THE VASCULAR ANATOMY OF THE TUBERS OF *NEPHROLEPIS*.

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[WITH THREE FIGURES IN THE TEXT].

INTRODUCTORY.

ALTHOUGH from the point of view of their biological significance the tubers borne on the underground stolons of *Nephrolepis* have been the subject of frequent comment[1], their vascular anatomy does not appear to have received the attention it deserves. The investigations of Professor Heinricher, who studied the tubers under artificial conditions of culture, while dealing in a most interesting manner with the biological problems, leave the vascular anatomy out of consideration, and since 1889 no reference has been made to it. In that year Lachmann[2] made the observation that the single strand traversing the stolon breaks up at the base of the tuber into a number of smaller strands usually concentric or rarely bicollateral in structure, which form a network lying in the peripheral part of the tuber, parallel to its surface, and converge again towards the apex of the tuber, there uniting into a single strand. Lachmann, however, did not describe the changes which the strand undergoes in order to give rise to the reticulate system traversing the periphery of the tuber; and as these form an interesting parallel to the mode of elaboration of the dictyostele from the protostele in the ontogeny of many Ferns, they would seem to be worthy of description.

The material for this work consisted partly of tubers of *Nephrolepis cordifolia* from the Cambridge Botany School, and partly of fresh tubers of the same species obtained from the Cambridge Botanic Garden through the kindness of the Curator, Mr. R. Irwin Lynch, M.A., to whom I wish to express my hearty thanks.

[1] Sperlich, A., Flora, 1906, p. 451; Sperlich, Flora, 1908, p. 341; Heinricher, E., Flora, 1907, p. 43.

[2] Lachmann, J.-P., "Contributions à l'histoire naturelle de la racine des fougères," Lyon, 1889, Thèse présentée à la faculté des sciences de Paris, pp. 155-6; Hofmeister, W., "Beiträge," etc., II. Abhandl. d. kgl. sächs. Ges. d. Wiss. V. Math.-Phys. Klasse III., Leipzig, 1857, p. 651.

Beyond the remarks contained in these two communications I am not aware of any reference hitherto made to the subject in question.

DESCRIPTIVE.

Several species of *Nephrolepis*[1] are now known to possess tubers, which are as a rule terminal swellings of short branches of the underground[2] stolons. The apex of the branch forms a minute mamelon at the distal end of the tuber. Only rarely, according to Professor Goebel's observations,[3] is the mamelon developed into a stolon while the tuber is still attached. The tuber is so completely protected by imbricating peltate scales that no part of its surface is left exposed. The fresh tubers examined by me contained enough sugar to give them a sweetish taste, and a copious brown precipitate with Fehling's solution confirmed the presence of a considerable quantity of a reducing substance. The outermost one or two layers of cells also contained a few starch-grains.

Fig. 1, A, illustrates the vascular relations between the stolon and the tuber. We shall follow the transition from the solid protostele of the stolon to the netlike stele of the tuber, as revealed by a series of transverse sections from the base upwards. But before describing these changes it will save some repetition to state that the manner in which the strands finally fuse up into the solid protostele at the apex is the reverse of the process of disintegration occurring at the base. In both these processes, however, individual variations are met with, which we shall later attempt to explain.

The strand of the branch-stolon penetrates the base of the tuber as a solid protostele for a few millimetres; its four or five protoxylems, hitherto more or less clearly seen,[4] may at this time become indistinct. The xylem then begins to dilate in a funnel-like manner and acquires a central mass of phloem which enlarges and is soon followed by pericyle, endodermis and ground-tissue in succession. The solid cylinder of xylem has been converted into a

[1] Heinricher, *loc. cit.*, p. 67. Tubers have also been recorded in *N. neglecta* by Lachmann. "Recherches sur la morphologie et l'anatomie des fougères," (Comptes rendus, CI, 1885, p. 605), and in *N. undulata* by Kunze (Bot. Ztg., 1849, p. 882) and by Hofmeister, (*loc. cit.*, p. 65); but these species may be synonymous with some of those mentioned by Heinricher.

[2] Under certain conditions, according to Sperlich (Flora, 1906, p. 454), tubers may be produced on the aerial stolons.

[3] Goebel, K., "Pflanzenbiologische Schilderungen I," 1889, p. 203. In one specimen at the Cambridge Botanic Garden, however, six of the tubers had produced stolons at their distal ends.

Attention may incidentally be drawn to the appearance of chlorophyll in the superficial layers of the young tubers as well as in some young underground stolons, *before* these organs have been exposed to light.

[4] Attention may here be drawn to a minor point, namely, that whereas in the aerial stolon there are usually four very well-marked protoxylem strands, in the underground stolons they are neither constant in number nor so well differentiated and regularly distributed.

hollow cylinder lined internally as well as externally by phloem, pericycle and endodermis, while the centre is occupied by a patch of ground-tissue which in this region is sclerenchymatous. This

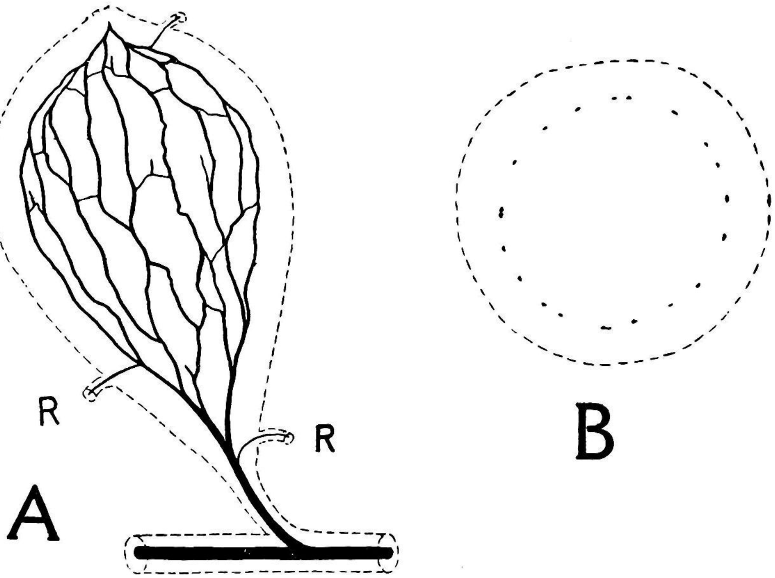

FIG. 1. *Nephrolepis cordifolia. A.*—Slightly diagrammatic representation of the vascular system of the tuber and its relation with that of the stolon. The broken line indicates the outermost limit of the cortex in both tuber and stolon. R, roots; their points of origin have no relation to the gaps in the reticulate stele of the tuber. *B.*—Transverse section of the tuber through its broadest part. *None of the gaps have any relation to leaf-traces*, whether rudimentary or other.

state of affairs does not, however, long persist, for, as the cross-section of the tuber increases, the stele also expands further and the xylem ring (Fig. 2, A) which has in places already become attenuated to only one or two layers of tracheides, becomes disintegrated into usually three or four arcs separated by gaps, with the result that the internal phloem becomes continuous with the external at the edges of the gaps. The arcs of xylem become further and further removed from the centre and from each other. Through the widening gaps first the internal pericycle, then the internal endodermis, and finally the central ground-tissue become continuous with the corresponding external tissues. The "pith" has meanwhile lost its thick-walled character and can no longer be differentiated from the cortex. As we pass distally from the base of the tuber, the arcs of xylem divide repeatedly by constriction and give rise to a considerable number of strands which anastomose with each other, forming an irregular network lying parallel to the surface of the tuber, a few millimetres inside it. In a transverse section of the tuber in its broadest part (Fig. 1, B) the vascular system appears as a ring of about a dozen or more tangentially flattened strands, each consisting of a plate of xylem completely

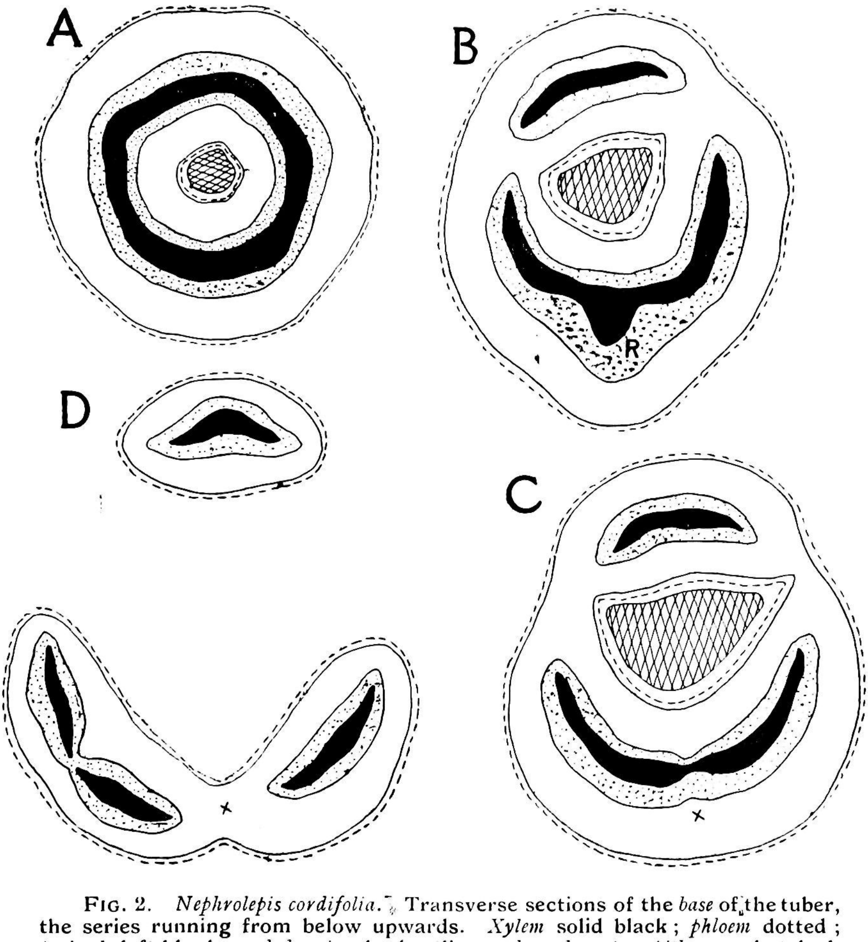

FIG. 2. *Nephrolepis cordifolia.* Transverse sections of the *base* of the tuber, the series running from below upwards. *Xylem* solid black; *phloem* dotted; *pericycle* left blank; *endodermis* a broken line; *sclerenchymatous pith* cross-hatched.

A has the appearance of a typical solenostele cut at a point where it is uninterrupted by a leaf-gap. In *B* a root-stand is coming off at R, and gives the impression that its exit is responsible for the gap (x) seen in *C* and *D*. In the two latter diagrams the detached root-stand is omitted.

surrounded by phloem, pericycle and endodermis. The xylem-plate is usually only one or two layers of tracheides thick, with the smallest elements at its two extremities. Distinctly spiral or annular tracheides could not be made out clearly. Bicollateral strands such as Lachmann found in *N. exaltata* were not seen.

The course of elaboration sketched above is very often slightly modified, inasmuch as the internal phloem may effect a junction with the external *before* any internal pericycle has made its appearance. (Compare Fig. 3, which is from serial sections of the *apex* of a tuber). The xylem-ring is thus converted into a horse-shoe: the gap of the horse-shoe is at first merely bridged over by external phloem, which is in turn overlain by pericycle and endodermis, but

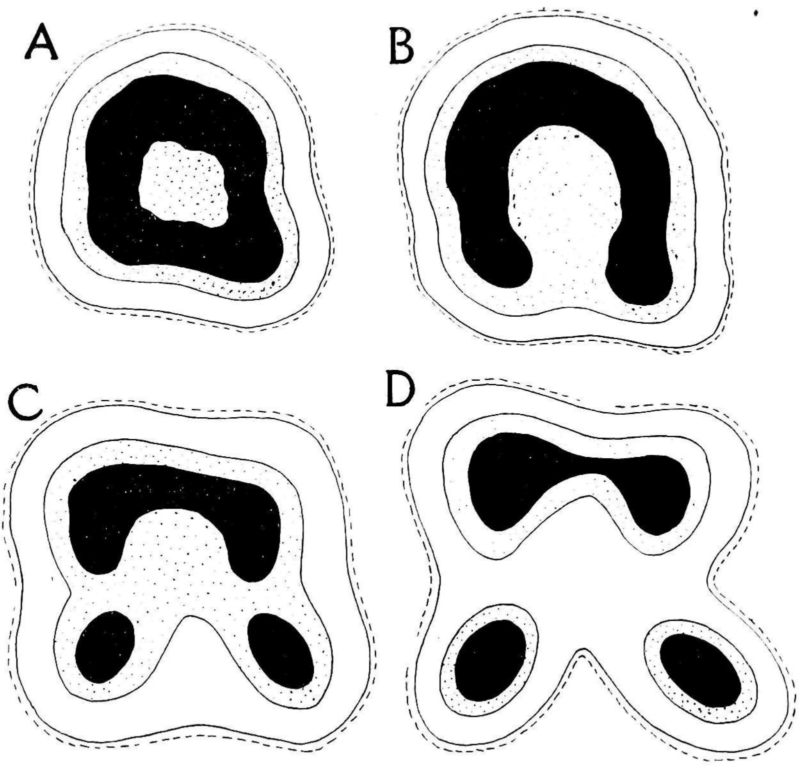

FIG. 3. *Nephrolepis cordifolia.* Transverse sections of the *apex* of the tuber, the series running from the apex downwards. The various tissues are indicated as in Fig. 2. Diagram *A* shows a stage resembling the "*Lindsaya*-type" of stele. For further explanation see Text.

it subsequently becomes invaded by the latter tissues in succession. Disintegration of the horse-shoe gives rise to three or four xylem-strands arranged in a ring. This process of disintegration may either begin before the pericycle has advanced far into the gap, so that we have the xylem-strands lying embedded in a single mass of phloem (Fig. 3, C); or it may be delayed till after the pericycle and endodermis have formed a complete internal lining to the xylem.

One cannot fail to notice the superficial but close similarity of some of the stages shown in Figs. 2 and 3 to those passed through by many fern-rhizomes during their individual development from the protostelic to the dictyostelic condition. Fig. 3, A, for example, is strongly suggestive of the "*Lindsaya*-type" of stele, while Fig. 2, A is exactly the appearance presented by a transverse section through the internode of a typical solenostelic fern. Neglecting for a moment the mode of origin of the gaps, the appearance of a transverse section through the middle of the tuber does not materially differ from that of a dictyostelic rhizome.

Roots arise promiscuously on the tuber, but sometimes they are almost confined to the narrow basal end and to the apical mamelon. As their strands are sometimes attached to the net-like stele at the base of a gap, sections through those regions (Fig. 2, B, C) give the impression that the gap is "caused" by the exit of the root-traces. An examination of Fig. 1, A will, however, show that the point of origin of the root-strands does not follow any rule.

It seems probable that the relative duration of the different stages in the transition depends largely upon the shape of the tuber. If the increase of diameter from the stolon to the tuber is gradual (as shown in Fig. 1, A) the expansion of the vascular system is correspondingly slow, and the intervening tubular stage, with internal phloem, pericycle and endodermis, is of appreciable length. If, on the contrary, the tuber is sharply marked off from the stolon the different stages in the transition succeed each other rapidly and may even overlap, so that the xylem-ring may become disintegrated before it has acquired an internal pericycle, endodermis and ground-tissue (Fig. 3, C). In the light of this suggestion some of the individual variations met with in the mode of transition may perhaps be satisfactorily explained. This view appears to find support in the fact that in the pear-shaped tubers examined the transition was more rapid at the apex than at the base (that is, the narrower end).

Professor Heinricher (*loc. cit.*, p. 71) has found that the shape of the tuber seems to be characteristic for each species and suggests that it may be a character of taxonomic value. Thus in *N. hirsutula* Presl *apud* Raciborski the tubers were pyriform, while in specimens of *N. tuberosa* (Bory, Willd.) Presl=*N. cordifolia* (L.) Presl they were found to be ellipsoid. In view of the confused condition of the taxonomy of the genus such a distinction would be welcome, but it is difficult to say what importance can be assigned to this character, for variations in the shapes of tubers from the same plant are not rare. In a few tubers from a specimen of the last-named species a complete transition from the pyriform to the ellipsoid could be traced. Some of the tubers were flattened, having grown against the wall of the pot, while others were distorted by small pebbles in the soil. A few were spherical.

THEORETICAL.

In the foregoing account of the vascular anatomy of the tubers the main feature of interest is that the different stages through which the stele passes from the solid, cylindrical to the net-like condition are closely similar to those seen in the ontogeny of the solenostelic and dictyostelic Ferns, in which the influence of leaf-traces is justifiably regarded as the dominating factor in the evolution of the cauline stele (Boodle, Gwynne-Vaughan, Tansley). My first impulse was to conceive of the tuber as possibly homologous with the "lateral plant" borne normally on the aerial stolon, which might have undergone swelling and a great reduction in the leaves, so that in its modified form it may serve as an underground organ for vegetative reproduction and water-storage. Certainly the position of the tuber on the stolon is exactly the same as that of a lateral plant, and the similarity in the stelar condition as traced from the base upwards encourages one in the hypothesis. The meshes in the network of strands might then be interpreted as leaf-gaps such as are known to exist in the Cactaceæ,[1] in spite of the extreme reduction of the leaves. The hypothesis is, however, not to be seriously entertained in view of the fact, already noticed by Heinricher (*loc. cit.*, p. 50), that the surface of the tuber shows no trace of leaves, even in a most rudimentary form.

Since then, none of the gaps can be looked upon as leaf-gaps, the stele in question is not entitled to be called even a perforated or dissected solenostele. Such a stele is not, to my knowledge, known to exist elsewhere among Ferns. It may be mentioned that in one underground stolon the strand was seen to break up into a few anastomosing ones arranged in a ring; these again fused up into a single strand at a point several millimetres from where the original strand divided. The portion of the stolon between these points showed neither any marked swelling nor any trace of leaves.

Structures which in external appearance (and apparently also in function) most closely approach *Nephrolepis* tubers are found in several species of *Equisetum* (*E. arvense*, *E. Telmateja*, *E. palustre*, *E. hiemale*) in which some of the internodes of the subterranean rhizome undergo swelling.[1] A point worth noticing is that in these

[1] Ganong, W. F. "Beiträge zur Kenntnis der Morphologie und Biologie der Cacteen." Inaugural-Dissertation. Cited by Jeffrey, E. C., Trans. Canad. Inst., 1900, p. 35 of Reprint.

also the strands diverge widely from the base and converge again towards the apex (*loc. cit.* p. 41, and Plate I, fig. 3). Tubers similar to those of *Nephrolepis* have also been recorded by Ule[2] in a species of *Hymenophyllum*, but unfortunately nothing more is known about these.

Since the behaviour of the vascular strands in the tubers of *Nephrolepis* cannot be explained as being due to any influence from leaf-traces, we must look for an answer to the problem elsewhere. For a plausible suggestion, which would apply equally well to the case of *Equisetum*, I am indebted to Mr. R. H. Compton who believes that an increase in the diameter of an organ tends to cause a corresponding dilatation of its vascular system. As he has pointed out in another connexion,[3] "the impression given . . . . . is that the stele takes the opportunity afforded by the increased diameter to acquire a pith and expand." While dealing with the factors in the evolution of solenostely Mr. Tansley[4] has remarked that an increase in the diameter of the stele would be necessitated by any broadening in the span of the C-shaped leaf-trace, to the attachment of which on an originally solid stele he has ingeniously traced the root-cause of the departure towards solenostely. In the case of *Nephrolepis* and *Equisetum* the great increase in the diameter of the axis may exert on the stele an influence similar in effect to that of the enlarging leaf-trace on the cauline stele. For the proper supply of food and water to a storage organ of large diameter, it would be necessary that the vascular system should not have the form of a solid axial cylinder, but of an expanded hollow stele.

The further change, from the tubular to the net-like condition may be taken to be a natural result of the enormous dilatation of the stele, and the concomitant thinning of the tube in places to produce the "perforations." Contrary to what is the case in the normal fern rhizome, where the dilatation of the stele is, comparatively speaking, slight, we may confidently believe that the mere thinning of the tubular stele would suffice to produce gaps in it. In fact, a suggestion of such a mode of origin for these perforations is visible in their irregular shape, in the frequent occurrence, at their edges, of thin blindly-ending strands, and in the varying width of the

1 Duval-Jouve, "Histoire naturelle des *Equisetum* de France," 1864, p. 6 ff.; Luerssen in Rabenhorst's Kryptogamen-Flora, iii., 1889, figs. 203, 206, 209.

2 Ule, E., Berichte d. d. bot. Ges., XV., 1897, p. (85).

3 Compton, R. H., "An Investigation of Seedling Structure in the Leguminosæ," Journ. Linn. Soc. 1912, p. 97.

4 Tansley, "Lectures on the Evolution of the Filicinean Vascular System," New Phytologist, 1907, p. 150.

ribbon-like strands composing the reticulate stele.

I wish to express my hearty thanks to Professor Seward for his kind interest in the work and also for revising the manuscript of this paper.

SUMMARY.

The strand of the branch-stolon penetrates the base of the tuber as a solid protostele for a few millimetres (Fig. 1, A), but rapidly expands in a funnel-like manner, acquiring, in succession, internal phloem, pericycle, endodermis and ground-tissue (Figs. 2 and 3). Sooner or later the funnel-like stele breaks up, while at the same time expanding enormously, into a hollow net-work of tangentially flattened ribbon-like strands (each concentric in structure), enclosing gaps of irregular shape and size. These strands converge again into a single protostelic strand. The latter as a rule ends in the apical mamelon, which contains the apical cell; but when the mamelon is developed into a stolon the strand is continued into the latter.

Root-strands arise promiscuously from this reticulate stele.

The process of fusion of strands at the apex is similar to the process of stelar disintegration at the base, the relative duration of the various stages in the transition depending upon the rapidity with which the tuber tapers towards its ends. This relation is inverse.

Attention is drawn to the superficial but close similarity of some of the stages in the transition to those passed through by many fern-rhizomes in their development from the protostelic to the dictyostelic condition. There being no sign even of reduced leaves on the tuber, the gaps cannot be traced to any influence from leaf-traces, which in normal fern-rhizomes have justifiably been held to be the dominating factor in the evolution of the cauline stele (Boodle, Gwynne-Vaughan, Tansley). It is suggested that the necessity of adequately supplying food to all parts of the tuber has "called forth" in the originally solid stele a dilatation great enough to transform it into a hollow net-work; this dilatation being similar to that "necessitated," according to Tansley, by the increase in the span of the C-shaped leaf-trace, to the attachment of which on an originally solid stele he traces the root-cause of the departure towards solenostely.

The reticulate stele of the tubers of *Nephrolepis* is unique because *all* the gaps in it are what have technically been called "perforations."

THE BOTANY SCHOOL, CAMBRIDGE,
March, 1916.