The Morphology of *Phylloglossum Drummondii*.

BY

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With eight Figures in the Text.

PHYLLOGLOSSUM was first described in 1843 by Kunze, in the *Botanische Zeitung*; its morphology was investigated in great detail by Bertrand in 1885 (5). Other contributors to our knowledge of the plant will be referred to as we proceed; they are, notably, Bower (1), Mettenius (9), Treub (12), and Thomas (13), who has given a detailed description of the gametophyte.

The observations recorded in the present paper were made on serial microtomed sections of two plants which, in their external features, showed no important points of dissimilarity; on the other hand, they were not precisely the same as regards their anatomy: the differences will be referred to in the description which follows.

EXTERNAL MORPHOLOGY.

A small plant (Fig. 1), about 1 to 1½ in. high; on the under side of the thickened lower part two tubers are borne, each upon what appears to be a relatively long stalk. Immediately above the insertion of these stalks, borne laterally to the thickened part, are the roots, which are horizontal, or almost so.

This thickened part, which is the stem, is much compressed vertically. On its upper surface it bears five or six subcentric fleshy leaves, each

FIG. 1. General appearance. *y.t.*, young tuber; *c.t.*, current season's tuber; *st.*, stem region; *r, r*, roots; *l*, leaves; *s*, strobilus; *p*, pedicel of strobilus.

tapering to a point. From the midst of the leaves arises the long peduncle, bearing terminally a small ovoid strobilus with closely overlapping bracts, spirally arranged.

INTERNAL ANATOMY.

The internal anatomy of *Phylloglossum* has been exhaustively described by Bertrand (5); in the present paper only the broader features will be considered.

The succeeding description will follow the microtomed sections from below upwards; the first structure which presents itself is:—

1. *The Young Tuber.* At the extreme tip this consists solely of an aggregate of parenchymatous cells, with well-marked nuclei; but at a very short distance above, this begins to be clearly differentiated from the peripheral layer, which is of regular, more or less radially elongated, empty cells. This peripheral layer persists throughout the entire length of the tuber; followed upwards, it presents a more or less strong thickening of the exterior cell-walls. Sections of the older tuber, at a higher level, also reveal a well-marked thickening on the radial walls of the peripheral cells.

FIG. 2. Diagram of transverse section of young tuber; *pe*, peripheral layer; *pa*, storage parenchyma; *me*, merismatic tissue.

Ascending, the sections show a gradual aggregation of the nucleated cells towards the centre, these being surrounded by a broad zone of homogeneous parenchyma, in which intercellular spaces are noticeably absent. The latter zone is doubtless destined to form the food-storage tissue, the nucleated cells being probably merismatic (Fig. 2).

Proceeding upwards, the central merismatic zone becomes smaller and smaller, ultimately breaking loose from the surrounding parenchymatous zone, and coming to lie in a cavity.

In the meantime the radial walls of the peripheral cells have acquired a well-pronounced thickening, particularly in the centre, so that they present a resemblance to the appearance often associated with an endodermis.

The next twelve sections in ascending order show simply a central cavity—indicating the existence of a rather long central channel (Fig. 4) in the 'stalk' of the tuber. This is borne out by the longitudinal sections, as shown in the diagram (Fig. 3).

One or two of the nucleated cells persist for a time around the edge of the central cavity as the transverse sections are followed upwards, so that the meristem tapers to a fine point (Figs. 3, 4); the segmentation

observed in the longitudinal and transverse sections does not, however, justify the conclusion that this meristem focuses upon a single apical cell.

In the meantime the sections have passed through the older tuber (Fig. 4). This latter, it will be seen, is really the tuber of the current season, the younger one, described above, being the tuber for the following season.

FIG. 3. Diagram of median longitudinal section. *y.t.s.*, strand of young tuber; *s.s.*, stem-stele; *r.t.*, *l.t.*, root- and leaf-trace; other letters as in Fig. 1. The numbers 2, 4, 5, 6, 7 indicate the levels at which the transverse sections shown in Figs. 2, 4, 5, 6, 7, respectively, were taken. The shaded portion denotes the meristematic tissue of the growing tuber. Xylem in thick black lines.

FIG. 4. Transverse section of young tuber, showing central cavity *ca*, with two meristematic cells at its edge. The older tuber (*c.t.*) also appears in section.

The older tuber presents a highly lacunar appearance below. This would be significant, but it is doubtful whether this is not due to indifferent preservation; there is no indication of lacunar structure in the parenchymatous tissue further up in the tuber—the aeration of the stem and tuber being provided, apparently, chiefly by the loose packing of the parenchyma cells.

Returning to the younger tuber, a few wood-elements appear, shortly above the extremity of the 'channel', in the centre of the sections (see Fig. 3). At no level do these exceed about a dozen in number; and in

many of the sections they are seen to be undoubtedly mesarch. The wood-elements are thus confined in this specimen to the stalk of the tuber; the body is entirely destitute of vascular tissue.

One or two notable differences were observed, however, in the second specimen examined: first, the bundle of the young tuber divided into two strands, which united further up, before joining the vascular system of the stem; second, a ring, more or less continuous, of somewhat degraded xylem was observed surrounding the central merismatic tissue of the young tuber. This ring, however, disappears before the stalk-region of the tuber is reached.

In the second specimen, moreover, three tubers appeared in section; one

FIG. 5. Transverse section, lower part of stem. Parenchyma left blank, xylem black. The young tuber strand, *y.t.s.*, has joined the main stele (*s.s.*). Five leaf-traces appear, two with included protoxylem cavities (*pxc*).

corresponding to the younger tuber, and two older ones—and this corroborates Thomas's statement in the *Proc. Roy. Soc.*, xix, p. 285.

These differences in the two specimens will be referred to later.

The two sections—old and young tubers—are now seen to approximate as we follow the sections successively upwards; the older begins to be cut somewhat obliquely, and two root-traces appear in longitudinal section. The latter evidently bend up rapidly at this stage (Fig. 3), as they are seen, three

in number, in clear transverse section shortly after the two tuber sections have merged. The roots are distinctly monarch, and resemble Stigmarian rootlets closely; a well-marked endodermis is present, and the ground tissue presents a highly lacunar appearance.

Further up, these root-traces are found somewhat nearer the centre of the section, having become connected laterally by other wood-elements running, at first, almost horizontally; at this point we are entering the lower part of the compressed stem.

2. *The Stem.* Proceeding as before with the sections in ascending order, leaf-traces begin to be 'pinched off' the stele thus formed, and these leaf-traces occupy the same relative positions previously taken by the root-traces. Leaf- and root-traces are thus continuous, a fact pointed out by Bower twenty-five years ago. The mode of exit of these leaf-traces is that typical of the *Lycopsidea*, there being no disturbance of the stele. The

leaves of *Phylloglossum* are thus anatomically microphyllous, so to speak, and may be compared usefully with *Isoetes* in this regard—the leaves in both being large as compared with the stem, although detailed examination reveals them, in both cases, to be characteristically microphyllous in their behaviour to the stele.

At a level where the three leaf-traces, corresponding to the three root-traces first observed, have progressed outwards to about midway in the cortex, the transverse section presents the appearance shown in Fig. 5. The leaf-traces are mesarch, the protoxylem in many cases being represented by cavities (see *postea*).

FIG. 6. Showing the U-shaped stele, with protoxylem-cavities. The strand of the young tuber has broken away from the stele, and is dying out. Five leaves appear, each with a single, small central vascular strand. There are no leaf-traces in this region: no more foliage leaves emerge.

The central stele is here similar to that seen in many of the Lycopodiales. The xylem-strand of the young tuber stalk has joined this main stele, which is a more or less continuous band of xylem enclosing a parenchymatous 'pith', and is roughly pentagonal. This is noticeably like *Psilotum* and many of the fossil *Lepidodendra*.

This condition, however, does not persist for any appreciable length of the stem; a little further up there is a distinct break in the xylem-band, on the side occupied, in sections at a lower level, by the young tuber. The stele thus becomes horseshoe-shaped; and although there seems to be a tendency to bridge over this gap, at first, by weakly developed tracheides, the gap may be said, approximately speaking, to persist until the base of

the peduncle is reached, at which point, we shall see, the stele breaks up into the vascular strands of the peduncle.

As we ascend, the original xylem-strand of the young tuber breaks away from the main stele; it ultimately disappears. In Fig. 6, taken across the lower part of the leaf region, we have a distinctly U-shaped stele, with the gap facing the former site of the young tuber. Five leaves are seen in section; and it will be well, perhaps, at this point, to digress with a brief description of the anatomical structure of—

3. *The Leaf.* The outline of the transverse section is roughly circular; a distinct peripheral layer is differentiated from the parenchyma which

occupies the greater portion of the section. In the centre is a single very small xylem-strand, consisting of six or seven wood-elements at most. In one case the xylem-strand was observed to be surrounded by a zone of tissue which was possibly phloem, although no sieve-tubes could be recognized.

Stomata occur evenly distributed over the epidermal layer, and leading into large air-spaces. The parenchyma seems to be traversed throughout by intercellular spaces; and the presence, in many of the sections, of radially elongated parenchymatous cells near the periphery suggests the existence of a rudimentary palisade tissue.

Let us now return to a closer examination of—

4. *The Stem-stele.* The investigation of the structure of the U-shaped

FIG. 7. The stele in detail. Protoxylem-groups appear at the free ends, and degraded groups form cavities in the body of the stele. A protoxylem-element, *px*, is seen clinging to the edge of one of the cavities.

vascular band yields some interesting results. It is surrounded by markedly homogeneous parenchyma, which is continuous into its concavity.

There appear to be several protoxylem-groups. One is observed situated in an exarch position at each free end; but what is more remarkable, several cavities are present in the body of the stele (Figs. 6, 7); and the presence in some cases of one or two small tracheides clinging to the sides of the cavities indicates that the latter represent degraded protoxylem-groups, comparable with those seen in *Equisetum*. These cavities appear in Bertrand's figures, and he expresses the opinion that they represent degraded protoxylem-groups. The xylem is thus, of course, mainly mesarch in development.

The position of the phloem in this stele would be of the most significant interest, but the closest examination has failed to reveal its presence in the stem.

5. *The Peduncle of the Strobilus*. This follows in the transverse sections in a continuous ascent from the stem region. The xylem of the latter breaks up, very soon after entering the peduncle, into isolated strands, very irregularly disposed; not in a circle, as has apparently been the general impression hitherto (Fig. 8).

Each strand encloses a protoxylem-cavity and is thus clearly mesarch in development. One or two small wood-elements cling to the edge of the cavity; and here the resemblance to the carinal canals of *Equisetum* is much more striking than in the stem-stele.

6. *The Strobilus region*. As we approach the base of the strobilus, one or two of the strands move outwards to the periphery of the section; these, we shall see, go to supply sporophylls. The first indication of the latter in the sections is the appearance of a tangentially elongated mass of parenchyma, entirely isolated from the section of the main axis, and destitute of vascular tissue. This is obviously the down-pointing free 'dorsal lobe' of the lowest sporophyll¹ (*dl*, Fig. 8). Opposite this, in the axis section and near its periphery, is the xylem-strand (*t*) which is going to supply the sporophyll.

FIG. 8. Transverse section of strobilus. The walls of seven sporangia are seen in section, *sw*. The section passes through the base of one sporophyll, before it has become free of the main axis. Xylem black, parenchyma shaded.

Fig. 8 shows the general appearance seen in a transverse section taken about midway across the strobilus. Dorsal lobes (*dl*), sporophylls (*sp*), and sporophyll traces are seen in section at different levels. The sporophylls, like the leaves, are seen to possess a small central vascular strand, the latter originating from the isolated bundles of the axis; one is shown, in partial longitudinal section, in the act of passing out into its sporophyll.

¹ Sykes (11).

The vascular system of the strobilus-axis thus appears to be an aggregation of sporophyll-traces; but at the extreme tip, above the level of departure of the highest sporophyll, a few xylem-elements are still to be seen in section, so that the system is in reality cauline in origin.

SUMMARY OF THE INTERNAL STRUCTURE.

The vascular system is embedded in closely packed parenchymatous tissue. The parenchyma is remarkably homogeneous in tuber, root, stem, and in the peduncle and axis of the strobilus; the sole differentiation is in the peripheral layer of empty, radially elongated cells, with thickened walls; the parenchyma, moreover, which is in immediate association with the stele, is more compact and of smaller cells than that of the main body of the cortex. The latter is traversed by large intercellular spaces. This peripheral layer is fairly constant in sections taken at all levels, and in all parts of the plant.

There is no indication of an endodermis, except in the root.

The vascular tissue consists of xylem only (except perhaps in the leaf). This is, for the most part, of typically scalariform tracheides.

The general course of the vascular system is briefly as follows: That of the lower portion of the stem is a medullated protostele, which breaks up below into the strands which supply the roots on the one hand, and the young tuber on the other. The leaf-strands are continuous with those of the roots, and leave the stele without causing any disturbance in its continuity.

The xylem on the side of the ring which faces the tuber rapidly thins out in an upward direction, and a level is soon reached at which there is a definite gap in the stele, so that 'pith' and cortex become continuous.

Before this gap is reached, a xylem-strand, corresponding in position to that occupied by the strand of the young tuber at a lower level, leaves the stele and takes a central course into a hump of tissue (*h*, in Figs. 3 and 6), which seems to represent what Bertrand calls the 'organ of Mettenius' (5); both hump and strand, however, soon disappear from the transverse sections as they are followed upwards.

The U-shaped stele breaks up above into the isolated peduncle-strands, each of which goes to supply a sporophyll. One or two, however, appear in transverse section above the level of the last sporophyll.

GENERAL DISCUSSION OF THE DETAILS OBSERVED.

1. The noticeable U-form of the upper part of the stem-stele is, perhaps, the most striking feature; it has no parallel in other Lycopodiaceae. It suggests, rather, an analogy to the upper part of the stem in *Tmesipteris*, in which the original protostele is disturbed by the outgoing leaf. As Bower points out, a similar appearance is seen in *Ophioglossum Bergianum*,

the U-shaped stele of which is remarkably like that now under discussion. This analogy to *Tmesipteris* is enhanced by the presence of what appear to be imperfectly developed tracheides bridging over the gap.

If there be any significance in this analogy, and the shape of the stele demands some such explanation, we must suppose that the gap indicates the presence, in an ancestral form, of a leaf, typically 'megaphyllous' in its behaviour to the stele. In this case we have a complete analogy to *Tmesipteris*, the lower leaves of which are clado-, and the upper phyllo-siphonic; and *Phylloglossum* presents yet another link between the Pteropsida and Lycopsida of Jeffrey.

The leaf-member which causes the gap must be regarded as entirely suppressed in the modern form, and there is no indication of the presence of a branch in its axil; the structure is, in fact, typically Filicinean. The gap never closes above; the U-shaped stele breaks up directly into the isolated strands of the strobilus pedicel.

It must be mentioned at this stage, however, that Jeffrey (8) denies that the gaps in the stele of *Tmesipteris* are foliar, and he points his denial by a strict definition of the term 'leaf-gap'; he emphasizes the closeness of the relation between the gap and the outgoing leaf. More than one botanist of distinction is less certain than Jeffrey upon this point; but, whatever may be the true case in *Tmesipteris*, the gap in the stele of *Phylloglossum* certainly complies with Jeffrey's criteria of a leaf-gap. In his paper (8) he evades this point by assuming, without offering any discussion upon the matter, that the opening in the stele of *Phylloglossum* is caused by the exit of the bundle which supplies the young tuber; the fact that this opening is found to face the site occupied by the latter at a lower level seems to lend some support to this contention. In this problem, however, we may derive considerable assistance from the stalked tuberous structures met with in certain Monocotyledonous plants, and described by Miss Robertson (10) in the case of the genera *Tulipa* and *Erythronium*. These 'stalked bulblets' or 'droppers' are the precise analogues of the *Phylloglossum* tuber, and serve the same fundamental purpose, namely, the exploration, so to speak, of the soil; the analogy is further enhanced by the fact that more than one tuber may be formed during a season¹—so that the tuber of *Phylloglossum* is essentially a means of vegetative reproduction; this consideration seems to lessen very considerably the fundamental phylogenetic importance which has been assigned to it.

Like the tubers we have described above, the stalks of the droppers are tubular, and bear small bulblets at the tips. Miss Robertson points out that the dropper is actually a continuation of the base of the leaf; and we may therefore suppose that the *Phylloglossum* tuber is a continuation of the suppressed leaf which we have postulated above; this contention is sup-

¹ See *supra*, p. 338, and Thomas (13).

ported by the relative positions of the gap and of the young tuber. Further, the morphology of the dropper is described as being partly foliar and partly axial; there is a vascular ring derived from the leaf; and this is represented in *Phylloglossum* by the ring observed in the tuber of the second specimen examined.¹ The 'axial' portion of the anatomy of the latter is, of course, represented by the central vascular strand (*y.t.s.*, Fig. 3).

Reasoning from analogy is admittedly dangerous; but the remarkable similarity in the structure and function of the tubers under discussion and the 'stalked bulblets' described in Miss Robertson's paper seems to lend no little weight to the supposition that a megaphyllous leaf existed in the ancestors of *Phylloglossum*, while the position and rudimentary nature of the 'organ of Mettenius' is very suggestive; it might very well represent the vestige of a megaphyllous leaf.

The habit of the plant further favours this suggestion; like the Monocotyledons, it is typically geophilous; and, as Bower has pointed out,² this habit conduces to reduction in the number of leaves and enlargement of the individual leaf—in other words it conduces to megaphylly.

2. The geophilous habit of *Phylloglossum* recalls some interesting parallels in other Pteridophyta. The adoption of this habit results in general reduction, as witness, for example, the modern pigmy descendants of the giant Calamariae; while there is no doubt whatever that *Phylloglossum* is extremely reduced, however primitive may have been the condition of its Lycopod ancestors; of this primitiveness we shall, however, have something to say further on. The latter may have been 'permanently embryonic Lycopods'—in which case it is not improbable that their remains would be as lost to us as are the embryonic stages of the ancient *Lepidodendra*; but their modern descendants are highly specialized in accordance with their special habitat. This is described in Cheeseman's Flora of New Zealand as 'barren clay hills' in the North island,³ and Thomas states that the plant flourishes best on a hill-top.

The thickening of the epidermal cell-walls is doubtless a xerophytic adaptation, designed for the purpose of providing a tegument to serve as a protection against the environmental conditions. Sclerenchyma is, however, entirely absent—a feature not surprising in so small a plant.

Similar degradation of the protoxylem occurs in many other forms which occupy special habitats—notably the Equisetales, *Sphenophyllum insigne*, the leaf of *Isoetes*, and many aquatic flowering plants.

3. The indefiniteness of the vascular system is also in accord with the habitat of the plant; and there is a striking resemblance in this regard between *Phylloglossum* and the Isoetaceae. In both cases we have a geophilous habit. The storage tuber of *Phylloglossum* is analogous to the thick tuberous stem of a form like *Isoetes Hystrix*, the storage parenchyma

¹ *Supra*, p. 338.

² Bower (4), pp. 231, 479.

³ Cheeseman (6).

in the former being paralleled in the latter by the strong development of secondary cortex. We are reminded, in this connexion, of the notably strong development of secondary cortex in many fossil forms.

The leaves, again, of the two forms are noticeably alike in shape, at least in the upper and greater part of their length; while in both, the leaves are large relatively to the stem, in spite of their 'microphyllous' anatomy.

The presence of phloem in the stem is much more problematical in *Phylloglossum* than in *Isoetes*; indeed it may be said to be entirely absent. True phloem probably exists, as we have seen, in the leaves of the former, the single leaf-bundle being concentric.

The mesarchy seen in the lower part of the leaf of *Isoetes* is reflected in *Phylloglossum*, in which plant, however, this condition is much more general, as it occurs throughout the leaf, in the upper part of the stem, in the peduncle and axis of the strobilus, and even in the strand of the young tuber.

In both *Isoetes* and *Phylloglossum* the vascular system is cauline, and the leaf-trace bundles leave the stele—a protostele in both cases—undisturbed by their exit.

The protoxylem cavities, so prevalent in *Phylloglossum*, occur constantly in the leaf of *Isoetes*.

The roots in both are monarch in structure.

In fact the external and internal morphology of the vegetative organs in the two plants are remarkably alike in fundamental points, suggesting additional evidence of the Lycopodinean affinities of *Isoetes*.

There seem at first sight, on the other hand, to be important differences in the structure of the reproductive organs. This feature, however, is mainly due to the adoption of the heterosporous habit of *Isoetes*. With this are probably connected the ligule and the 'velum'—structures which have been paralleled with those found in the integumented sporangia of *Miadesmia*; many may consider, in fact, that *Isoetes* has advanced beyond mere heterospory; it has made the first step towards seed-production. We may suggest that the homosporous *Phylloglossum* could not proceed so far, at least in this direction; but in specialization for spore dispersal it is a decided advance upon *Isoetes*, as its sporangia are aggregated into a very definite and pedicellate cone. It shares, of course, with *Isoetes* the constant Lycopod character of one sporangium to each sporophyll.

The structure and development of the individual sporangia have been exhaustively described by previous authors; it will suffice to recall here the fact that the sporangium is typically Lycopodinean, and of the less specialized, *Urostachya*, type.¹

4. Let us now proceed to consider the question of the primitiveness, or otherwise, of *Phylloglossum*.

¹ Sykes (11).

The striking similarity of the development of this plant to the embryonic stages of *Lycopodium* has led many to regard it as a 'permanently embryonic form of Lycopod'. This has led to the conclusion that *Phylloglossum* is a relatively primitive form, and this receives a certain amount of support from the gametophytic characters; but the fact that more than one tuber may be formed in a season, with the consequence that the tuber is probably a merely adventitious organ of vegetative reproduction, seems to militate very forcibly against such a conclusion.

The anatomy, moreover, seems to point to extreme specialization. The latter is, doubtless, largely biological in significance, and comparatively recent in descent; but the gap in the upper part of the stem-stele can scarcely be regarded as other than an ancestral character, and one of considerable importance.

If the gap is a leaf-gap, as seems by no means unlikely, then *Phylloglossum* is no more primitive than *Tmesipteris* or *Ophioglossum Bergianum*; in fact, it is less primitive, for reduction has led to the complete suppression of the megaphyllous leaf in *Phylloglossum*.

This suppression is not without parallel in the Pteridophyta. In recent *Equiseta* the leaves are extremely reduced, but the gaps in the stele are now generally admitted to be leaf-gaps.¹ In *Ophioglossum simplex* we have an exact parallel with the suggested condition in *Phylloglossum*, for, although leaf-gaps are present in the stele of this species, the megaphyllous sterile laminae which cause them, so to speak, are altogether absent; and as Bower points out, 'it is thought that *O. simplex* forms the end of a series of reduction of the vegetative system, consequent on . . . habitat: that as *O. intermedium* . . . shows . . . only a reduced lamina, so in *O. simplex* the reduction having proceeded further has resulted in the complete elimination of the sterile blade.'

It is suggested that *Phylloglossum* stands at the end of a similar reduction series, of which the transitional forms have been lost. If this be so, we can no longer regard it as a primitive form, at least, so far as the vegetative organs are concerned; while in specialization for spore-dispersal it stands as high as any of its Lycopodinean allies.

We may summarize our conclusions briefly thus:—

1. In view of its anatomical structure, *Phylloglossum*, like *Tmesipteris*, is 'microphyllous' in its lower portion, and 'megaphyllous' in the upper—thus occupying a position intermediate between Pteropsida and Lycopsida.
2. The general degradation of the vascular system, coupled with the geophilous habit, suggests that *Phylloglossum* has undergone considerable reduction recently in descent.

¹ Gwynne-Vaughan (7); but Jeffrey (8) is a notable exception to this statement.

3. This reduction has resulted in the complete suppression of the megaphyllous leaves, a condition comparable with that presented by *Ophioglossum simplex*.

4. The similarity in respective habits and structure of *Phylloglossum* and *Isoetes* go to support the Lycopodinean affinities of the latter.

5. *Phylloglossum*, far from being a primitive form, is highly specialized.

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It should be stated that the present investigation was carried out in the Botanical Department of Goldsmiths' College, University of London.

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