

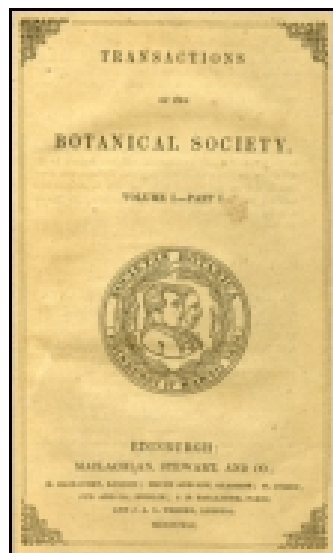
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### The Relation between the Lenticels and Adventitious Roots of Solanum Dulcamara

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13. Diagram of vascular supply of pistil.—*o.* = ovule; *ov.w.* = ovarian wall; *s.v.* = stylar vessels; *f.v.* = funicular vessel; *c.c.* = chalazal cup; *d.v.* = dorsal vessel.

14. Pistil showing basal flange.—*b.f.* formed by expanded epidermal cells; *v.k.* = ventral keel.

15. Ventral, and 16, profile view of stigma, showing the ventral groove.

17-23. Outline drawings of pistils.—17 = *laciniosa*; 18 = *viscosa*; 19 = *kurdica*; 20 = *Hookeriana*; 21 = *Fenzlii*; 22 = *approximata*; 23 = *rupestris*.

THE RELATION BETWEEN THE LENTICELS AND ADVENTITIOUS ROOTS OF *SOLANUM DULCAMARA*. By JAMES A. TERRAS, B.Sc., Lecturer on Botany, Edinburgh. (With Plates.)

(Read 11th January 1900.)

The existence of a definite relationship between adventitious roots and lenticels was recognised for the first time in 1826 by De Candolle (3), as the result of an investigation into the modes of rooting exhibited by a number of cuttings taken from the most varied species of woody plants; and subsequent authors, though differing widely as regards the degree of interdependence of these structures and the functional causes which underlie the connection between them, have never denied the primary fact that the great majority of those lateral adventitious roots, which under favourable conditions are found growing out from the surface of many woody stems, take their origin below lenticels.

Stahl (7), in his classical work on the development and anatomy of lenticels, cited *Solanum Dulcamara* as a species in which nearly all the adventitious roots arise below lenticels, but attempted no explanation.

Fourteen years later, Beijerinck (2) called attention to the remarkably large number of root rudiments occurring on the stem of this plant, and to the facility for vegetative propagation which it in consequence possesses, but made no reference to the connection between these roots and the lenticels, which, indeed, he scarcely mentions.

Klebahn (4), in 1884, figured a lenticel of *S. Dulcamara*, but made no mention of the subjacent root, and the first connected account of the relationship in which these two

structures stand to one another is to be found in a paper by the same author (5) published in 1891, and containing an account in considerable detail of the anatomical features of the fully formed root rudiment, without, however, touching on the question of its origin or mode of development, while he barely does more than refer to the lenticel, which he regards as raised on a small papilla, the projection of which above the general surface of the stem is accounted for by the growth of the underlying rootlet.

The root itself he correctly describes as exhibiting all the anatomical characters of a typical root of the species, though it remains in a state of arrested development so long as the environment of the stem is normal, and only commences to elongate under the influence of excessive moisture.

A superficial examination of any portion of the mature stem of *S. Dulcamara* will in most cases show the surface to be covered with the small papillæ above mentioned, which on the older and thicker portions often reach a height of 1 or 2 mm., and appear as rounded warty excrescences, with rough, nearly vertical, sides, and flat or slightly pointed apices.

Each papilla is accompanied by one or more small dark-coloured lenticels, placed either close to its base on the surface of the stem, in the angle which it makes with the stem, or even on the sides of the papilla itself, though but rarely on its apex, from which, however, the outer layers of cork are not unfrequently abraded, giving a rough surface, at first sight not unlike a lenticel, but easily distinguishable therefrom by the entire absence of the characteristic complementary cells; and this arrangement of parts, which may be looked upon as typical of the mature papilla, is generally to be found on all stems of more than two years of age.

On stems in their second year of growth the papillæ are in general less sharply limited, and appear as rather low dome-shaped protuberances with a smooth rounded surface, bearing on their flanks a pair of small lenticels. These are somewhat elongated in the direction of the axis, and are usually placed near the base of the protuberance, though their number and relative positions may vary considerably,

as many as three being not uncommon, while, on the other hand, they are frequently reduced to one.

They are generally placed laterally, but may occasionally occupy an oblique position, and may even, though but rarely, be found in the median plane longitudinally above or below the papilla.

On shoots of the current year no papillæ whatever are at first recognisable, and they do not make their appearance till a considerable amount of elongation has taken place and the season is well advanced. Small superficial elevations may then be observed on the stem, at or near the base of the year's growth, and as the shoot increases in age these appear at progressively higher levels, till in late autumn, when growth has completely ceased, they may be found within one or two internodes of the apical bud, while those first formed at the base of the shoot have already assumed the characters of second year's papillæ, and, like them, bear lateral lenticels.

The relative number in which these structures appear varies greatly in different plants, and even in different parts of the same plant, their formation seeming to depend to a considerable extent on the degree of transpiration to which the branches are exposed. Plants inhabiting moist situations, such as the margins of deep ditches, etc., have in general their stems almost entirely covered with papillæ, while individuals living in dry airy positions are, on the other hand, nearly devoid of them. In the case of plants growing in hedges and thickets where the surrounding vegetation supplies a considerable check to air movements and thereby limits transpiration, papillæ are especially abundant on the protected twigs, while those which project above the surrounding herbage, and are thus more exposed, are comparatively free from them. Papillæ are also not unfrequently found in larger numbers on the lower than on the upper surface of horizontal branches growing near the ground, and, as Beijerinck (2) has pointed out, wherever a branch of this kind comes in contact with the soil the root rudiments concealed within the papillæ on its lower surface grow out into functional roots.

Although plants growing in dry places never bear so large a number of papillæ as those in moister situations, it

is extremely rare to find an individual from which they are entirely absent, though in some cases they may be reduced to one or two in an internode.

*The Stem.*—In *S. Dulcamara* the leaves are arranged in a two-fifths spiral, and at each node two vascular bundles unite under the base of the leaf; of these, one arises from the similar vascular union below the leaf two internodes lower down, and the other from that below the next lower leaf, *i.e.* the leaf three internodes below the first, consequently each internode is traversed by five primary vascular bundles, the position of which is indicated on the surface of the young stem by a corresponding number of well-marked ridges.

The primary bundles are, as has been pointed out by De Bary (1), bicollateral in structure, while the internal phloem, itself of considerable thickness, is also accompanied by isolated phloem strands. The bundles are of considerable width in the tangential direction as compared with their rather small radial diameter, and are split up into a number of narrow wedges, each composed of from two to eight radial rows of xylem elements, by a varying number of medullary rays, which extend from the inner limit of the xylem to the outside of the external phloem, without however traversing that on the inner face of the bundle.

These rays are identical in structure with those laid down in the secondary wood, through which they also are continued, both being as a rule but one cell wide tangentially, and from ten to fifteen high, while in both the component cells retain their protoplasmic contents and are rectangular in outline, with the radial diameter about one-third of the height, and somewhat greater than the tangential width.

Under normal conditions the course of such a medullary ray through the phloem till it comes in contact with the inner wall of the pericycle may be readily traced, owing to the regularly radial arrangement of the, in most cases, single row of cells, which, moreover, differ individually, both as regards shape and contents, from the elements of the phloem by which they are bounded on both sides.

Its course within the xylem is equally well defined, but as the walls are now lignified, though thinner than those

of the ordinary xylem elements, it is necessary to depend on the abundant protoplasmic contents of the cells as a means of identification, and, in unstained sections, they are only recognisable with difficulty.

The stem, with its five vascular bundles, is bounded externally by an interrupted circle of isolated sclerenchymatous fibres, of rectangular, roughly square section, and of considerable length, but which in the young state appear to be only partially lignified, as it is in old stems alone that they give any reaction with phloroglucin or aniline sulphate.

These fibres are not limited to the regions immediately external to the primary bundles, but in general occur singly at intervals round the stem, though here and there a group of eight or nine may be found united together by their radial walls, in which case the group generally lies on the outer edge of a bundle. Although occasionally thus united side by side, they are seldom duplicated radially, and when this does occur, both elements clearly result from the division of a single mother-cell.

In longitudinal sections, the outer sieve tubes of the external phloem are readily seen abutting directly on these fibres, which must therefore be looked upon as representing the pericycle, along with the intervening thin-walled cells required to complete the circle, though these latter are in no way specially characterised, and are only distinguishable from those of the succeeding layer by their position and generally smaller size.

In the majority of young stems this fibrous layer is immediately surrounded by a complete circle of rather large cells, especially rich in starch, which is, however, also to be found in the other cells of the cortex, though in somewhat smaller amount, and although the characteristic dot on the radial walls is apparently absent in the stem, there seems no reason to doubt the identity of this layer with the endodermis.

The remainder of the cortical tissue, which generally reaches a thickness of from five to ten cells, is composed of rounded, thin-walled parenchyma, often containing traces of starch, and with large intercellular spaces.

*The Root.*—The first indication of the appearance of adventitious roots on *S. Dulcamara* takes place at a

comparatively early period, and apparently with remarkable regularity, the initial stages being found only during the formation of the first ring of wood, and in general shortly before or shortly after it has reached half its ultimate thickness, though here considerable variation may occur.

The greater preponderance of root-bearing papillæ, which may frequently be observed on old than on young stems, is probably to be explained by the greater proximity of the former to the surface of the soil, and the consequently greater degree of moisture in the surrounding atmosphere during the period of their development. However this may be, the roots underlying these papillæ may, in the great majority of cases, be traced back without difficulty to within the first ring of wood, even when the stems on which they appear are eight or nine years of age, and one or two centimetres in diameter.

The young roots generally bear a definite relation to the primary vascular bundles of the stem, which, as has been already pointed out, are of considerable tangential width, a point which has here a certain importance, as the roots do not usually arise opposite the median plane, but generally nearer either the right or left hand edge of a bundle, so that papillæ are seldom placed directly on the longitudinal ridges, which in the young stem are the superficial indications of the subjacent bundles, but in most cases on the intervening flat surface.

Though the situation of the root on the circumference of the stem is thus to a certain extent defined, no rule whatever appears to be followed with regard to its longitudinal position, and papillæ seem to arise with equal readiness on the bundle throughout any part of its course.

Van Tieghem and Douliot (8), in their account of the origin of lateral rootlets, state that the adventitious roots which arise from the underground stems of *S. tuberosum* originate in divisions taking place in the single layered pericycle, while the cells of the phlœm parenchyma assist in the formation of the basal part of the central cylinder; and the endodermis forms a digestive cap.

In the species now under investigation, the roots, on the other hand, apparently owe their origin to the proliferation

of the extracambial cells of one or more medullary rays, those implicated being generally situated near one or other margin of the bundle, but still within it, though in rare cases this relation is somewhat difficult to determine, owing to the secondary growth of the stem in thickness. Of these rays, one, two, or as many as three, may be concerned in the formation of a single root, but, where more than one is so employed, the intervening patches of phloem are always very narrow.

When a root is about to arise, those cells of the ray which are situated in the phloem region of the bundle undergo a remarkable series of changes, their nuclei enlarge, they become richer in protoplasm, and at once commence to divide irregularly in all three directions, thus forming a small protuberance with a conical base, which tapers gradually inwards towards the xylem, at the margin of which it is continuous with the internal xylar portion of the ray, and is here of necessity reduced to not more than two cells in tangential width, and in most cases to only one; while the outer rounded apex of the papilla is, on the other hand, composed at this stage of a convex surface, with a perimeter of five or six cells, and generally lies in contact with the inner surface of the pericycle, which is easily recognisable by its fibres. At about this stage, the thin-walled cells of the pericycle, opposite the apex of the papilla, also undergo segmentation, usually dividing, in the first instance, by radial walls, but so irregularly as to render it a matter of great difficulty to determine what part they take in the formation of the root.

Lemaire (7) mentions the occurrence of a somewhat similar irregularity in the initial divisions, which give rise to the adventitious roots of *Tecoma radicans* and *Ficus repens*, both of which further resemble *Solanum* in that their roots arise on the stems in a subaërial position, though, in both cases, all the tissues of the root are formed from the pericycle.

In this connection the behaviour of the pericyclic fibres is of some interest. Though normally the root in its outward course altogether avoids these elements, it not unfrequently happens that a single fibre or small group of

fibres is situated nearly, if not quite, opposite the end of the rhizogenetic medullary ray, and sometimes in direct contact with it.

As the papilla increases in length, these fibres become curved outwards before it; and when, owing to their ends being securely fixed in the tissue above and below, the resistance of the long, tough elements becomes too great to allow of further displacement, they cut into the apex of the root, forming therein a deep, narrow groove, at the bottom of which they may be recognised, though in a somewhat crushed condition, even when the root has reached a stage of comparative maturity.

As the groove so formed extends to the extreme apex of the root rudiment, and cuts through both root cap and periblem, the conclusion seems unavoidable that no cells external to these fibres can have any part in the origin of the root papilla, thus excluding at least the endodermis from all participation in the formation of this structure.

The remaining thin-walled cells of the pericycle undoubtedly divide, but as regards the part which they play in the formation of the root I am at present unable to make any definite statement, though, from a consideration of the arrangement of the cells in median longitudinal sections through somewhat older root rudiments, it seems improbable that they do more than give rise to the root cap, while the cortex appears to arise from the divisions of phloem parenchyma cells on the flanks of the medullary ray, from which the central cylinder takes its origin.

In the younger outgrowths no differentiation into root cap, cortex, and central cylinder is observable, but all three may be distinctly recognised in median longitudinal sections, at a stage so early that no trace of the existence of a root rudiment can be perceived on the surface of the stem. The characteristic dot on the radial walls of the endodermis of the root does not, however, appear till much later, not indeed till the superficial protuberance is almost fully formed and the xylem of the central cylinder is beginning to undergo lignification. It is, however, easily recognisable at the end of the first year in median longitudinal sections which have been double stained in Magdala-red and Malachite-green, the latter of which

colours all lignified and corky elements, while the former is exclusively absorbed by protoplasmic and cellulosic structures.<sup>1</sup>

*The Phellogenetic Divisions.*—The initial divisions of the phellogen, which in this species arises in the cells of the epidermis, are purely centripetal in direction, and, under normal conditions, the few centrifugal divisions which ultimately occur do not take place till a later period.

The origin of the rootlet, however, considerably precedes the first appearance of phellogen, and the relative rate of growth of these two structures is, in general, such that by the time the root has penetrated to within two or three cells of the outer limit of the primary cortex the phellogen has undergone from one to three centripetal divisions, with the result that the outer persistent portion of the original epidermis is separated from the dividing layer by one or two rows of cork cells.

This relation between the rates of growth of these two almost independent tissues, though fairly constant, is subject, as might be expected, to certain variations. It may, for example, happen that for some reason the origin of the root is somewhat delayed or its growth retarded in comparison with that of the phellogen, as indeed appears to occur normally in the case of the last formed roots of a year's growth.

On the other hand, the elongation of the root rudiment may altogether outstrip the formation of phellogen, a condition which may be readily brought about artificially by placing in water a shoot of the current year, after removal of as much of its basal portion as exhibits well-marked papillæ. When so treated the young root rudiments already formed in the stem increase so rapidly in length as to force their way to the exterior, perforating both cortex and epidermis before even a trace of phellogenetic division has appeared in the latter.

Every stage intermediate between these two extremes

<sup>1</sup> The sections are soaked in a saturated aqueous solution of Malachite-green till deeply stained, and then treated directly with a saturated alcoholic solution of Magdala-red, washed rapidly in absolute alcohol followed by organum oil and mounted in balsam,—a method of obtaining a double stain for which I am indebted to my friend Dr. Campbell Brown.

may be met with as an occasional variation, probably induced by the action of environmental differences, but under ordinary conditions one or two layers of cork are, as above mentioned, in general laid down before the root reaches to within a distance of two or three cells from the actively dividing phellogen. When, however, this position has been approximately attained, the phellogenetic divisions in the cells immediately opposite the root entirely lose their centripetal character, and there is initiated a series of centrifugal divisions, which, commencing opposite the apex of the root, extend laterally in the phellogen, and eventually result in the formation of a lenticular mass of secondary cortex, with its greatest thickness in the centre opposite the root, but becoming gradually thinner till it disappears in the circumference of a circle, whose diameter is in general about three times that of the root in front of which it originates.

This secondary tissue is entirely composed of thin-walled parenchyma cells, somewhat rectangular in outline, and with but a few small intercellular spaces between their slightly rounded angles.

Considering the relation between the position occupied by the apex of the root, and the period at which the development of this tissue takes place, as well as its exceptional character, it is difficult to avoid the conclusion that its formation must be looked upon as the external evidence of the response made by the actively dividing cells of the phellogen to the pressure exerted on them by the elongation of the root.

The rapidity with which these centrifugal divisions succeed one another in the line of the rootlet's advance is somewhat remarkable, and in general exceeds that of the normal centripetal divisions, taking place at the same time in the unaffected portions of the phellogen. Indeed, the time required for the completion of the whole lenticular mass of tissue, which in its centre often reaches a thickness of twelve or thirteen cells, is frequently less than that occupied by the deposition of a single layer of cork.

This rapid localised deposition of secondary cortex by the phellogen is the primary cause of the formation of protuberances on the surface of the stem, and these, at

least during the earlier portion of the first year, owe almost their entire elevation to it, as the comparatively slow elongation of the root confines it for a considerable period within the primary cortex, where it can exert but little direct influence on the height of the protuberance above it. Later in the season, however, it begins to press heavily on the internal surface of the secondary cortical tissue, and soon penetrates into it, pushing before it the upper and outer layers, and thus greatly increases the elevation of the papilla.

The centrifugal divisions of the phellogen continue even after the apex of the root has pierced the inner layers of the lenticular mass of tissue, but at this period the rate of elongation of the root generally exceeds to a considerable extent that of the formation of secondary cortex, with the result that the former gradually penetrates deeper and deeper into the latter, and, in the majority of cases, entirely pierces it before the end of the second year, though instances are not wanting in which some layers of secondary cortex are still recognisable between the apex of the root and the cork cells covering the outer end of the papilla, as late as the end of the fourth year, so that the root, it would appear, may stop short of reaching the phellogen. This, however, is not of common occurrence; and in most cases when the papilla is fully mature, the root apex may be seen to be covered only by a few cells of cork, or even, owing to the abrasion of the cork layers, to be entirely without protection.

*The Lenticels.*—Towards the end of the first year one or two typical lenticels appear, as above mentioned, on the lateral flanks of the superficial protuberances.

These arise generally to right and left of the root apex, and apparently owe their origin to a return to the centripetal mode of division taking place in certain circumscribed patches of the phellogen, which, however, instead of laying down ordinary cork tissue proceed to deposit the loose, rounded complementary cells so characteristic of lenticels. As the remaining portions of the phellogen covering the protuberance continue to divide in a centrifugal direction, the lenticellar areas become depressed below the rest of the dividing layer, while their rapid formation of comple-

mentary cells ruptures the layers of cork above them, and thus opens the lenticel to the atmosphere.

The structures so formed persist apparently throughout the life of the plant, and can almost, without exception, even in stems of eight or nine years of age, be found at or near the bases of the papillæ, to which, indeed, they are confined.

#### CONCLUSIONS.

I. That in *Solanum Dulcamara* the adventitious roots do not arise below or grow out through lenticels, as is apparently the case in the majority of plants.

II. That, as the origin of the root precedes the appearance of phellogenetic divisions, it is entirely independent of lenticellar formation.

III. That the protuberances on the surface of the stem are not lenticels, but result from the formation of a mass of secondary tissue, which originates in the reaction of the phellogen to the pressure set up by the elongating root below it.

IV. That the lenticels only appear after the protuberances are fully formed.

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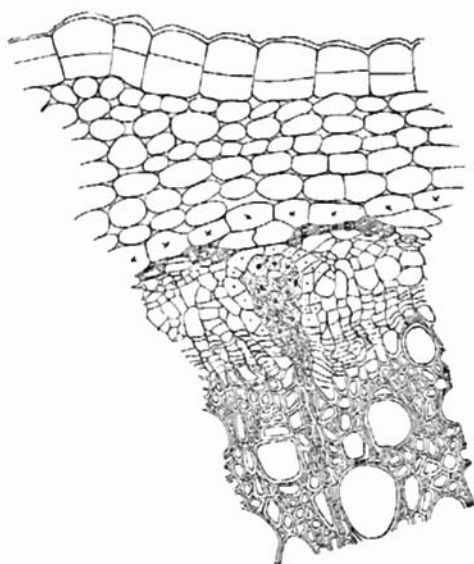


PLATE I.

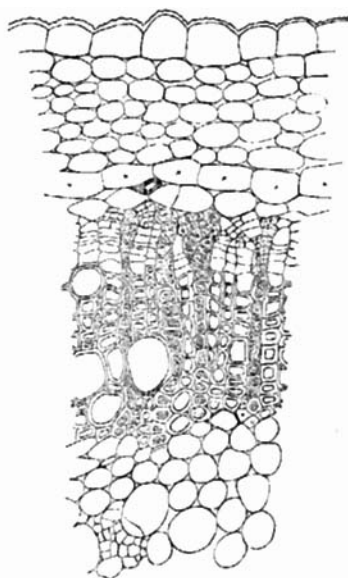


PLATE II.

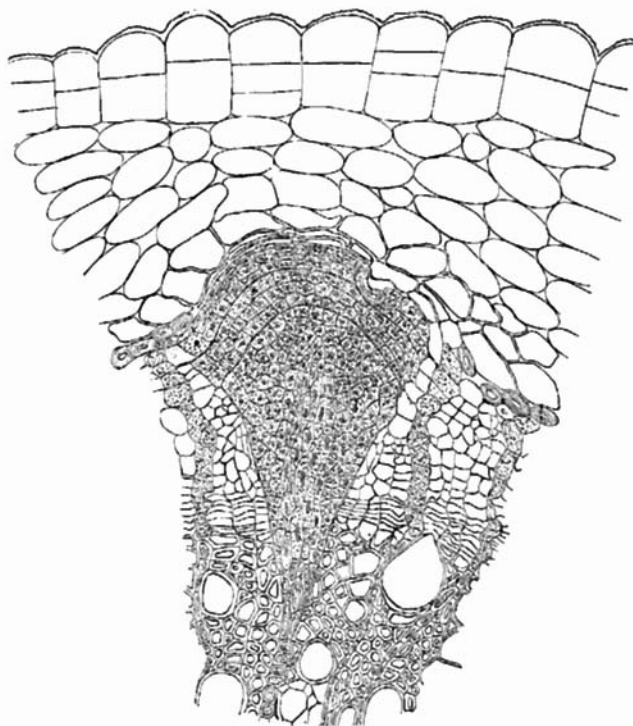
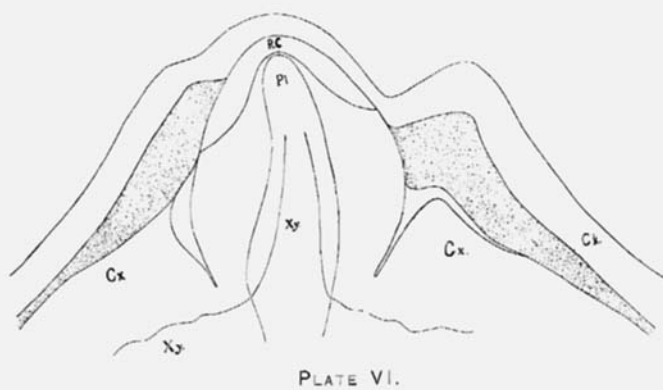
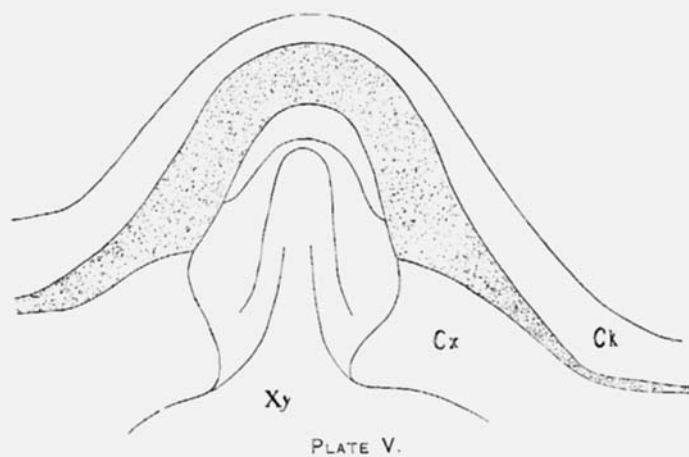
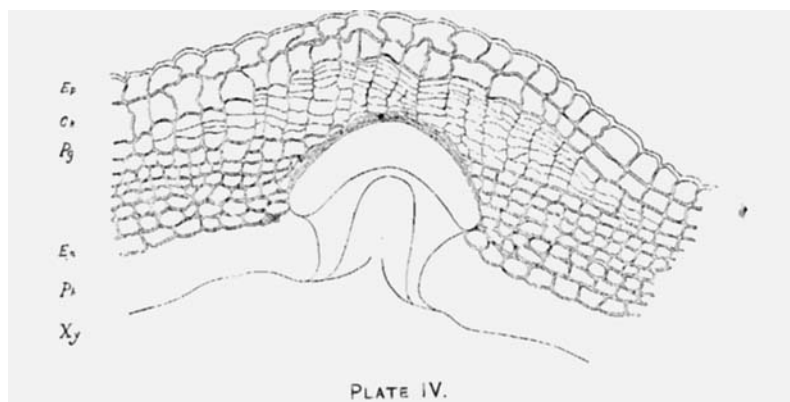


PLATE III.



## EXPLANATION OF FIGURES.

## PLATE I.

- Fig. 1. Early stage of root, the outer cells of the medullary ray dividing. The cells marked  $\times$  are endodermal.
- Fig. 2. Later stage endodermis as before. Numerous pericyclic fibres; thin-walled pericycle cell opposite root apex, dividing radially; marked cells outside medullary ray tissue represent cells of the phloem region which have become meristematic.
- Fig. 3. Root showing three regions. Pericyclic fibre commencing to cut a groove in the apex; endodermis not recognisable owing to growth in thickness of stem.

## PLATE II.

- Fig. 1. Formation of lenticular mass of secondary cortex opposite apex of root, which has already penetrated its base—*ep*, epidermis; *ck*, cork; *pg*, phellogen; *en*, probable position of endodermis; *ph*, phloem of stem; *xy*, wood of stem.
- Fig. 2. Older stage of root. Mass of secondary cortex dotted and partially perforated by the root.
- Fig. 3. Mature papilla. Secondary cortex entirely pierced. Root in resting state.

CONTRIBUTIONS TO THE FLORA OF SPITSBERGEN, ESPECIALLY OF RED BAY, from the Collections of W. S. BRUCE, F.R.S.G.S., Naturalist to the Prince of Monaco's Expeditions of 1898 and 1899. By R. TURNBULL, B.Sc., Lecturer on Botany, School of Medicine, Edinburgh.

(Read 8th March 1900.)

In a former communication (9th February 1899) to this Society, I gave an account of the flora of Hope Island, and mentioned Mr. Bruce's first visit to Spitsbergen in the Prince of Monaco's steel yacht, the "Princesse Alice," in 1898. Since the publication of that paper, I have learned that Mr. Leigh Smith collected plants from Spitsbergen and Hope Island, and a record of them is contained in the "Journal of Botany," vol. xiv., 1876.

Some of the plants in the present collection were gathered by Mr. Bruce in 1898, but most of them were obtained during the second voyage of the "Princesse Alice" to Spitsbergen, in 1899.

An account of the two voyages, and a map of Spits-