies the upper half of the stele, and the phloem the lower.

Van Tieghem in his earlier work[2] states that the first vessels are formed at a single point in the circumference (thus making the xylem monarch), and describes the root-bundle as being inserted on the stem with its xylem downwards and phloem upwards. Thus he had not at that time discovered the rotation afterwards described by him. He goes on to show that the root of *Ophioglossum* corresponds in structure to half the root of *Botrychium*; and says that, to refer the structure in *Ophioglossum* to the diarch type of *Botrychium*, it is only necessary to suppose that a dichotomy (producing monarch branches such as he here claims for roots of *Botrychium*[3]) takes place in the cortex of the stem, and that the upper branch is constantly abortive. This would mean that he interpreted the xylem as truly monarch, a view which he abandoned afterwards; for in the Traité de Botanique[4] the xylem is described as diarch. It is curious that the

[1] Russow, Vergl. Unters., in Mém. de l'Acad. Imp. des Sciences de St.-Pétersbourg, vii. sér., t. xix, No. 1, 1872, p. 122, and Taf. xi, Fig. 31.

[2] Van Tieghem, Symétrie de structure des plantes, Ann. des Sci. Nat., Bot., v. sér., t. xiii, 1870–71, p. 107.

[3] l. c., p. 109.

[4] Second edition, 1891, p. 1394.

orientation as described by him comes out wrong, both on his earlier and later interpretations, when compared with *Botrychium*[1].

Holle's paper has been referred to above for the relation of roots to leaves. According to his account the lignification of the leaf-trace proceeds acropetally, and when it reaches the part opposite the young root, it then proceeds outwards into the root and upwards in the leaf-trace. This simultaneous lignification in the adjacent organs is important physiologically for the purpose of conduction to the young leaf; but, as mentioned above, the junction has not always the appearance of direct continuity. Holle[2] also states that, if one disregards the fusion of the leaf-traces of the lowest two leaves into the solid stele at the base of the adventitious plant, the trace of the first leaf is continuous with the bundle of the posterior part of the parent-root, while the trace of the second leaf is continuous with the bundle of the anterior part of the parent-root. This is probably roughly correct.

Van Tieghem's theory of the monarch root of *Ophioglossum vulgatum*, as given in his Traité de Botanique[3], has been quoted above, and is that it represents a diarch root with one phloem-group abortive.

Rostowzew[4] states that the stem of *Ophioglossum vulgatum* possesses secondary thickening of very short duration, but gives no details, reserving them for a more complete memoir. The later paper is written in Russian[5], and no detailed abstract appears to have been published, but there is an explanation of the figures in German. None of the illustrations, however, refer to secondary thickening. There is a figure[6] of a transverse section of a young root-stele showing

[1] Van Tieghem, Symétrie, &c., p. 105.

[2] l. c., p. 314.

[3] Van Tieghem, Traité, p. 1394.

[4] Rostowzew, l. c. (Oversigt), p. 72.

[5] Rostowzew, Beiträge zur Kenntniss der Ophioglosseen; 1. l'*Ophioglossum vulgatum*; Moscow, 1892.

[6] Plate II, Fig. 14.

the first two protoxylem-elements, which in this case are a considerable distance apart.

In his first paper he describes the stele of the root as being always monarch, though he states that he has sometimes seen protoxylem at two opposite points: but he adds, 'Thus the root in this case appears to be diarch, but it becomes afterwards monarch, because the lower part of the phloem does not develop.' Thus he apparently regards the xylem as representing a diarch plate, and one of the two phloem-groups as absent. The dichotomy of the root is described[1] by him, and the stele of the root is stated to become concentric before the branching, several phloem-elements appearing on the lower side of the xylem, and the two steles after the dichotomy being at first concentric.

The above description is not very definite as to the amount and distribution of the phloem, and is supplemented by the observations of Poirault[2], who says that the stele before division possesses several sieve-tubes on the lower side[3], but that these are scattered and not grouped as in the normal phloem-mass[4]. The other details of the dichotomy need not be referred to here, but this occurrence of scattered sieve-tubes on the lower side of the xylem is quoted because the same thing sometimes occurs in the mother-root near the base of the adventitious plant, on both sides of the latter. It may be explained as a local development of the part of the phloem which is normally abortive (viz. the lower parts of the two phloem-masses).

Poirault[5] describes another anomaly as occurring in roots of *Ophioglossum vulgatum*, namely, the occurrence of a second phloem-group, *similar* to the normal one, on the lower side of the xylem, these two phloem-groups being connected by a series of sieve-tubes round the ends of the xylem-mass.

[1] l. c. (earlier paper), p. 75.

[2] Poirault, Journal de Botanique, t. vi, 1892, p. 70.

[3] He writes 'upper side' by mistake.

[4] This agrees with a figure in Rostowzew's Russian memoir (Fig. 10) representing the young stele of a dichotomised root.

[5] Poirault, l. c., p. 70, and Comptes-rendus, 1891, p. 967.

This anomaly was traced by him for a distance of 30 cm. with no sign of dichotomy. This is referred to again in a later paper[1], and the conclusion arrived at that the anomaly is due to the root preparing for division, where the processes of the dichotomy proceed slowly, the first stage being very persistent, or that it is a case of abortive dichotomy.

The view given in the earlier paper[2], that it was a case of return to diarch structure, is given up, as it had been suggested by a supposed case of another species in which monarch roots (of the type of *O. vulgatum*) as well as diarch and triarch roots occurred. This was found to be due to the roots of two species being mixed in the material used.

In this case of *Ophioglossum vulgatum* with two phloem-masses, no definite conclusion can be drawn without a knowledge of the development of the xylem-mass.

Poirault states that after dichotomy the roots have only one phloem-group, and are not concentric, as described by Rostowzew.

The observations in Bower's paper[3] concerning the monarch structure in *Ophioglossum* have been quoted above. His conclusion, that the xylem is monarch, has been confirmed by the facts described in the present paper, but the latter do not tend to support the view of the primitive character of monarchy in *Ophioglossum* to which he inclines.

I am indebted for material of *Botrychium Lunaria* to Mr. J. Lloyd Williams of University College, Bangor. The rest of the material, with the exception of the young plants of *Botrychium virginianum* sent by Mr. Jeffrey, was obtained from the Royal Gardens, Kew.

I wish to express my thanks and obligation to Dr. D. H. Scott, F.R.S., under whose direction this research has been made, for his kind advice and criticism throughout the work.

[1] Poirault, Recherches sur les Cryptogames vasculaires, Ann. des Sci. Nat., vii. sér., t. 18, 1893, p. 144.

[2] Journal de Botanique, t. vi.

[3] Bower, l. c.

Summary.

1. The root of *Ophioglossum vulgatum* is monarch as regards its xylem, but the phloem has an indication of the presence of two protophloems.

2. Monarch structure also occurs at the base of diarch rootlets in *Ophioglossum pendulum* and *Botrychium Lunaria.*

3. The root-stele of *Ophioglossum vulgatum* has probably become monarch by reduction from diarch structure, viz. by the abortion of one of the *xylem*-groups and the fusion of the two phloem-groups.

4. A small amount of secondary thickening takes place in the root and stem of *Ophioglossum vulgatum*, xylem-elements only being added.

5. Secondary thickening also occurs in the root-bases of *Botrychium Lunaria.*

EXPLANATION OF FIGURES IN PLATE XX.

Illustrating Mr. Boodle's paper on the Ophioglosseae.

Abbreviations :—*e.*, endodermis ; *p.*, parenchyma ; *ph.*, phloem ; *s. t.*, sieve-tubes ; *px.*, protoxylem ; *t.*, developing tracheides.

Fig. 1. *Ophioglossum vulgatum.* Transverse section of young stele of root (near apex). Most of the sieve-tubes are differentiated, but only one tracheide (*px*). *a* is the position in which the second tracheide appeared in this root ; *pp*, position of the two protophloems. × 270.

Fig. 2. *Ophioglossum vulgatum.* Young stele of root in a transparent preparation ; slightly diagrammatic. The tracheides are of course not all in one plane, but are included in the drawing as if they were. × about 150.

Fig. 3. *Ophioglossum vulgatum.* Parts of first two elements of the protoxylem more highly magnified to show the thickenings more accurately. The first tracheide is marked *px* at about the same point as in Fig. 2. × 375.

Fig. 4. *Ophioglossum pendulum.* Transverse section of stele of rootlet within the cortex of the parent-root, showing monarch structure. × 135.

Fig. 5. *Ophioglossum pendulum.* Stele of same rootlet when free, showing diarch structure. × 130.

Fig. 6. *Botrychium Lunaria.* Base of rootlet showing monarch structure. × 275.

Fig. 7. *Botrychium Lunaria.* Same rootlet becoming diarch. × 275.

Fig. 8. *Ophioglossum vulgatum.* Stele of root in cortex of stem, showing change of orientation. × 88.

Fig. 9. *Ophioglossum vulgatum.* Transverse section of root, showing five partly lignified developing tracheides (*t*). × 130.

Fig. 10. *Ophioglossum vulgatum.* Part of transverse section of root more highly magnified, showing one developing tracheide with its protoplasmic contents. × 365.

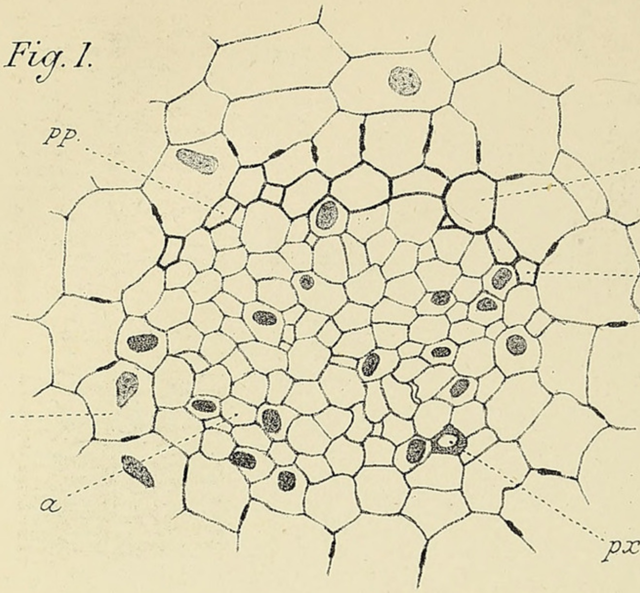
Fig. 11. *Ophioglossum vulgatum.* Longitudinal section of root, with nucleus (*n*) and protoplasm in the developing tracheide on the left. × 375.

Fig. 12. *Ophioglossum vulgatum.* Transverse section of one bundle of petiole. × 130.

Fig. 13. *Ophioglossum vulgatum.* Part of one vascular bundle of the stem cut transversely, with five developing tracheides. × 130.

Fig. 14. *Botrychium Lunaria.* Transverse section of stele of root-base in the cortex of the stem, showing secondary thickening. × 195.

Fig. 1.



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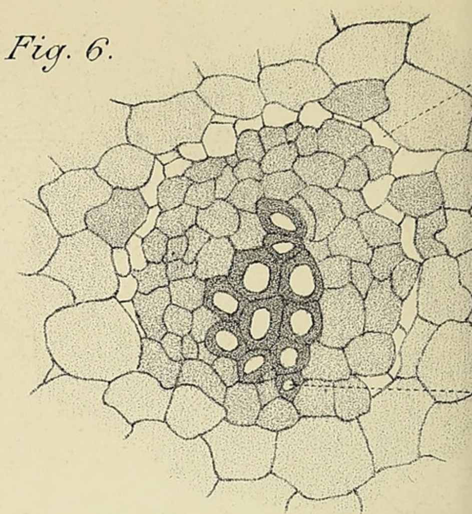

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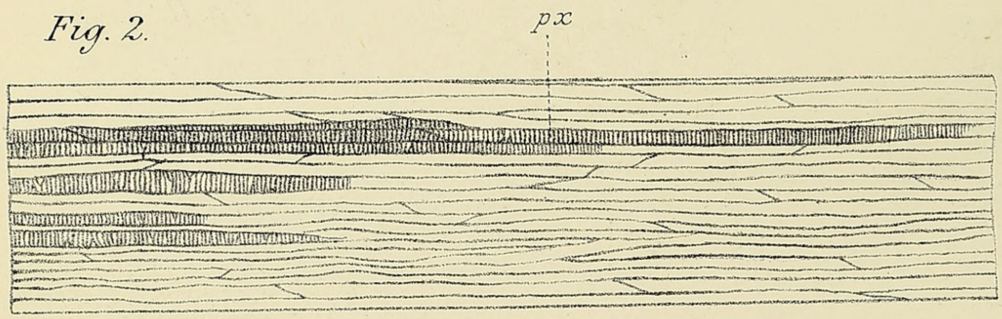

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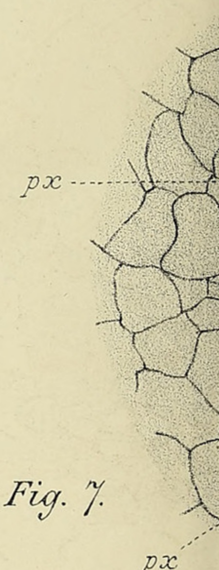

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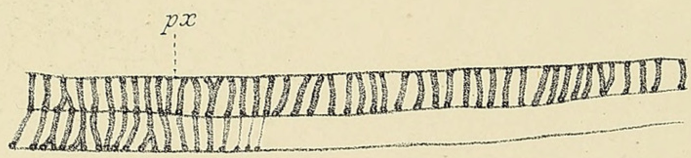
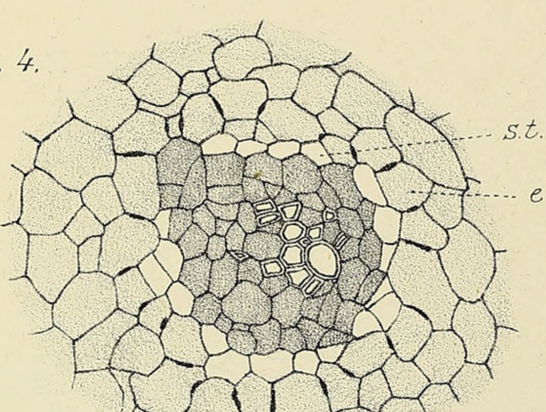


Fig. 8.

Fig. 4.



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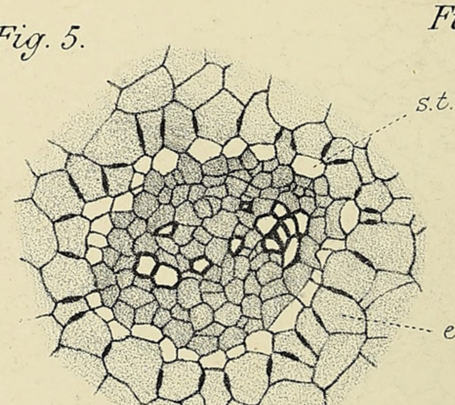

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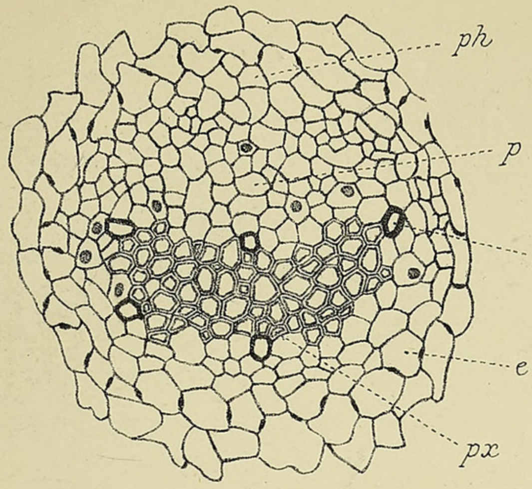

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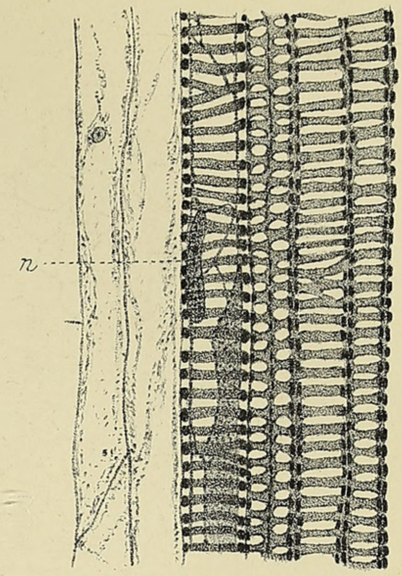

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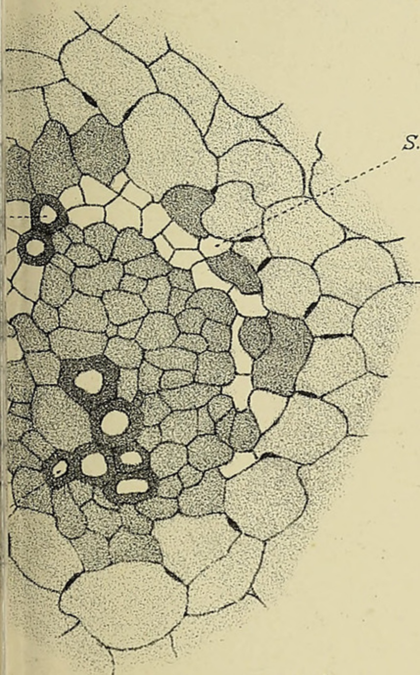

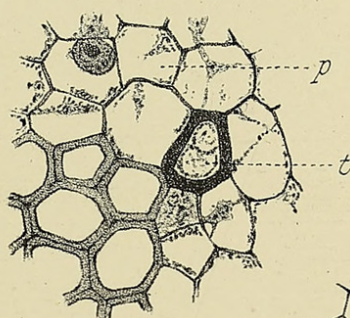

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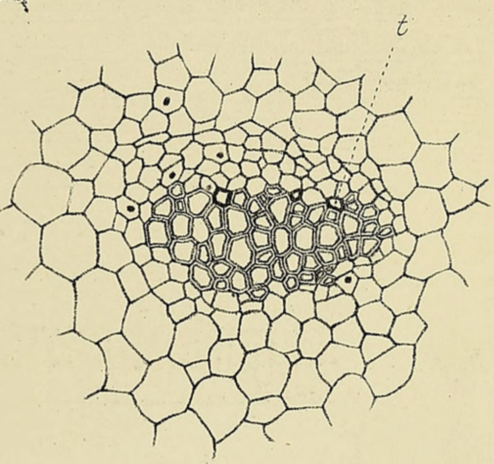

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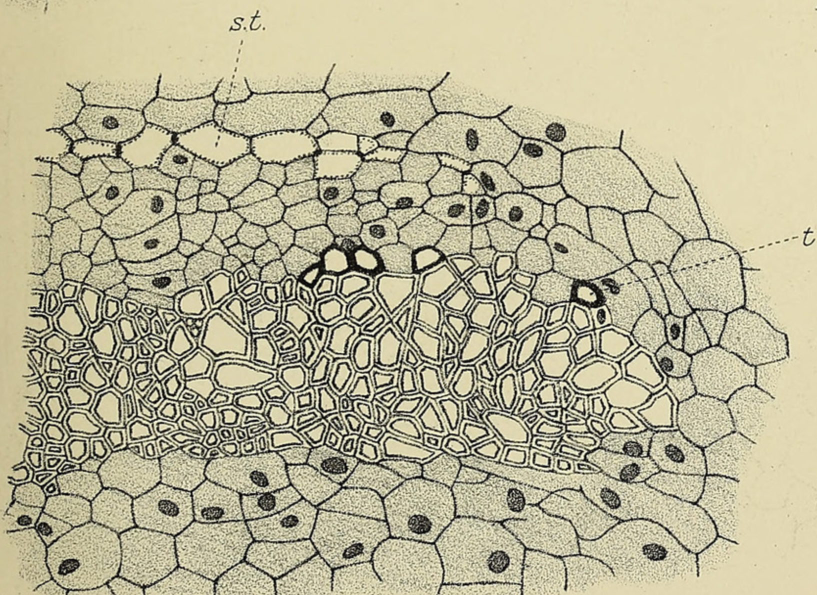

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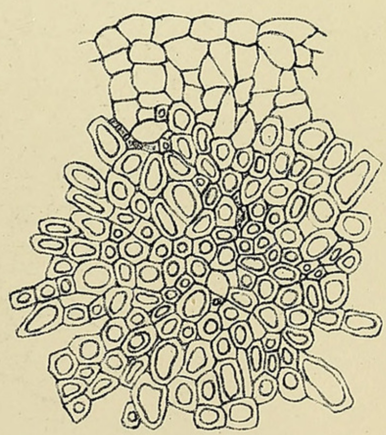

Fig. 14.

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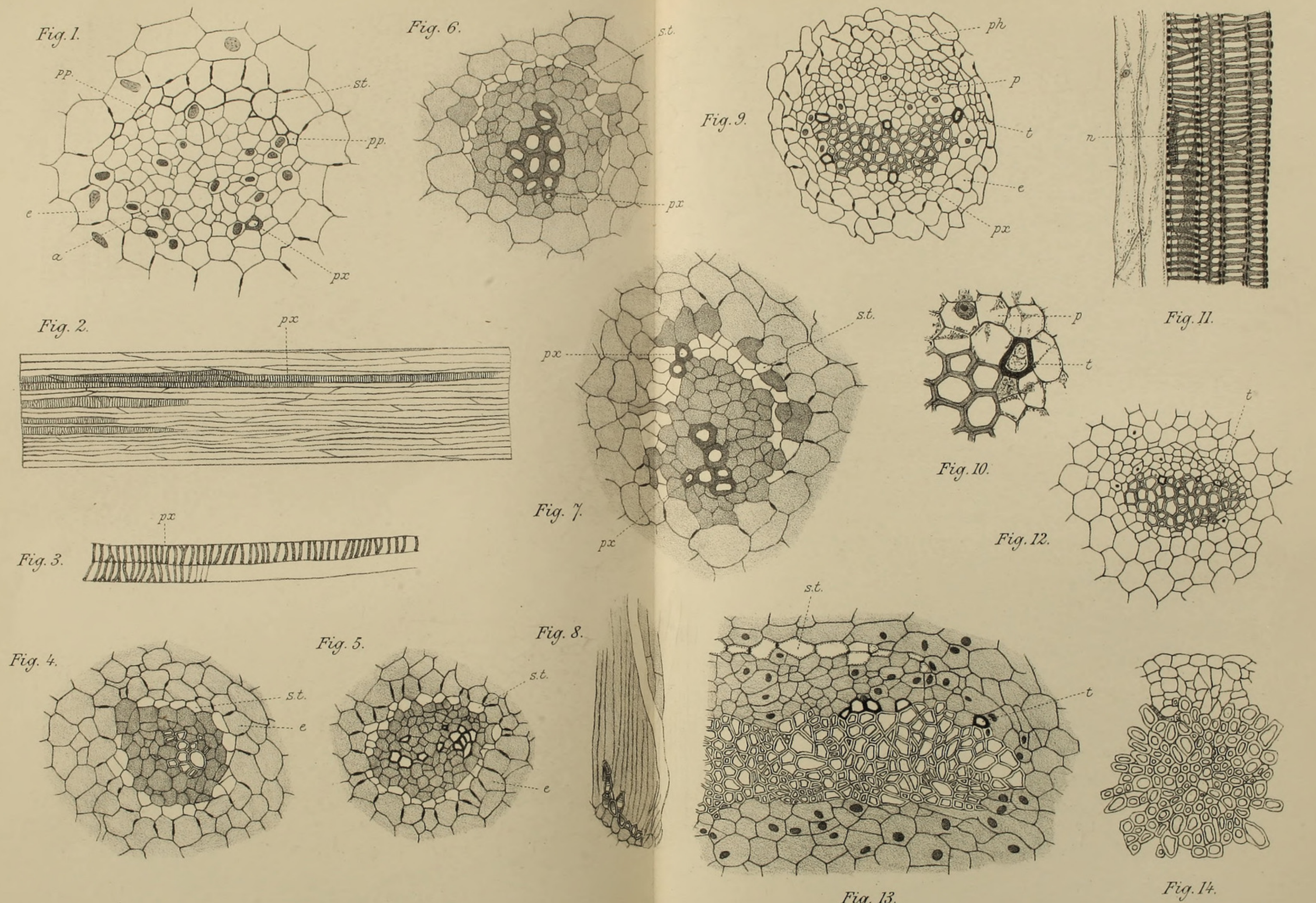

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