

XII. *On the Development and Morphology of Phylloglossum Drummondii.**By Professor F. O. BOWER.**Communicated by W. T. THISELTON DYER, F.R.S.*

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[PLATES 71-73.]

PART I.—THE VEGETATIVE ORGANS.

WITHIN the last twelve months the interest of Botanists has been centred afresh in the investigation of the *Lycopodinae*. It is sufficient to refer to the recent writings of BRUCHMANN,* TREUB,† and SOLMS-LAUBACH,‡ to indicate how actively the investigation of these plants is being pursued. It had long been the wish of the author of this paper to obtain material for the careful investigation of the less known members of the *Lycopodinae*, and especially of *Phylloglossum*; the authorities of the Royal Gardens at Kew made this known to BARON FERDINAND VON MUELLER, and from him there were received during the latter half of 1884 two consignments of living tubers of *Phylloglossum Drummondii*, as well as a supply of mature plants preserved in alcohol. The tubers germinated successfully, in the propagating pits at Kew, and the material was thus at hand for the investigation of the development and histology of this little known plant. As circumstances will for the present prevent the author from continuing his work, and as the *Lycopodinae* are now one of the focal points of botanical interest, it appears desirable that the chief facts thus far acquired should at once be published, while a discussion of these results, and their bearing upon recent observations of other forms, may for the present be postponed. The structure and development of the sporophore generation only will be described at present. Many of the plants now growing at Kew already bear immature sporangia, but the description of their development will be deferred till the sporangia have arrived at maturity, and until attempts have been made to germinate the spores: the general treatment of the subject will be better in place when it is seen what results, if any, are acquired from those cultures of the spores. For similar reasons it would be both inconvenient and inopportune now to review the writings already published by various

* 'Botanisches Centralblatt.'

† "Études sur les Lycopodiacées." 'Ann. du jardin botanique de Buitenzorg,' vol. iv., p. 107.

‡ "Der Aufbau des Stockes von Psilotum Triquetrum." 'Ann. du jard. Buitenzorg,' vol. iv., p. 130.

authors on *Phylloglossum*. This memoir will therefore deal merely with the observations recently made by the author; in some points it will be seen that they confirm the observations of previous writers, in others they are not in accord with them: they will be placed in relation with those of other authors when the investigations, which are still in progress, have been as far as possible completed.

Structure of the Tuber during the resting stage.

The tubers as sent over from South Australia were in the mature condition, and undergoing a period of rest. The upper parts of the plants which produced them had already died off. In no case was there evidence of more than one tuber being produced by one parent plant.

In this condition the structure of the tuber is as follows: it consists of an ovoid solid mass of tissue, connected at its upper end with the stalk by which it was attached to the parent plant. This stalk widens out near the apical end of the tuber (*i.e.*, that nearer the parent plant), and is there hollowed, covering in the broad organic apex of the tuber, which thus has the appearance of being of endogenous origin. A transverse section of the stalk which bears the tuber shows a nearly circular outline. The chief bulk of the tissue consists of thin walled parenchyma, with intercellular spaces: in this may be recognised a point where the cells are of smaller size, and for the most part without intercellular spaces (fig. 1, *c*): in many cases a transverse section will show a cavity between these cells (*c*, fig. 2), and this is especially marked in sections taken near the tuber, or near the attachment of the stalk to the parent plant. At the point in question lies the original channel of communication of the apex of the tuber with the outer air; as will shortly be seen the apex of the tuber is of exogenous origin, but the channel of communication becomes closed during development. Further, a vascular strand of small size may be seen cut through in the transverse section (*xy*, fig. 1); it consists of a few elements with lignified walls, which are, as shown by longitudinal sections, spirally or reticulately thickened. At the periphery is a layer of epidermis, with peculiarly thickened walls: it is continuous with a similarly developed layer covering the tuber externally (see below). Passing downwards to the tuber itself, the stalk widens out, and becomes hollowed; the vascular strand spreads laterally, so as to assume a funnel-like form, covering the apex of the tuber; but it stops short about the level of the apical cone, and is not continuous into the fleshy tissue of the tuber.

The mature tuber itself consists of a central bulky mass of thin walled parenchyma, which is entirely undifferentiated: there are intercellular spaces. The cells are filled with store materials, *viz.*, protoplasm, starch and oil. Towards the periphery of the tuber the cells have little or no contents, and the last two or three layers below the epidermis thus form a more transparent band, the elements being often squeezed out of shape. The superficial layer is developed as a clearly defined epidermis (figs. 3, 4); the cells themselves are of oblong form, their radial walls are strongly thickened and

stratified, and are also pitted; irregular pits are found in the outer part of them, which has accordingly a reticulate appearance when seen in surface view; clearly marked pits are also found occasionally near the internal limit of the radial walls (fig. 4). These thickened walls give a mauve colour with SCHULZE'S solution, and are not stained by an acid solution of aniline sulphate: it is thus shown that they are not lignified. Some superficial cells grow out as root-hairs, which are sometimes cut off by a wall from the parent cell (as shown in fig. 3, *h*). As might have been expected, stomata have not been seen in the epidermis of the tuber. An investigation of the base of the tuber shows that in the mature state this epidermis is continuous over it: a longitudinal section of a tuber in course of development shows no trace of those characters which are peculiar to the root, a conclusion which is equally borne out by the mature structure.

Passing now to the apex of the tuber, median longitudinal sections show that the mode of division of the cells up to the period of maturity is that known as the \perp mode of division.* I have not in any case observed any wedge-shaped cell at the apex in this stage of development of the axis (fig. 6). The arrangement of the cells as seen in superficial view from without is represented in fig. 7; it is suggested that the four cells marked (*x*) may be initial cells in this particular example, but it is not insisted that this is universally the case. As will be seen later, there is some inconsistency in structure of the apical meristem of this plant, and as the number of tubers investigated has been necessarily small, I am not prepared to assert that the structure of the apex above described is uniform for all mature tubers. Before germination there is no sign of formation of appendicular organs, the apex of the tuber is broad, slightly conical, and quite smooth.

Germination of the Tuber.

The living tubers, which were sent over in the dry state, were germinated with success in the propagating pits at Kew; the first plants made their appearance above ground about one month after they were sown. The tubers were of very variable size, and the character and number of the organs formed depends, in great measure, upon the size of the tuber. Thus it has been found that where the tuber is small, foliage leaves are formed, together with roots (one or more), and one new tuber; the number of the leaves also depends upon the size of the tuber, being sometimes only one, where the tuber is very small. Where the tuber is relatively large, sporangia are produced, their position and arrangement being as already described by other writers; in this case the tuber will also produce foliage leaves, roots (one or more), and one new tuber, as in the former case. As there is a difference in the mode of development of the plant, according as sporangia are formed or not, it will be necessary to deal with the two cases separately; it is however to be borne in mind

* See PRANTL, "Unters. zur Morph. der Gefässkryptogamen." Heft i., p. 4.

that, as far as observation extends, the starting-point is in either case the same. If we leave the size of the tuber out of account, there is in the structure of the apex of the mature tuber no indication by which it has been possible to decide beforehand whether the tuber will produce sporangia or merely vegetative organs.

Before entering on the details of the process of germination, it will be well to state what the results of that process are, as shown by mature plants. Of the twenty-two mature plants which were preserved in spirit, seventeen bore sporangia, five had only vegetative organs. From a careful comparison of them the following conclusions have been drawn, viz. :—

(A.) Where sporangia are produced, the number of foliage leaves is 3–6; the number of roots 1–3, usually 3. Two tubers are found in all cases, one of these being the spent tuber of the previous year, the other the new tuber.

(B.) Where sporangia are absent, the number of foliage leaves is 4–7; the roots 1–2, usually 1. As before two tubers are present, and it may be stated that in no case have more tubers than two been observed: if it is constantly the case that only one new tuber is formed during each period of activity, it is obvious that there can be no increase in number of individuals by means of the tubers.

Taking, first, the more simple case, where the germinating tuber produces only vegetative organs, the conical apex elongates, and a massive rounded outgrowth appears upon it: this is the first leaf. The position of this first leaf is lateral, though in some cases more clearly so than in others: its position relative to the parent plant which produced the tuber has not been found to be constant in those cases where it was possible to judge on this point; thus, it has been found in some cases to be inserted on the side of the axis more remote from the parent plant; again, it has been observed in other cases to be lateral as regards the parent plant. As will be pointed out below, the other organs developed later, have more or less clearly defined positions, relative to the first formed leaf, and consequently we may conclude generally, that as regards the position of its organs, the germinating tuber develops independently of the plant which produced it: this conclusion might well be anticipated since the parent plant is in a state of advanced decomposition before the tuber begins to germinate. Where the tuber is a small one, and the supply of reserve materials is therefore small, the leaf which appears first may be the only one developed: this has been the case in the plants represented in figs. 8 and 9: in both of these, the solitary leaf is the most prominent member of the plant. I am not in a position to state definitely that in these cases the leaf is clearly of lateral origin on the apex of the tuber, though the natural conclusion would be that it is lateral, and this view is supported by a comparison with the other types of development of the plant, to be described below.

In one irregular example represented in fig. 10, there are apparently two leaves of equal size. This case may be compared with that shown in fig. 20 at a more advanced stage of development.

Where a single leaf is formed first (and this is the case in the large majority of specimens) it is usually followed by two of approximately equal size, which are formed laterally on the apex of the tuber, and are disposed one on either side of the first formed leaf. This is clearly seen to be the case in the specimens represented in figs. 11 and 12 (lii.). This pair of leaves may be again followed by a second pair (fig. 13, liii.); but here again irregularities of arrangement may, and often do occur: thus though in fig. 14 their general arrangement is the same as that above described, the leaves do not in this case appear as successive pairs. From the examples cited it is evident that there is no strict constancy in number, or arrangement of the leaves; their number is seen to vary from one to five, and the number as seen in the mature plant may be occasionally higher still, as many as seven have been seen in one mature specimen. It may be again noted that the larger number of leaves is usually associated with the absence of sporangia. The arrangement of the leaves also shows some inconstancy, there being in the majority of cases one leaf formed first, and followed by successive pairs; in other cases the order of succession and position being less regular. In those examples in which the arrangement of the leaves, and their order of appearance on the apex are most regular, it is clear that we have to deal with a *successive whorl* of leaves. Such successive development of members of a whorl is well known to exist in certain flowers, as for example in *Reseda*, the flowers of the *Papilionaceæ*, &c. The successive formation of the whorl of leaves derived from a node of *Chara* may also be cited. Further, the irregularities of arrangement and succession of the leaves in *Phylloglossum* acquire additional interest when it is remembered that in the genus *Lycopodium* irregularities are also prevalent, and have always presented difficulties to those who attempt to reduce morphological description to strict formulæ. The leaves originate on the apex of the tuber as rounded masses of meristematic tissue, in which no single apical cell is to be distinguished; divisions of the superficial cells by periclinal walls are frequent, and it is only at a comparatively late period that a superficial layer of epidermis becomes apparent.

Returning now to the central point around which the leaves are disposed, it is at no time a prominent cone in those plants which do not form sporangia. According to the strength of development of the leaves it is liable to be more or less displaced; this is most clearly seen in those plants in which only one leaf is produced (figs. 8, 9), here the apex of the tuber assumes a lateral position at the base of the solitary leaf. Even in those cases where the successive whorl of leaves is most complete, the apex becomes displaced, owing to the more rapid development of the earlier formed leaves (fig. 13). At an early period the apex thus displaced becomes depressed; it grows slowly in length itself, while the tissues immediately surrounding it advance more rapidly, the result is a conformation of the surface as seen at (*a*) in figs. 8-14. A longitudinal section shows the depression still more clearly (fig. 15). There can be little doubt that, in those plants which do not form sporangia, it is actually the apex of the plant which becomes thus depressed, since the depression appears constantly in

an approximately central position, notwithstanding differences in number and arrangement of the leaves. Following still the changes of external conformation, it is found that the young tuber begins to project, since the growth of tissue is continued actively round the apical depression (fig. 16, *a*); it gradually becomes inverted and elongated, as the result of a special localisation of intercalary growth (figs. 17-20). Meanwhile the swelling of the tuber begins by increase of the tissues lying below the depressed apex (fig. 20). Further details of the development of the tuber, as illustrated by sections, will be given below.

In some cases a leaf smaller than the rest and of later development is to be seen inserted above the tuber (fig. 18); its position is, as a rule, not directly above the tuber (fig. 17). A leaf holding this position has been observed by other writers, but it is by no means of constant occurrence, and its occasional appearance illustrates once more how great is the irregularity of number and position of the leaves in *Phylloglossum*. The description above given of the development of those simpler plants of *Phylloglossum* which do not bear sporangia coincides with the structure of those plants when mature, and it may especially be noted that in the mature plant there is no trace of an apical cone or bud to be found in a central position at the base of the leaves, an observation which completely bears out the view that in these plants it is actually the apex of the plant which gives rise to the new tuber.

While the development of the tuber is progressing, an outgrowth makes its appearance on the opposite side of the plant to that on which the tuber is formed; it is situated at a point below the insertion of the oldest leaf. It arises as a smooth rounded cone; there is no sign of any rupture of the tissues, indicative of endogenous origin, its outer surface being unbroken and glossy; as it grows older a slight excrescence appears at its apex, the convexity of its surface being there greater; this outgrowth ultimately develops as the first root (*r*, in figs. 9, 16*b*, 18, 19, 20). In one plant this outgrowth did not appear as a simple cone, but, as shown in fig. 21, two cones appeared, joined laterally, a mode of development which may well be compared with that exceptional development of the leaf shown in fig. 20. As far as external observation is concerned, it may be concluded from the above description that the root is of exogenous origin. This is borne out by the results derived from the study of sections, which will be detailed below.

The second alternative mode of development remains to be described, viz., that in which the plant forms sporangia. As above stated, this appears to occur only on the germination of large and well-developed tubers. The formation of leaves and their order of succession appear to proceed in the same way as above described, but it is to be noted that the number of ordinary vegetative leaves is usually smaller in sporangium-bearing plants than is the case in plants of purely vegetative development. When sporangia are to be formed, the apex of the plant is convex, and grows on in an erect position; on it are formed successive leaves, which originate like the ordinary foliage leaves, but remain of relatively small size, while the axis which bears them

becomes elongated below the insertion of the lowest of them (figs. 22-25). As to the arrangement of the leaves on the cone I have nothing to add to the description of previous writers. It will be seen from figs. 22-25 that the first two leaves of the cone correspond roughly in position to the second pair of leaves in fig. 13.

Since in sporangium-bearing plants the apex of the main axis continues its growth, and gives rise to the sporangium-bearing cone, it is clear that there must in this case be a different origin for the tuber than that described for the purely vegetative plant. Up to a stage of development, such as is shown in fig. 23, no trace of a new tuber has been observed; but subsequently a depression is seen at a point near the base of the pedicel, which is surrounded by a circular weal (fig. 24); this is the young tuber, which is again shown in a more mature condition in figs. 25, 26. It would thus appear that in those plants in which the main axis develops as a sporangium-bearing cone, the new tuber is of adventitious origin, and exogenous. It does not bear any constant relation to the leaves, though, as has been observed in mature plants, a leaf of smaller size than the rest is occasionally inserted immediately above the attachment of the new tuber (fig. 27). A supernumerary leaf of this sort has been observed in four out of eleven specimens of mature sporangium-bearing plants. In plants of this type the roots originate in the manner above described.

The chief points in the development, as seen on germination of the tuber, having been described, as far as their external characters are concerned, the description of the development of the tuber and of the root, as illustrated by sections, may now be proceeded with. If a median longitudinal section be cut from a plant, such as that represented in fig. 13, it will present an outline as shown in fig. 15. At the point marked (*a*) there is a slight depression, which indicates the first origin of the new tuber. Seen under a higher power the arrangement of the cells appears as in fig. 28. Here it is evident that growth and cell-divisions, especially periclinal divisions, are less frequent at the point (*a*) than in the tissues immediately surrounding that point: the result is that the point marked (*a*) becomes depressed, while the surrounding tissues gradually overarch it (fig. 29), leaving only a narrow channel open above the apex. Finally the channel which is seen still open in fig. 29 is closed up, and the apex of the new tuber is thus completely covered in by the more rapidly growing tissue which surrounds it (fig. 30). It is to be observed that the apex thus covered in is in the first instance of very small area, and in the case of fig. 29, it appears to be only a single cell in width: whether this is always the case I am not in a position to state. Subsequently divisions appear in the cells at the base of the depression (fig. 30), which are repeated, and as the tuber increases in bulk the apical cone also increases in width, until finally in the mature tuber it is a massive structure of convex form, such as is seen in fig. 6. Even before the apex of the new tuber is thus covered in by the increasing bulk of the tissues surrounding it, growth is localised in a special way in the more deeply seated tissues: this growth results in the whole body of the tuber being made to project beyond the general surface of the axis, while, since the

intercalary growth is more strong on the lower than on the upper side of the new tuber, the whole body of it becomes inverted, in a manner not unlike that already well known in the tubers of certain orchids.* Fig. 31 represents in general outline the form and position which are thus assumed by a developing tuber: the apex (*a*) still maintains an oblique position; above it is a small cavity, more clearly seen in the specimen drawn under a higher power in fig. 32; from this cavity the now closed channel, which originally communicated with the open air, may be traced upwards, as seen in figs. 31, 32, till on approaching the outer surface it again widens out as a funnel-like depression (shown in fig. 33), which may often be recognised even in the mature plant (fig. 26). It may further be noted that a vascular strand, already described as existing in the stalk of the mature tuber, runs down from the main body of the plant till it approaches the apex of the new tuber; but, as above stated, it stops short before reaching the new apex. It may here be again remarked that among the plants grown at Kew no case has been observed of the formation of more than a single tuber: if this be uniformly the case with *Phylloglossum*, there can be no increase in number of individuals by means of the tubers, and at present no other form of vegetative reproduction is known in this plant: this would lead us to expect that the plant depends for its multiplication upon the germination of its spores, and this will enhance the interest which attempts to raise the plant from spores would naturally arouse.

If a median longitudinal section be cut through the conical outgrowth which ultimately develops as the root, while it is still young, its structure is seen to be such as is shown in fig. 34. It is clear from such preparations that there is no question of endogenous origin of the outgrowth, since the outer margin of the section is continuous, smooth, and unbroken from the surface of the axis, over the whole of the swelling. There can be no doubt that the whole outgrowth is of exogenous origin. The superficial cells are subject to both periclinal and anticlinal division, and consequently there is no clearly marked dermatogen; this is the case for all the other organs of the plant while young. As the outgrowth increases in age and size, periclinal divisions, which may already be observed at the point of greatest convexity in fig. 34, become more frequent, and being repeated in the same cells, result ultimately in the formation of a root-cap, which may then be recognised externally as the slight excrescence at the apex, as above described; the root-cap is thus derived in this case from superficial cells, and the whole root is of *exogenous origin*. In *Phylloglossum* another plant is added to the list of those in which the root is described as being of exogenous origin†: it is interesting to note that among them is *Isoetes*, in which the first root of the embryo is stated to originate from superficial cells.‡

* IRMISCH. "Biologie und Morphologie der Orchideen." Leipzig. 1853.

† Compare GOEBEL. "Vergleichende Entwicklungsgeschichte," p. 350.

‡ SADEBECK. "Gefässkryptogamen," p. 229.

It has been above stated that the mature leaf is of simple form, and almost cylindrical: a transverse section of it shows an almost circular outline, limited peripherally by a more or less regular epidermis, in which are numerous stomata of simple structure, and distributed uniformly on all sides (fig. 36). Below the epidermis is a massive, thin-walled mesophyll, arranged almost uniformly all round: there are large intercellular spaces, and respiratory cavities. The more peripheral cells have their longer axis disposed obliquely to the outer surface (fig. 37), while in those which are nearer the centre of the leaf the longer axis is directed longitudinally: thus in the transverse section the cells nearer the centre of the section appear almost circular. At the centre of the transverse section there is a small and simple vascular bundle, consisting only of four or five xylem elements, surrounded by tissues with cellulose walls, and small cell-cavities with protoplasmic contents. Longitudinal sections show that the xylem elements are elongated, with annular or irregular spiral thickening: there is no clearly marked phloem, and no bundle-sheath. The more central portion of the mesophyll consists of elongated and pointed elements (fig. 37); the oblique terminal walls where two such elements adjoin one another are of irregular thickness, and as seen in surface view are marked with shallow pits: there is no special character of their cell-contents, and a nucleus is present. It seems probable that this tissue replaces the phloem not only anatomically, but also physiologically, in fact that it is a rudimentary type of phloem. It is thus seen that the vascular bundle of the leaf is of a very simple type.

A peculiarity of structure is to be noted in the parenchyma at the base of the leaf. There the intercellular spaces are large, and into them there project numerous peg-like outgrowths from the walls of the adjoining cells (fig. 40); these are similar to those already well known as existing in the parenchyma at the base of the leaf in many ferns. The substance of which they are composed gives the following reactions: (1) They swell slightly with strong potash solution, and become less highly refractive, but do not lose their clearly defined outline; they do not stain with SCHULZE'S solution, even after previous treatment with potash, though the adjoining walls give a deep blue stain; (2) in sulphuric acid they behave similarly to the middle lamella, that is, they resist its action longer than the layers adjoining the protoplasm; (3) with methylene blue they stain very slightly or not at all. From these reactions it is clear that the outgrowths are not composed of ordinary cellulose; but it is difficult to define what their substance really is; it would appear, however, that it is not slightly cuticularised cellulose, such as described by LUERSSEN for similar outgrowths in ferns.*

A transverse section of the peduncle, or sporangium-bearing axis, shows an epidermis with stomata; its outer wall is thick, and is covered with cuticle, and a narrow cuticularised layer. Beneath the epidermis is parenchyma, with large inter-

* "Ueber Intercellularverdickungen im parenchymatischen Grundgewebe der Farne." Sitzungsber. der naturforsch. Gesellschaft zu Leipzig, 1875, p. 76.

cellular spaces, the cells being rounded, with thin walls, and containing protoplasm with chlorophyll granules. Here again there is no clear limit between the outer tissue and the vascular tissue; on passing from the periphery inwards the intercellular spaces become smaller, and in the tissues immediately surrounding the xylem they are almost or entirely absent (fig. 39); there are, however, intercellular spaces between the elements of the xylem themselves. The thin-walled tissues surrounding the xylem show characters similar to those of the tissue in a similar position in the leaf, which suggest for them a similar function. The elements of the xylem are tracheides with annular or irregular spiral and reticulated thickening of the walls.

A transverse section of a mature root shows a structure which coincides with that of the simpler forms of root in the *Lycopodinae*. There is no clearly defined epidermis; cells of the superficial layer grow out as simple root hairs. There is a broad band of cortex with large intercellular spaces; it is limited internally by the bundle-sheath, which is not a definite layer of cells, but is, as in *Lycopodium*, a somewhat irregular band of cells with corky walls (fig. 41); between this and the vascular tissues an irregular band of cells with cellulose walls intervenes, which may represent the pericambium. The vascular tissues consist of a single group of xylem elements, and a single group of elements of the phloem. No example of branching of the root has been observed.

As regards the distribution of the vascular bundles in the whole plant, and their mutual relations, there is considerable irregularity; this might be anticipated from the irregularity of number and arrangement of the leaves, &c., as above described. From each leaf one bundle of the leaf-trace passes into the axis; one strand passes from the axis into each root, and, as above described, one vascular strand passes into the stalk of the tuber. These are the fundamental points on which the arrangement of the vascular tissues is based. Taking first the simple case where only vegetative organs are formed, the vascular system was found, in two specimens, each with four leaves and one root, to be disposed as shown in fig. 42A. The bundles from three of the leaves united in the axis to form one trunk, which was continuous downwards directly into the single root. The bundle from the fourth leaf, probably the latest formed or supernumerary leaf, was traced directly downwards into the stalk of the tuber, without its being connected with the other bundles. This arrangement is a very simple one, and is obviously less efficient than those to be described below, since the vascular system here consists of two disconnected portions. In another specimen having five leaves, two roots and a new tuber, the vascular system was found to be disposed as shown in fig. 42B. The bundle passing down from one leaf, obviously from its position the first formed leaf of the successive whorl, divided in the axis into three strands; of these one passed to the stalk of the tuber (*t*), the other two curved to right and left, and finally coalesced with those descending from the other leaves, to form two trunks which passed directly into the two roots (*r*).

In those plants which bear sporangia, seated on an elongated stalk or peduncle, a

composite bundle passes down that stalk, the structure of which is shown in fig. 39. At the base of the stalk, about the level of the insertion of the foliage leaves, this composite bundle separates into strands of varying number, according to the number of the other organs of the plant; two examples from such plants are shown in figs. 43A, B. In these it may be observed that the general plan is in both cases the same, though there is a difference in the number of the roots; also in (A) the strand which passes to the tuber (*t*), is derived directly and solely from the axis, while in B the bundle of the tuber (*t*) is derived partly from the axis and partly from the leaf (*l_i*), which is situated above the insertion of the tuber, and appears to be the supernumerary and latest formed leaf, described above as being of inconstant occurrence. These few examples will suffice to show that there may be considerable variety in the arrangement of the vascular system of *Phylloglossum*, and that the irregularities are closely connected with the variations of arrangement of the organs.

Concluding Remarks.

The above description applies only to the vegetative organs of *Phylloglossum Drummondii*. The description of the structure of the sporangia, their development, and the possible results of their germination must be deferred for the present. In the light of TREUB'S recent researches on the *Lycopodiaceæ*, the development of the vegetative organs of *Phylloglossum* acquires additional interest, and a comparison immediately suggests itself between the early stages of development of the sporophore of *Lycopodium*, and the germination of the tuber of *Phylloglossum*. It can hardly have escaped the notice of those acquainted with TREUB'S memoir, that in certain points the correspondence is very marked, and it may be well to point out those characters where the similarity is most striking. As regards the general conformation of the plant of *Phylloglossum* while young, a comparison may well be drawn with the young plant of *Lycopodium cernuum* shown in fig. 1, Plate XVI. of TREUB'S memoir. At the base is a parenchymatous tuber ("tubercle embryonnaire" of TREUB), which corresponds in position and structure, though not in size, to the tuber of *Phylloglossum*; in both cases it is composed uniformly of parenchymatous cells, and in both plants the superficial cells may develop as root hairs. In that same figure three leaves are represented similar in their form and position to those of the simpler plants of *Phylloglossum*. As yet no root is visible in the young plant of *Lycopodium*, and, similarly in *Phylloglossum*, the formation of the first root is subsequent to the appearance of the leaves. The foot, which is not shown in the figure of *Lycopodium*, is absent in *Phylloglossum*, but it is to be remembered that in this plant the place of the foot is taken physiologically, if not morphologically, by the stalk of the young tuber. Thus the correspondence of parts, as regards their external form, between the young plant of *Lycopodium cernuum* and *Phylloglossum* is very close. The chief difference is in the relative size of the tuber; in *Phylloglossum* the development of the tuber, and storing of nutritive materials in it, precede the development

of the new organs at the apex, an arrangement which is well adapted to the growth of the plant under circumstances which alternately favour and prevent vegetative activity. In the young *Lycopodium* the supply of nutritive materials is drawn by the foot from the prothallus as it is wanted by the young sporophore. It is further to be observed that the same difficulty has been experienced by Dr. TREUB in distinguishing the morphological character of some of the young organs (*l.c.*, p. 130) as meets us also in the case of *Phylloglossum*: shall an outgrowth which appears not clearly lateral, such as that described as the first leaf in *Phylloglossum*, be designated a leaf or not? It is only to be expected that such difficulties should arise as we investigate plants which are low in the scale of development, and especially when we observe the development of their embryos. As regards the origin of the root, there is no doubt that in *Phylloglossum* it is exogenous, and that the first root is adventitious. In *Lycopodium cernuum* also the origin of the first root is comparatively late, and it is adventitious. I cannot think, however, that the one example shown by TREUB (Plate XVII., fig. 1) excludes the possibility of the first root being of exogenous origin, and it is to be observed that other figures (*e.g.*, figs. 2, 3, 4 of Plate XVII.) seem rather to point to an exogenous than an endogenous origin. It may also be observed that the connexion of the vascular bundles of the leaves and root, and their absence in the tuber ("tubercle embryonnaire") in *Lycopodium cernuum* correspond with the distribution of the bundles in *Phylloglossum*. Taken as a whole, and discounting the absence of the foot, and the storage of nutritive materials in the tuber before the development of the apex to form leaves and other organs, it may be said that the whole development of *Phylloglossum* from the tuber is strikingly similar to the embryonic stages of *Lycopodium* as described by TREUB. A comparison of the two leads clearly to the conclusion that, provided the sporophore generation of *Phylloglossum* corresponds in its more important points to that of *Lycopodium*, we may regard *Phylloglossum* as a form which retains, and repeats in its sporophore generation, the more prominent characteristics of the embryo as seen in *Lycopodium cernuum*; it is a permanently embryonic form of Lycopod.

DESCRIPTION OF THE FIGURES.

PLATE 71.

- Fig. 1. Part of transverse section of the stalk of a mature tuber: xy = the strand of xylem. c indicates the position of the channel, which is in this case completely closed. ($\times 175$.)
- Fig. 2. Part of a similar section: here the channel (c) is still open. ($\times 175$.)
- Fig. 3. Peripheral part of a transverse section of a mature tuber, showing the superficial epidermis, with peculiarly thickened walls, and one root-hair (h). ($\times 130$.)

- Fig. 4. A small piece of epidermis of the tuber, showing under higher power the thickened, stratified walls, with pits as described in text. ($\times 325$.)
- Fig. 5. Median longitudinal section of the base of a young tuber. ($\times 325$.)
- Fig. 6. Median longitudinal section of the apex of a mature tuber. ($\times 130$.)
- Fig. 7. Apex of mature tuber as seen from above. ($\times 325$.)
- Fig. 8. Apex of a very small tuber, after germination for fifteen days. l_i =the first, and in this case the only leaf. a =apex of new tuber. ($\times 20$.)
- Fig. 9. A similar specimen more advanced. l_i =first leaf, t =new tuber, a =apex of new tuber, r =root. ($\times 20$.)
- Fig. 10. Apex of tuber germinated for thirteen days, showing a rather unusual disposition of parts, viz., two leaves of equal size (l), apex of new tuber (a), and a small outgrowth ($l?$), which may be a young leaf. ($\times 20$.) A, seen from above; B, lateral view.
- Fig. 11. Apex of tuber germinated thirteen days: l_i =first leaf, l_{ii} =pair of subsequent leaves, a =apex of new tuber. ($\times 20$.) A, seen from above; B, lateral view.
- Fig. 12. Apex of a similar tuber germinated ten days. ($\times 20$.)
- Fig. 13. Apex of a strong tuber which has, on germination, formed a first leaf (l_i), and two subsequent pairs (l_{ii}), (l_{iii}), a =apex of new tuber. ($\times 20$.)
- Fig. 14. Apex of a strong tuber after germination thirteen days: l =the four leaves, a =apex of new tuber. ($\times 20$.) A, lateral view; B, seen from above.
- Fig. 15. Outline of a median longitudinal section of a germinating plant similar to that represented in fig. 13.
- Fig. 16. A, frontal aspect of a plant germinated for twenty days; B, lateral view of the same. r =root. ($\times 20$.)
- Fig. 17. A more advanced plant with three leaves (l), new tuber (t_2) with the apex at (a), sh =sheath.
- Fig. 18. A plant after germination for three months. l =ordinary leaves, l^* =last formed smaller leaf, t_1 =original tuber, t_2 =new tuber, r =root, sh =sheath. (\times about 5.)
- Fig. 19. A similar plant. ($\times 5$.)
- Fig. 20. A plant germinated three-and-a-half months. l =two leaves, in this case connate. (\times about 5.)
- N.B.—All the figures 8–20 represent plants of purely vegetative development which would not produce sporangia.
- Fig. 21. A young plant seen from above, and showing two connate roots; ap =apex of sporangium-bearing axis, which has formed two leaves (l_1). ($\times 20$.)
- Fig. 22. Young plant germinated thirteen days, and developing a sporangium-bearing axis. A, as seen from above; B, lateral aspect. ($\times 20$.)
- Fig. 23. Young plant rather more advanced, showing leaves (l) and sporangium-bearing axis, but no sign of a new tuber. ($\times 20$.)

PLATE 72.

- Fig. 24. A more advanced plant, showing, in addition to the parts seen in fig. 23, a new tuber (t_2), and two roots (r). ($\times 20$.)
- Fig. 25. A plant germinated about five weeks, showing the same parts as fig. 24. c =sporangium-bearing cone. ($\times 5$.)
- Fig. 26. A mature plant, showing the arrangement of parts. l =leaves, r =roots, t_1 =old tuber, t_2 =new tuber, a =sporangium-bearing axis. ($\times 3$.)
- Fig. 27. A mature plant with similar parts, with the addition of the supernumerary leaf (l).
- Fig. 28. Median longitudinal section of a new tuber in its first stage of development, compare fig. 15. The depression of the surface at (a) is already apparent. ($\times 175$.)
- Fig. 29. A similar section through an older tuber; the depression at a is deeper, and the channel above it is already beginning to be closed up. ($\times 175$.)
- Fig. 30. A similar section through a still older tuber; the channel is here completely closed. ($\times 325$.)
- Fig. 31. An older tuber drawn under low power (20) to show its general outline.
- Fig. 32. Apex of a similar tuber, with the completely closed channel. ($\times 325$.)
- Fig. 33. Opening of the channel of same tuber as fig. 32, at the external surface. ($\times 130$.)
- Fig. 34. Median longitudinal section of a root in early stage of development. Compare fig. 16. ($\times 175$.)

PLATE 73.

- Fig. 35. A rather older root. The periclinal divisions in superficial cells are very regular. ($\times 175$.)
- Fig. 36. Transverse section of a mature leaf. ($\times 130$.)
- Fig. 37. Median longitudinal section of a mature leaf. ($\times 130$.)
- Fig. 38. Two elements from a longitudinal section of the mature leaf. ($\times 325$.)
- Fig. 39. Central part of a transverse section of a mature peduncle. ii =intercellular spaces in the xylem. ($\times 175$.)
- Fig. 40. Part of a transverse section of the base of the leaf, showing peg-like projections into the intercellular spaces. ($\times 325$.)
- Fig. 41. Part of a transverse section of a root, showing the vascular tissue, surrounded by an ill-defined bundle sheath ($b. sh.$).
- Fig. 42A, B, vascular systems of two plants bearing no sporangia. l, l , bundles from leaves. t , bundle running to tuber. r , bundle running to root.
- Fig. 43A, B, vascular systems of sporangium-bearing plants. ax =bundle running down the stem.

Fig. 1
x 175

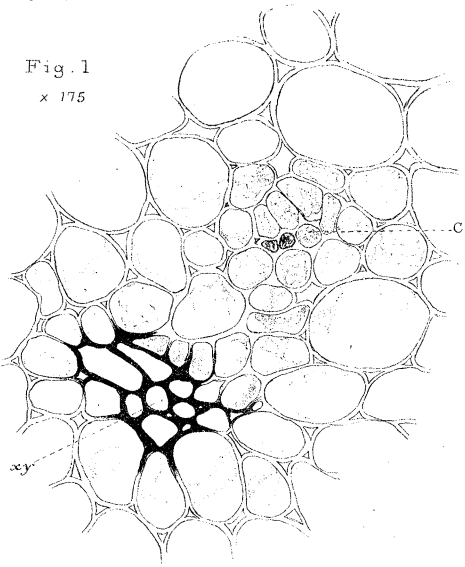


Fig. 3 x 130.

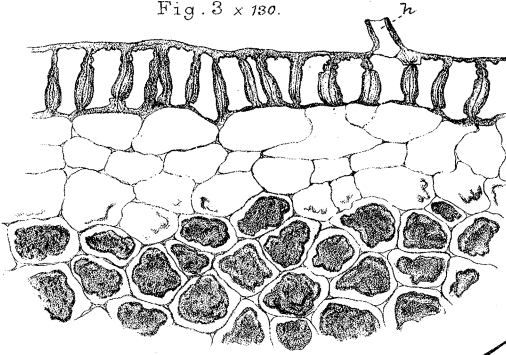


Fig. 4 x 325

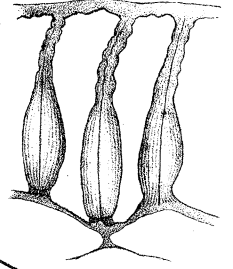


Fig. 5
x 325

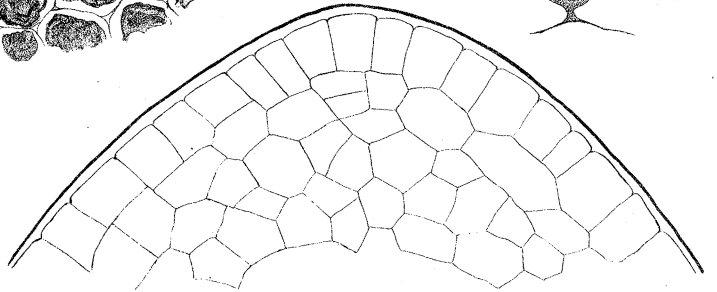


Fig. 2
x 175

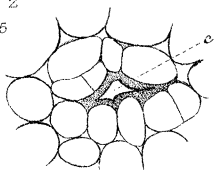


Fig. 6
x 130

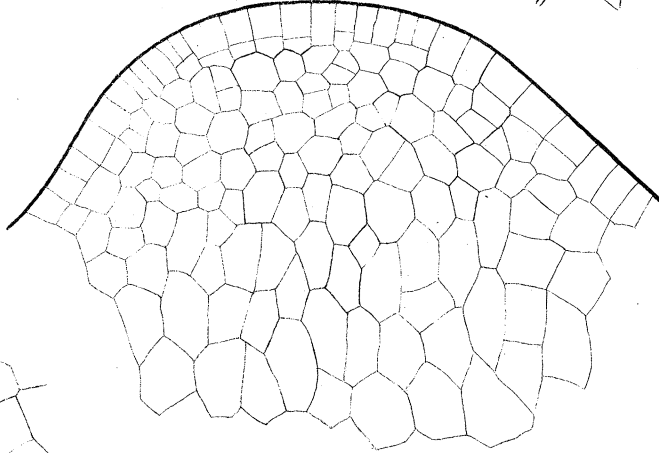


Fig. 8 x 20



Fig. 10
x 20

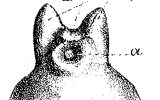
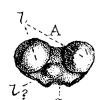


Fig. 7
x 325

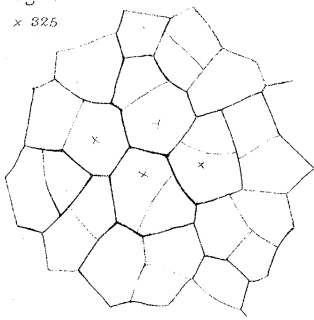


Fig. 9
x 20

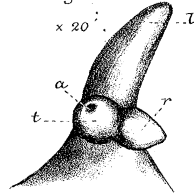


Fig. 11
x 20

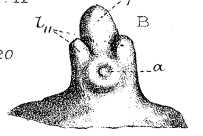


Fig. 12
x 20

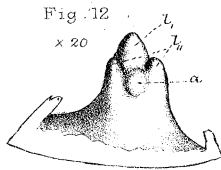


Fig. 13
x 20

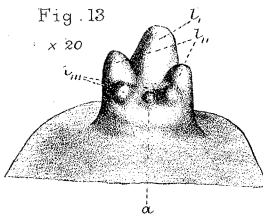


Fig. 14
x 20

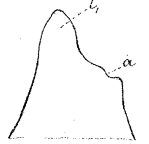
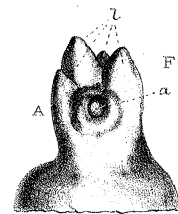


Fig. 15
x 20

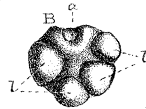


Fig. 16
x 20

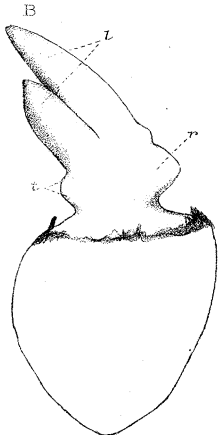
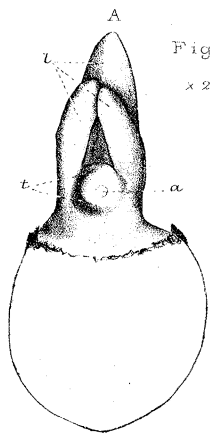


Fig. 17 x 20

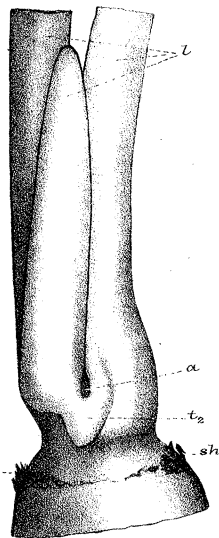


Fig. 18
x 5

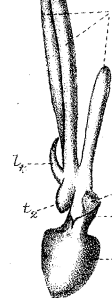


Fig. 19 x 5

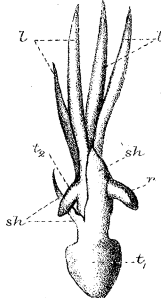


Fig. 20
x 5

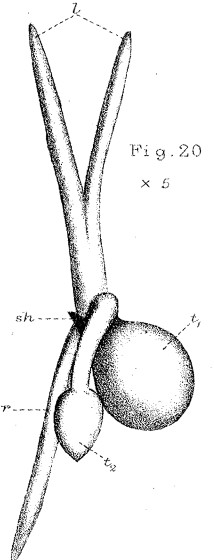


Fig. 21
x 20

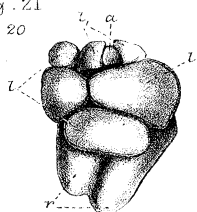


Fig. 22
x 20

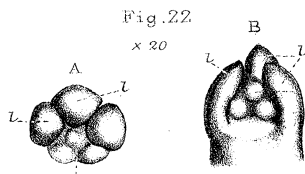
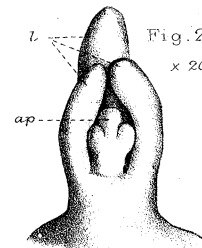


Fig. 23
x 20



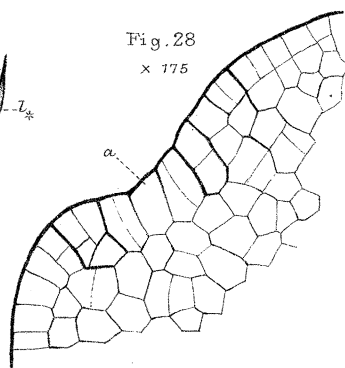
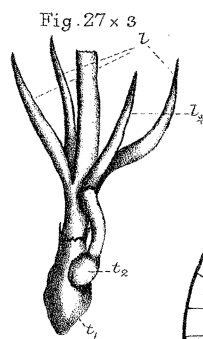
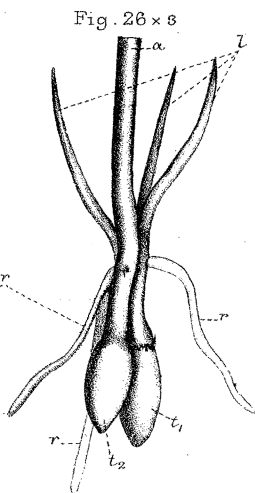
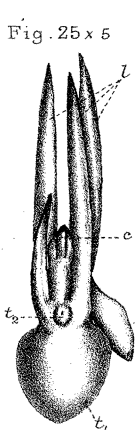
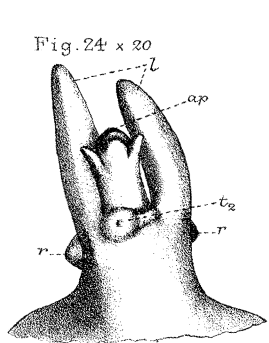


Fig. 29 x 175

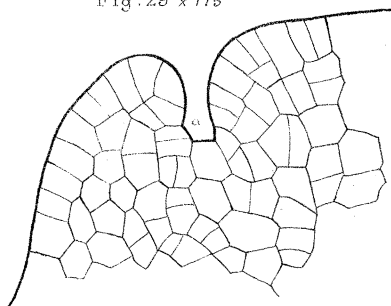


Fig. 30 x 325

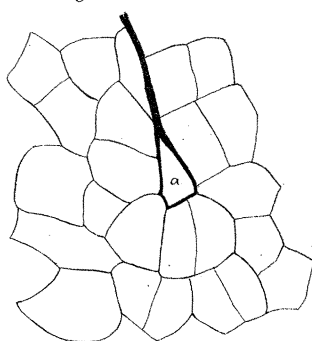


Fig. 31
x 20

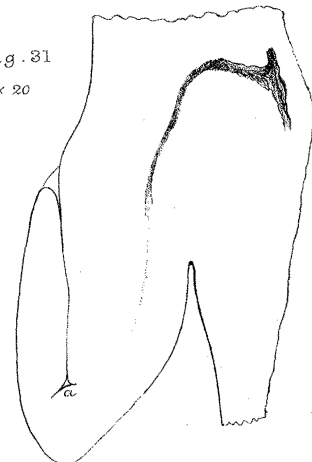


Fig. 34
x 175

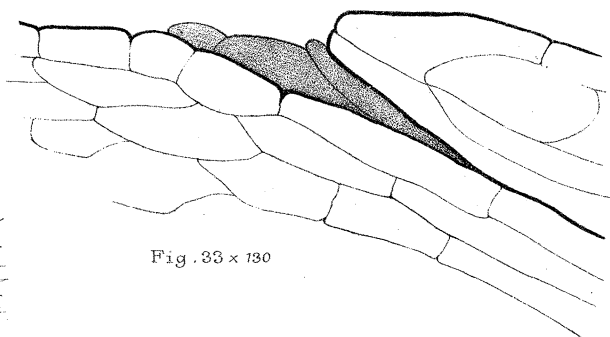
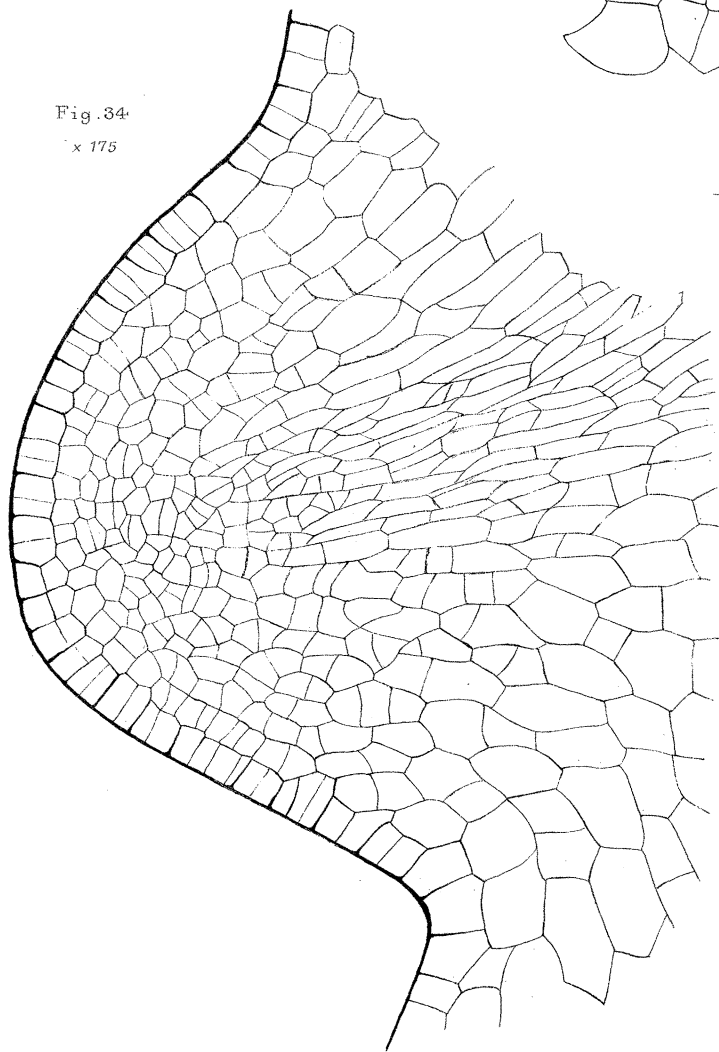


Fig. 33 x 130

Fig. 32
x 325

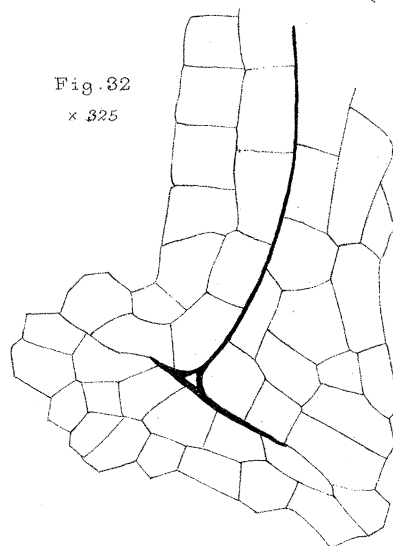


Fig. 35
x 175

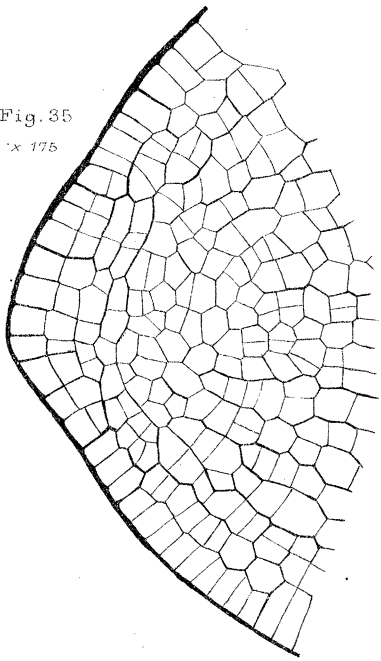


Fig. 38.
x 325



Fig. 36
x 130

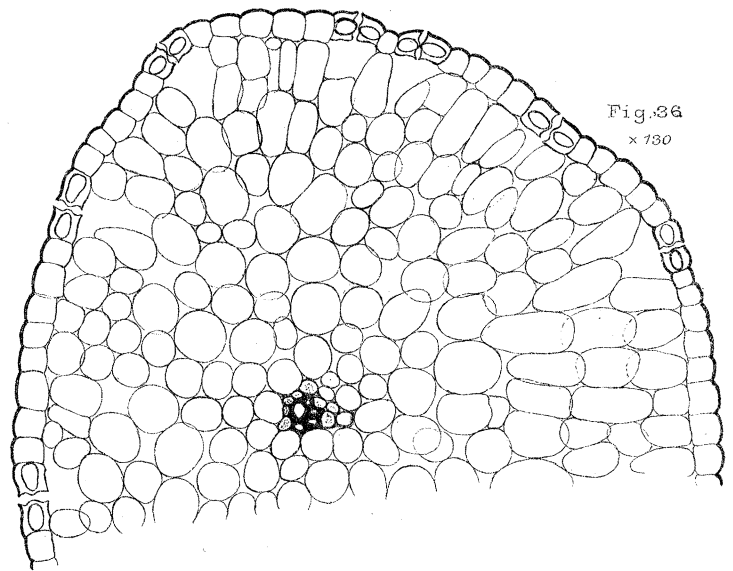


Fig. 37 x 130.

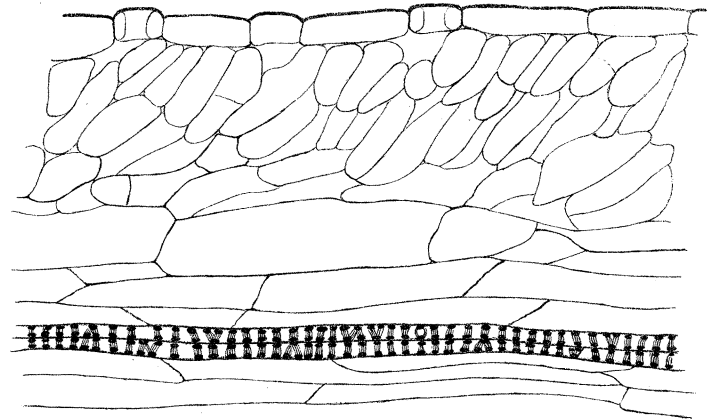


Fig. 39
x 175

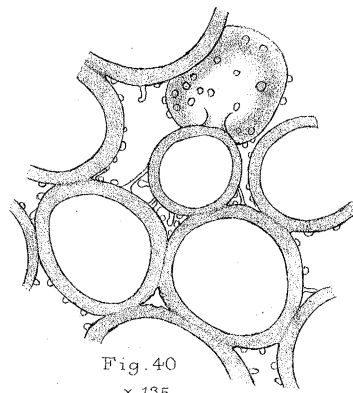
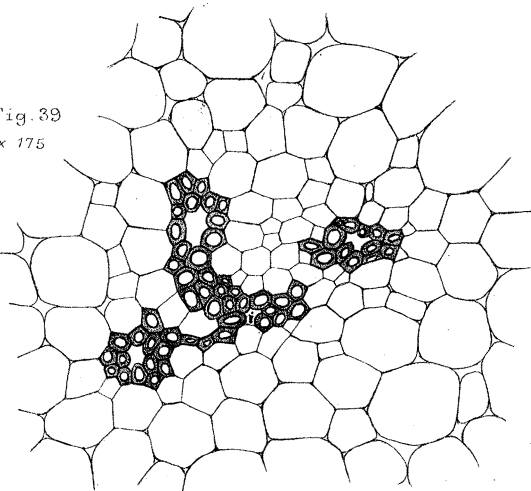


Fig. 40
x 135

Fig. 42. A

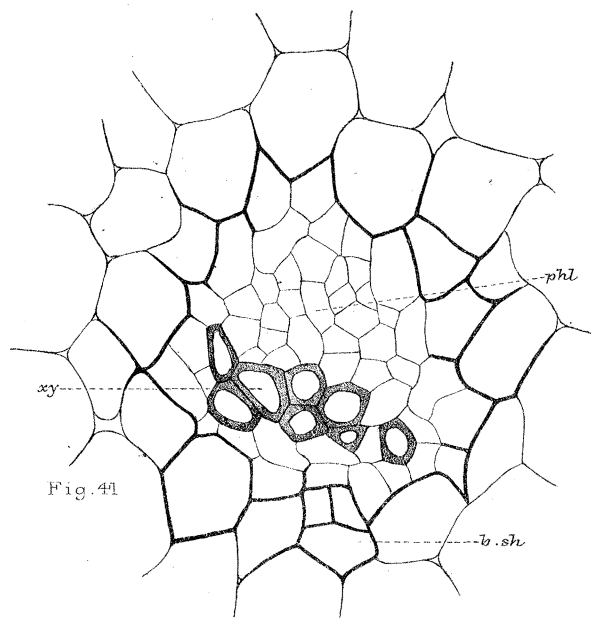
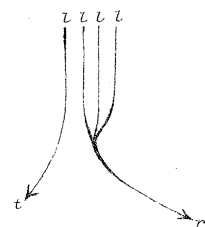


Fig. 41

Fig. 42. B

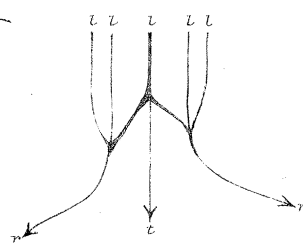


Fig. 43.

