

THE ANATOMY OF *NEPHROLEPIS VOLUBILIS* J.Sm.,
WITH REMARKS ON THE
BIOLOGY AND MORPHOLOGY OF THE GENUS.

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[WITH PLATE IV AND SEVEN FIGURES IN THE TEXT].

I. INTRODUCTION.

THE subject of this paper is a description of a species of *Nephrolepis* (*N. volubilis* J.Sm.)¹ collected near Kuala Lumpur, Federated Malay States, by Mr. F. T. Brooks during 1914. In spite of its many interesting features, this plant does not seem to have been previously investigated.² The enormously long stolons which enable the young plants arising on them to climb trees to a very considerable height, the entire absence of roots on these lateral plants, and the presence on them of coiled tendril-like stolons which suggest contact irritability, are features of biological interest which seemed worth investigating; the mode of branching of the stolons and the structure of the lateral plants were followed out in some detail. Unfortunately, no part of the mother-plant was available, nor is the latter represented in any of the specimens at the Kew Herbarium; each contributor seems to have collected only a portion of the long stolon bearing some lateral plants.

It may be mentioned that several of the systematic authors who have described this plant refer to the stolon as if it were the main axis of the plant.³ I am indebted to Mr. Boodle for the discovery of this error.

During the work, comparisons with other species of *Nephrolepis* were frequently necessary, and a few of these observations are included below. These would have been inaccessible to me had it not been for the kindness of Dr. Stapf, who granted me the privilege of dissecting dried material from the Royal Herbarium,

¹ Christ, "Farnkräuter der Erde," p. 288, 1897; Clarke, Trans. Linn. Soc., Bot. II, 1879, p. 541, pl. 78. Synonyms are *N. radicans*, Kuhn, Ann. Mus. Bot. L.B. iv., 285; *Polypodium radicans*, Burm. (oldest name).

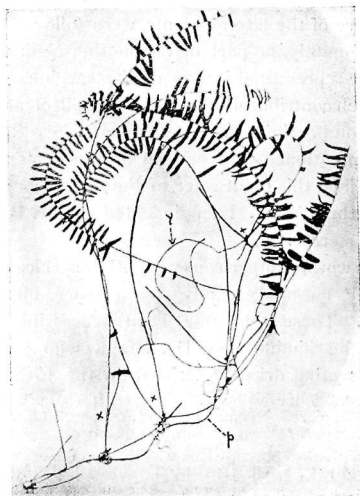
² The only anatomical observations which can refer to this plant are in a paper (Ann. Sci. Nat. V, t. xii, 1869) by Trécul, called "Remarques sur la position des trachées dans les Fougères." The author, in a footnote on p. 245, alludes to the outstanding anatomical features of a fern which he elsewhere (Ann. Sci. Nat. V. t. x, 1869, p. 351) regards as probably a *Nephrolepis*, but which he was unable to identify. His brief account, so far as it goes, agrees largely with that set forth below, and it is likely that his plant was the same.

³ Clarke, l.c.; Christ, l.c.; Diels in Engler u. Prantl, Nat. Pfl.; van A. van Rosenburgh, "Malayan Ferns," 1908, p. 161.

Kew, and of Mr. R. I. Lynch, M.A., Curator of the Cambridge Botanic Garden, who helped me with fresh material. To both my sincere thanks are due. I have also to thank Mr. Ridley and Mr. C. H. Wright for help in identifying the specimen of *N. volubilis*.

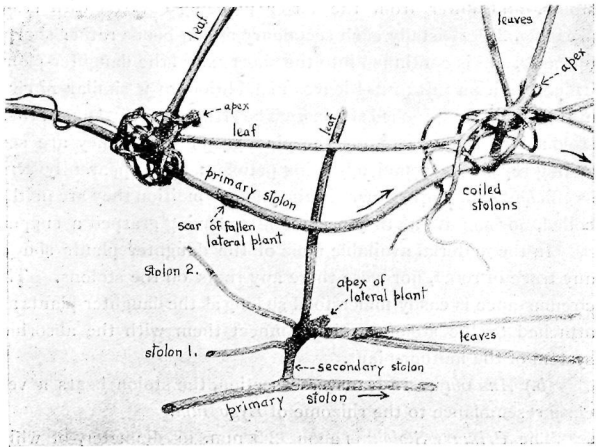
II. METHODS.

Special mention may be made of the way in which the diagrams in Text-fig. 4 were obtained. The stele of the primary stolon being only loosely attached to the cortex, it is easily dissected out. When freshly removed it is cylindrical, but on being left to dry up, it assumes the shape of a fluted column of which the ridges correspond to the exarch protoxylem strands, and the grooves were filled by the now badly shrunken thin-walled phloem and pericycle. On such specimens, prepared from regions where the stolon branches, the successive bifurcations of the protoxylem strands can be traced with ease.



TEXT-FIG. 1. *Nephrolepis volubilis*. Photograph (much reduced) of portion of primary stolon *p* (loosely twining) bearing several lateral plants (*x*). Repeatedly coiled stolons are seen at the points of origin of the lateral plants. At *y*, a young stolon which has not yet grasped a support.

Phlobaphene is commonly found in ferns, impregnating the walls of ground tissue cells just outside the endodermis, and is well-known for its great resistance to acids.¹ Of a piece of the stolon about half a centimetre long kept in concentrated chromic acid for some days, all parts had been destroyed except the phlobaphene in the inner cortical layers, which was left intact as a black hollow cylinder. This method may perhaps be of use in following the intricate vascular structure of certain other ferns, in which the phlobaphene-containing layers closely invest the vascular strands.



TEXT-FIG. 2. *N. volubilis*. Natural size photograph showing three lateral plants. The cut ends of the primary stolon show the single axial strand. Scabs cover the secondary stolons and the lateral plants.

III. DESCRIPTION OF *NEPHROLEPIS VOLUBILIS* J.SM.

(a.) *External Features and Distribution.* This species, which ranges in distribution from Northern India, through the Malayan Region to New Guinea,² is distinguished chiefly by its peculiar habit. The main axis gives rise laterally to stolons of unusual length which, instead of creeping about on the substratum as in the other species of the genus, scale forest trees up to a height of 16 metres and thus raise the young plants, produced on them at intervals, far above the level of the ground vegetation of which the mother-plant forms a

¹ Walter, *Bibliotheca botanica*, iv, p. 15, 1890.

² Christ, l.c.

part. The particular specimen that Mr. Brooks saw was at least 10 metres in height and was scrambling over bushes on to a tree at the outskirts of a forest.

The stolons are stiff, cylindrical organs, devoid of ramental scales in the older parts; the surface is smooth, except for the scars of fallen branches (Text-fig. 2), or for occasional dormant buds.¹ Faint brown spots mark the positions of lenticel-like structures, while the minute scars of fallen ramental scales are also distinguishable. Short branches, which may be called secondary stolons, come off at frequent intervals almost at right angles to the primary stolon, and differ from the latter in being covered with scales (Text-fig. 2).² Distally each secondary stolon bends rather sharply upwards, and is continued into the short axis of the daughter-plant,³ which carries a tuft of 2-4 leaves in addition to a similar number of thin, wiry, unbranched stolons. The striking appearance of these stolons is well illustrated by the photograph where they are seen coiling repeatedly round adjoining petioles; they apparently serve as efficient climbing organs. In the young condition they are neither coiled, nor so stiff, as they become after having grasped a support.

In the material available none of the daughter plants showed any trace of roots, nor were there any roots on the stolons. This circumstance is easily understood so long as the daughter-plants are attached to the stolons which connect them with the absorbing system of the mother-plant.

(b.) *Anatomy*. In transverse section, the stolon bears a very close resemblance to the rhizome of *Lygodium*.

The *Primary Stolon*⁴ is about 2.5 mm. in diameter, of which about 1 mm. is formed by the *xylem-cylinder* in the form of a fluted column composed of tracheids and parenchyma. In transverse sections (see Pl. IV, figs. 1 and 2) the parenchyma appears as tortuous 1-3-seriate chains of thin-walled cells with normal contents. In longitudinal section, these cells appear in vertical rows and are

¹ Sperlich, Flora, 1906, p. 463, pl. iv, fig. 2 (*N. cordifolia*).

² At this stage it should be made clear that there is no marked line between the "lateral plant" and the "secondary stolon." In fact, it may even seem advantageous to leave out the term secondary stolon, and consider the lateral plant as arising directly on what we have termed the primary stolon.

³ One case was observed where it was continued into a short piece which was identical in character with the primary stolon, the latter becoming arrested. This piece again produced a branch exactly like a primary stolon, and itself became arrested.

⁴ Already described for *N. exaltata* by Lachmann ("Contributions à l'histoire naturelle de la racine des Fougères," Lyon, 1889) and by Chandler (Ann. of Bot., 1905, p. 392) and Sperlich (l.c., p. 464 ff.) for *N. cordifolia*.

several times longer than broad, with horizontal or oblique end-walls, probably forming a connected system. The cells store abundant oval starch-grains in the mature parts of the stolon. The metaxylem elements are all finely scalariform and develop centripetally, the larger tracheids being nearer the centre. The protoxylem consists of narrow annular and spiral tracheids grouped in 7-9 distinct *exarch* strands forming the ridges on the xylem-cylinder. Each protoxylem strand is traversed by one or two longitudinal rows of parenchyma cells.

The *phloem* is *continuous* round the xylem, and the proto- and meta-phloems are easily distinguishable on account of the much larger elements of the latter. Taking the metaphloem first, the sieve-tubes occur in distinct crescentic groups occupying the bays between the protoxylem ridges, and separated from the latter and from the metaxylem by one or two layers of parenchyma. The largest sieve-tubes of each group occur in the middle of each bay. Their walls are thin and give the cellulose reaction with chlor-zinc-iodine; the contents are scanty and often closely applied to the walls in a thin layer containing the usual refringent granules, which become yellow with this reagent. The granules were sometimes seen filling the whole cavity of the sieve-tubes, but were often aggregated against the walls in groups which seem to mark thin places, though neither callus nor sieve-pores were visible. The phloem-parenchymatous cells are few in number and, in sharp contrast to the sieve-tubes, are full of cytoplasm and possess large deep-staining nuclei. The protophloem lies immediately outside the metaphloem, forming a well-defined layer of narrow cells about 2-4 deep. It closely follows the contour of the metaphloem, *passing over the protoxylem ridges as a continuous wavy mantle* (well seen in Pl. IV, fig. 1). But for this continuity round the protoxylems the structure of the stolon would be remarkably root-like.¹

The shallow bays in the protophloem are filled up by the thin-walled *pericycle*, which is 4-5 cells thick at the bays, but only two cells at the ridges so that its outer limit is circular.

The *endodermis* is a single layer of tabular cells with their radial walls approximately in seriation with those of the outermost pericycle layer. These walls are not thickened but stain yellow with chlor-zinc-iodine. In older parts of the stolon all the endoder-

¹ So long as this continuity exists no doubt can be entertained regarding the cauline nature of the stolon. In this relation, Heinricher's simple experiments (*Flora*, 1907, pp. 57, 63, 72) are valuable as being in the nature of demonstrations. See p. 266 below.

mal walls give this reaction. Some of the endodermis cells were found to be traversed in the radial direction by peculiar struts (Pl. IV, fig. 2) loosely attached by their flat ends to the respective tangential walls, and often becoming free by one or both ends. In unstained preparations, these objects appear homogeneously yellow and translucent. They stain bright red in gossypimine or safranin but remain unaltered in chlor-zinc-iodine. Their significance is obscure but they may serve a mechanical function similar to that ascribed by Schwendener¹ to the so-called Casparian strips on the radial endodermal walls of many plants.

The *cortex* falls into two well-marked zones. The inner consists of about a dozen layers of cells. The walls of the layer immediately in contact with the endodermis are extremely thick, perforated by deep, straight pits, and thickly impregnated with phlobaphene. Eau de Javelle quickly bleached this substance; the lamination of the walls became evident, and a *violet* colour with chlor-zinc-iodine showed the presence of cellulose.² The remaining cells of the inner cortex are large, and rounded or oval in cross-section, with abundant triangular inter-spaces. In the younger parts of the stolon, these cells have thin walls, numerous chloroplasts and large oval starch-grains. As the stolon becomes older the walls become thickened and pitted, and to some extent impregnated with phlobaphene, while the contents gradually disappear, the tissue assuming a purely mechanical function.

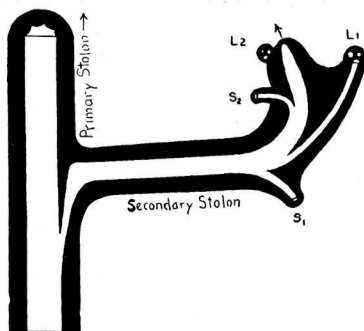
The outer zone of the cortex consists of about ten layers of rather narrow cells with lignified³ walls, closely packed without inter-spaces. In regions corresponding to overlying stomata, however, the cells of this otherwise air-tight sheath are thin-walled and loosely packed as in the lenticels of higher plants, and the sub-stomatal chamber is thus brought into communication with the air-system of the inner cortex. These channels persist long after the death of the stomata.

2. The *Secondary Stolon* is, in the main features of its anatomy, very similar to the primary stolon, but has a thinner xylem-core and relatively wide cortex, which is uniformly thick-walled, except for its one or two innermost layers which are left thin-walled. The air-space system is much reduced. In the endodermis, the "struts" (see above) are much shorter. The pericycle

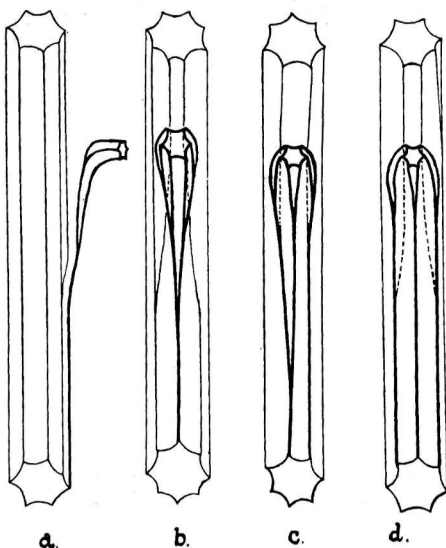
¹ Haberlandt, "Physiological Anatomy," p. 371, Engl. Transl., 1914,

² Sperlich states that these walls are suberized in *N. cordifolia* (l.c., p. 467).

³ This was confirmed by Wiesner's phloroglucin and hydrochloric acid test, as well as by ammoniated fuchsin.



TEXT-FIG. 3. *N. volubilis*. Diagrammatic longitudinal section through the lateral plant and the region of branching of the primary stolon. S_1 S_2 , two stolons arising on the lateral plant. L_1 L_2 , leaves, each possessing three strands. Cortex black, vascular strands white.



TEXT-FIG. 4. *N. volubilis*. Diagrams to illustrate behaviour of protoxylems in region of branching of primary stolon. The vertical fluted column is the xylem-cylinder of the primary stolon, the ridges being the protoxylem strands. The protoxylems supplying the secondary stolon are represented in bolder lines. The broken lines in *b*, *c*, *d*, represent the portions of strands passing behind the secondary stolon. *a* is a side view of *b*. For further explanation see text.

is practically uniform in thickness all round. In the sieve-tubes the refringent granules are more numerous and the protoxylem groups often fewer by one or two than in the primary stolon.

The mode of origin of the secondary stolon¹ is illustrated by the diagram in Text-fig. 3. The branch strand is thin to start with, and runs for a couple of millimetres nearly parallel to the vascular cylinder of the primary stolon and still enclosed in the cortex of the latter, at the same time gradually widening out. Then it sharply turns away almost at right-angles to its previous course, forming a striking knee-like bend. Attention may here be called to the resemblance of this mode of branching to the origin of the so-called "axillary branches" in the Hymenophyllaceæ and the Botryopterideæ. A comparison of Text-fig. 3 with Boodle's² figure of a longitudinal section through the region of branching in *Trichomanes radicans* is interesting, even if it only brings out a superficial resemblance.

At the actual point of branching, forked or V-shaped tracheids (all scalariform) were seen, similar to those observed by Boodle³ in *Lygodium*. The tracheids in the ascending part of the branch-strand are very short and more or less distorted.

The behaviour of the protoxylem strands is interesting. Text-fig. 4 shows diagrams drawn from steles actually dissected out, and based on several specimens which could be reduced to the three types, *b*, *c*, *d*. In this figure, *a* represents a side-view of *b*. The preparation for the branching of the stolon is often apparent as much as half-a-centimetre below the point where the stolon forks. One, two or three of the protoxylem-strands of the primary stolon, which are destined to supply the secondary stolon, pass upwards and divide as shown (thicker lines) the branches gradually spreading round the metaxylem cylinder of the secondary stolon to the extent that the latter becomes free from the main. The median protoxylem is entirely given over to the branch-supply, but each supplementary one, when present, partly supplies the branch, and is partly continued into the main. The number of protoxylem-groups in the main stolon, above and below the point of branching remains

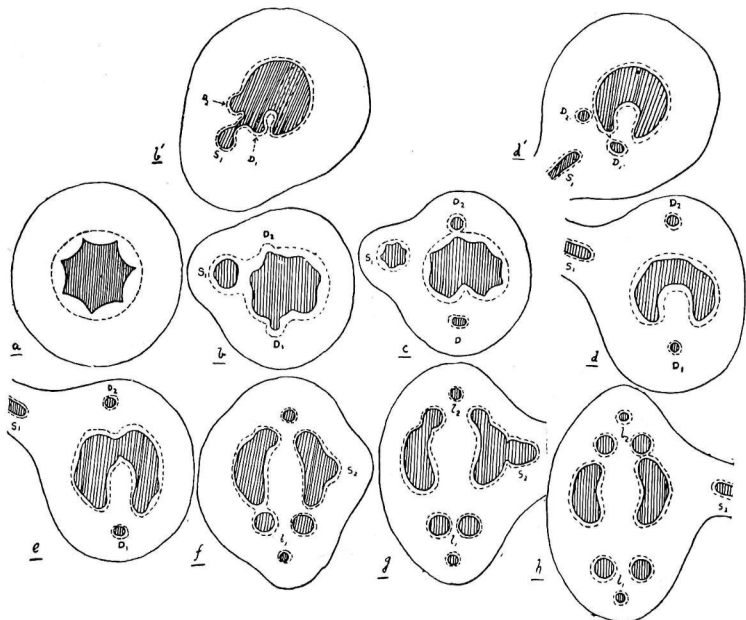
¹ Though Sperlich (l.c., p. 462) goes into the branching of the stolons in *N. cordifolia*, the relations of the vascular structures have not been elucidated.

² Boodle, Ann. of Bot., 1900, fig. 28, pl. xxvii.

³ Boodle, Ann. of Bot., 1901, pp. 367-8.

In one preparation of *N. rufescens* var. *Whitmanni* two or three V-shaped tracheids were seen fitted together in a row, while in another one two curved sieve-tubes were observed similarly arranged.

more or less constant: the diagrams illustrate the different ways in which this object is attained.



TEXT-FIG. 5. *N. volubilis*. Serial sections through basal part of lateral plant. *a-h* are from one plant, *b'* and *d'* from another to show the varying relative positions of the stolon- and leaf-strands. S_1 S_2 , first and second stolons; D_1 D_2 , dorsal strands of first and second leaves, respectively. Xylem shaded, endodermis shown as a broken line.

3. The internal structure of the *Lateral Plants* in *Nephrolepis*, except for Trécul's¹ short account of his unnamed plant, remains undescribed. A comparison of the lateral plant in *N. cordifolia* with Chandler's² description of the "sporeling" of that species revealed certain differences which will be noted below (p. 263). It is unfortunate that for *N. volubilis* such a comparison is impossible till plants raised from spores are available, but a description of the lateral plant may be given.

¹ Trécul, l.c. p. 245.

² Chandler, l.c. p. 389.

The changes that occur at the base of the lateral plant are shown in Text-fig. 5. They comprise the origin of two stolons (s_1 , s_2) and two leaves (l_1 , l_2). The stolon bundles never leave gaps. Concurrently with the origin of the first stolon, two small strands are separated off from the central cylinder, one on each side of the stolon (D_1 , D_2); these form the dorsal strands of the two compound leaf-traces, *there being no simple traces in the lateral plant*. The solid central cylinder rapidly becomes horse-shoe shaped, (c , d , d') by an invagination of the cortex, which pushes the endodermis, pericycle and phloem before it. The dorsal strand of the first leaf (D_1) turns round so as to lie opposite the invagination. This small strand is clearly not responsible for the relatively huge gap which it subtends and which rapidly deepens, giving the cauline strand a distinctly horse-shoe like form as seen in section (d). In fact the dorsal strand does not contribute at all to the formation of the invagination. The latter presently breaks through to the opposite side of the horse-shoe, dividing it into two large curved strands (e , f). It is clear that this stage cannot be called a dictyostele, for the gaps are not leaf-gaps. From the ends of the large strands opposite D_1 , two relatively large ventro-lateral strands are constricted off, and these three together form the first leaf-trace (l_1) which is compound.

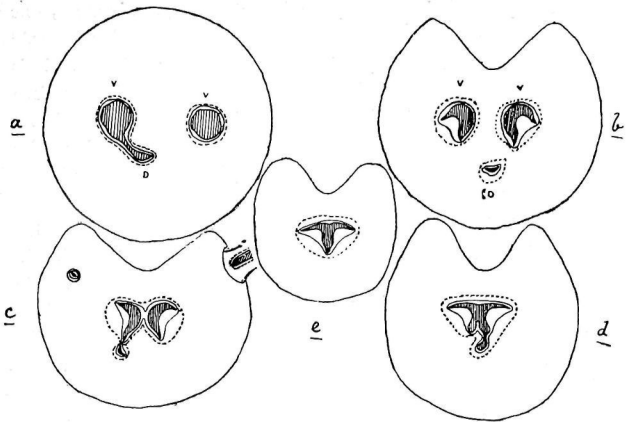
It may be pointed out that by the separation of the two ventro-lateral strands, the gap, from whose sides they come off, becomes larger, and the first leaf-trace may, in a sense, be said to be responsible for a portion of the gap, though not for its initiation.

A second stolon (s_2) arises exactly like the first and at the same time the second leaf-trace (l_2) is completed, exactly like the first.

Before the first gap (that opposite the first leaf-trace) is closed up, the dorsal strand of the third leaf arises at a different point on the cauline stele, causing a distinct gap, and being followed at a higher level by its two ventro-laterals. A fourth leaf may soon arise similarly, so that the vascular structure at the apex of the lateral plant is a primitive form of dictyostele.

Beyond a rough numerical correspondence there is not much to suggest any relation between the stolon and the leaves. The origin of a stolon is frequently, but not always (as shown by b' , d' in Text-fig. 5) along a radius at right-angles to the one on which the nearest leaf is situated.

The stolons borne by the lateral plant, which may become tendril-like, are similar to the secondary stolons in internal structure.



TEXT-FIG. 6. *N. volubilis*. *a-e* Serial sections through leaf from base towards apex. *a* is at the extreme base, *e* very near the apex. Xylem shaded, protoxylem solid black, phloem within the continuous line, endodermis, a broken line.

The petiolar structure was described for *Nephrolepis* in general terms by Trécul¹ long ago, though no figures were given. These may now be given for *N. volubilis* (Pl. 4, fig. 3; Text-fig. 6). Immediately before the three leaf-trace strands enter the petiole, the dorsal anastomoses with one of the vento-laterals (*a*) but it soon becomes free again. The petiole at this stage is circular in section. The usual adaxial groove soon appears on it, and at the same time the outline of the xylem portion of each strand, nearly circular at first, becomes crescentic in the manner shown (*b*) the positions of the protoxylems being indicated in solid black, while the metaxylem is shaded. Phloem completely surrounds the xylem, being particularly abundant in the deep bays at the outer side of each ventro-lateral strand. The strands to the pinnæ are given off from the adaxial horn of each crescent (*c*). The dorsal strand, passing up through the long rachis, anastomoses alternately with the two ventro-laterals twice or thrice with each. Ultimately, however, it loses itself into one of them (*d-e*). Meanwhile, the latter approach each other (*c*) by their convex sides and fuse along the middle-line, forming the T already mentioned by Trécul (*e*).

The stage *e* deserves notice on account of its similarity to a transverse section of the petiole of *Lygodium japonicum*. As in that

¹ Trécul, Ann. Sci. Nat. V, t. 10, 1869, pp. 351-2.

plant, the parenchymatous xylem has "three prominences, one median and two lateral, where the first formed tracheids occur,"¹ while between these are bays where the phloem is thickest. It is interesting to find near the tip of the leaf of a Polypodiaceous fern a stage recalling the primitive condition of *Lygodium*. The almost identical plan of structure, as seen in a transverse section, of a *Lygodium* stem and the stolon of *Nephrolepis volubilis* has already been referred to (p. 254).

Nephrolepis leaves are well-known to bear chalk-glands on the upper surface of the pinnæ. These have been described by Poirault² in species of *Polypodium*, and very similar ones were found in *N. volubilis*. The photograph (Fig. 4) on Pl. 4 is intended to show the "spoon" shape in vertical longitudinal section, mentioned by Poirault. The large, round or oval black bodies are apparently resinous, but some of them are the prominently staining large nuclei of the parenchymatous cells between the swollen reticulate tracheids. A couple of spiral and annular tracheids are seen in the vein coming up to the gland.

IV. OTHER SPECIES OF THE GENUS.

Having reviewed the anatomy of *N. volubilis* we may pass on to the consideration of a few of the other species which were examined.

(1) *N. cordifolia*. Sperlich's³ excellent account of the stolons of this plant leaves little to be said. From the base of the numerous roots on the stolon a longitudinal groove extends towards the apex of the stolon, sometimes for a considerable distance, so that a cross-section through this region is not quite circular. Each groove always overlies one of the four protoxylem strands of the stolon, the roots arising in four orthostichies.

The mode of branching of the primary stolon shows no important difference from that in *N. volubilis*. On account of the small size of the stele, it is not possible to dissect it out neatly enough to show the behaviour of the protoxylem strands in the secondary stolon, though it is clear that one of the four protoxylems of the primary stolon is continued into the secondary, while serial transverse sections in the region of branching lead to the belief that the further branching of this strand is on the same general plan as in *N. volubilis*.

¹ Boodle, l.c., p. 366, fig. 4, pl. xix.

² Poirault, Ann. Sci. Nat. VII, t. 18, p. 250 ff.

³ Sperlich, l.c., p. 464.

A study of the lateral plant revealed certain interesting differences from Chandler's¹ account of the sporeling. The most striking feature in which the lateral plant differs is the comparative rapidity of its development. This difference may perhaps be explained by the fact that the two kinds of plants start life at different stages, the lateral plant having a better start than the sporeling, on account of the ready-made channels of food- and water-supply afforded by the well-developed stolon at its base. This comparative rapidity of development finds expression in the fact that the first leaf may be well-developed and possesses a compound leaf-trace, whereas in the sporeling it is not till after the fourth leaf² that such a condition is reached. The primitive stage of the simple arc-like trace described by Chandler on p. 391 is also thus skipped over by the lateral plant.

(2) *N. Whitmanni*. I am indebted to Mr. Lynch for kindly ascertaining that this is a garden variety of *N. rufescens* Presl. Material of the stolons and of lateral plants obtained from the Cambridge Botanic Garden, showed such a close correspondence in external and internal structure and in the mode of branching, even in details, with *N. cordifolia*, that no more need be said about it. The stolons in one specimen had attained a length of nearly two metres, and were still growing vigorously.

(3) *N. rufescens triplinatifida*.³ In the usual structure of the stolons this plant is identical with the above, and is only mentioned here because one case of branching was seen (? abnormal) which looked exactly like that mentioned by Lachmann⁴ for *N. Duffii*. Transverse sections showed that the preparation for the division of the axial strand began at a distance of not less than three centimetres from the actual fork. A root arose in the neighbourhood of the fork, but not exactly at that level; its bundle ran for about 2-3 mm. inside the cortex of the stolon before entering it.

(4) *N. Duffii* (according to Goebel⁵ a mutation from *N. cordifolia*). A photograph is given (Pl. IV, fig. 5) of a cross-section of the forking stolon in order to show the relation of the four protoxylem groups of each arm with one another and with the root-strand. The latter has apparently been given off by the stolon on the right-hand side,

¹ Chandler, l.c., p. 389.

² Chandler, l.c., p. 391.

³ According to Baker (Ann. of Bot., 1891, vol. V, p. 331) a garden form of *N. acuta* Presl., itself closely allied to *N. rufescens* Presl.

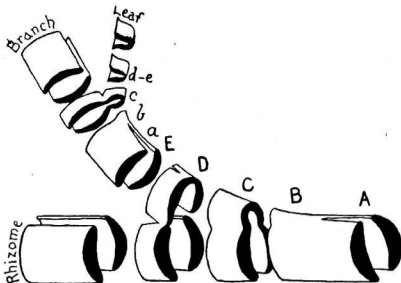
⁴ Lachmann, l.c., pp. 149-50., Pl. V, figs. 17-20.

⁵ Goebel, Flora, 1907, p. 42.

whose protoxylems show evident sign of derangement, the one opposite the root-strand having become reduced in size.

It must be pointed out that it is by no means general for a root to appear at the level of the bifurcation. On the other hand, several may be present at or near the point. It is true a case where a root arises at the bifurcation is strongly suggestive of a rhizophore arising at a bifurcation of the stem in *Sellaginella*, as Lachmann points out.

(5) *N. ramosa* Moore. Herbarium material only was available of this species and of *N. altescandens*. No stolons are borne, but the rhizome itself is slender and creeps on the trunks of trees. The rhizome frequently gives off side-branches which bear distant leaves in two rows, alternately right and left, like the main rhizome itself. The branch has an internal structure, and leaf-arrangement, identical with that of the main axis, so that only the internodal structure and the mode of origin of the branch and the leaf need be described (see Text-fig. 7 and Pl. IV, fig. 6).



TEXT-FIG. 7. *N. ramosa* Moore. Diagram of vascular skeleton to show the origin of a branch-trace from the rhizome, and of a leaf-trace from the branch. In the natural position the two meristemes of the stem are dorsal and ventral, with the gaps right and left. The cut ends of the strands are shown black. A-E, stages in the origin of the branch trace; a-e, corresponding stages in the origin of the leaf-trace. Note the great similarity in the corresponding stages. At d-e the leaf-trace is almost divided into two strands.

The vascular cylinder at the internode consists of two curved strands facing each other (Text-fig. 7, A), but separated from each other, and surrounded by a thick layer of sclerenchyma (black in the photograph on Pl. IV, fig. 6). Each of the strands has its own phloem, pericycle and endodermis, and they lie in the dorso-ventral plane, the gaps between them being thus respectively on the right and left. These gaps are very long, for they overlap in spite of the fact that the leaves are more than 2.5 cm. distant on the thin wiry rhizome.

In preparation for the origin of a branch, the gap on the side on which the branch is to arise is closed by the bundles approaching each other and finally fusing (*B*) by their margins. The portion of the xylem where this fusion occurs, at the same time bulges out sideways as an arc (*C*) seen in section, to the formation of which the two strands have contributed equally. This arc is the branch-trace. It soon frees itself first from one (*D*) and then from the other cauline strand, and at this stage passes out as a C-shaped strand into the branch, with its gap facing the main rhizome. Very soon, however, its opposite side opens, and the internodal structure of the main axis is thus established in the branch (*E*).

*The mode of origin of the leaf-trace is almost identical with that of the branch, and need not be described fully.*¹ On entering the petiole the C, which is formed exactly like the branch-trace, but is smaller, becomes very much attenuated on its abaxial side, and may even split into two strands corresponding to the two internodal strands. This division, however, is only momentary, and the leaf-trace very soon assumes the form shown in Pl. IV, fig. 8,² its adaxial margins turning outwards and becoming engaged in supplying the pinnæ. In addition to peltate scales (*s*) the sides of the rachis bear curious stiff, mostly unicellular hairs (*h*).

(6) *N. altescandens* (Colla) Baker. This species from Juan Fernandez, is closely related to the above,³ and the agreement extends to anatomical characters. The internode has exactly the same structure as in that species. The origin of the leaf-trace is different; each internodal strand constricts off a small strand which forms half of the leaf-trace (Fig. 7, Pl. IV) which thus at its origin consists of two separate small strands instead of a single large one. The two leaf-strands on entering the petiole join each other and the resulting strand assumes the form shown in Fig. 8, Pl. IV.

The origin of the branch is exactly the same as in *N. ramosa*. Fig. 7, Pl. IV shows a section which happens to have passed through a point where a leaf and a branch were both being given off from the rhizome, diametrically opposite to each other. (Such a case was met with only once, the usual course being for the leaves and the branches to come off from the rhizome at consider-

¹ In one specimen from the Kew Herbarium (Pl. IV, fig. 6) the tracheids near the middle of one of the internodal strands were either very narrow or absent, forming a break in the xylem, though the phloem passed round the bundle in the normal way. This interruption was not seen in a specimen from the Cambridge Herbarium.

² This figure will do equally well for *N. ramosa* and *N. altescandens*.

³ Christ, l.c., p. 288.

able distances apart). In the figure referred to, the two leaf-strands are still just attached to the ends of the cauline strands on the one side, while on the other the arc-like branch-trace is constituted by the attenuated portion of the xylem-ring.¹

From the foregoing account of the species of *Nephrolepis* three interesting facts emerge. Firstly, an evident tendency in the genus for the products of branching of the stolon to remain adnate to one another for shorter or longer distances, so that their respective vascular strands lie more or less parallel to each other and enclosed within a common cortical envelope, before they finally become free. Secondly, the great uniformity in structure and mode of branching of the stolons in the different species, even when their habits are divergent. Thirdly, the great similarity of structure, in *N. ramosa* Moore, between the basal part of the leaf, and the stem on which it arises, and the exactly similar way in which the leaf- and branch-traces respectively originate. In this respect *N. ramosa* agrees with *Trichomanes radicans* and other members of the Hymenophyllaceæ.

It may also be mentioned here that in the two closely allied species *N. ramosa* and *N. altescandens*, we see the transition from the simple arc-like leaf-trace of the former to the more advanced double trace of the latter.¹

V. BIOLOGICAL OBSERVATIONS.

There is abundant literature dealing with the biological aspects of *Nephrolepis* centred especially on the tubers and the stolons. Three of the most recent papers, two by Sperlich,² one by Heinricher,³ contain a series of highly interesting observations on the growth and development of the tubers and stolons, studied by the latter author under artificial conditions of culture. Of these results the most remarkable appears to be Heinricher's exposition of the great plasticity of the stolons which, moreover, can be controlled by the cultivator. For instance, by merely covering the rhizome over with earth he was able to transform it into a stolon which bore leaves *directly*, and possessed a single axial strand.⁴

¹ It must here be stated that the above account of *N. ramosa* and *N. altescandens* is based on a limited amount of dried material.

² Sperlich, *Flora*, 1906, p. 451; *Flora*, 1908, p. 341.

³ Heinricher, *Flora*, 1907, p. 43.

⁴ l.c., p. 63. See also pp. 57, 72.

It may be instructive to study the behaviour of the vascular strands at the origin of such leaves borne directly on the stolons, and to ascertain whether such a stolon agrees with the normal stolon in internal structure.

A few remarks on the stolons of some *Nephrolepis* plants which I had the opportunity of observing at the Cambridge Botanic Garden may now be made. The plants were all in the same house (Tropical Fern House).

(1) *N. Whitmanni*.—In a wire cage hanging vertically down about 8 feet from the ground. The primary stolons, $1\frac{1}{2}$ -2 feet long, were all seen growing directly downwards. They bore no roots, unlike the stolons of all the specimens that were not in hanging pots; and were less frequently branched than usual.

(2) *N. Whitmanni*, *N. davallioides* (Sw.) Kze., and *N. todeoides*.¹—One specimen of each in a pot placed on a table covered with moist pebbles. In each case most of the stolons arising from the stock on different radii, on reaching the edge of the pot, passed close over the edge and then grew obliquely outwards and downwards towards the table at an average angle of about 45° to the table, the tips in each case being above the level of the table.² They bore secondary stolons usually only on their lower sides, and these grew vertically downwards, never, however, touching the table.

(3) *N. cordifolia*.—A large specimen bore over 35 stolons, 34 of which, after passing over the edge of the pot, grew vertically downwards, the single exception growing obliquely outwards and downwards at about 45° . Several of the vertical stolons, on reaching the moist table passed underneath the pot.

(4) In an unnamed specimen growing in a pot, the stolons were mostly growing downwards but adhering to the outside of the pot.

No definite solution could be arrived at regarding the varying behaviour of the stolons in the above four cases. Number 1 might suggest positive geotropism but the stolons, especially when long, would hang down merely by their weight. Number 3 is a partly similar case, but the passing of the stolons under the pot suggests positive hydrotropism, which is also suggested by Number 4.

Although it did not appear likely that these directions of growth were due to mere chance, (because of the considerable

¹ This is probably a garden variety.

² This appearance was afterwards seen illustrated (in fig. 90, p. 477 in Gard. Chron. 1, 1887) for *N. rufescens* var.

uniformity of behaviour of the stolons in each individual pot), some of the vertical stolons in pot 3 and some in pot 2 (*N. todeaoides*) were artificially propped up on wooden sticks so as to remain horizontal. After a week or ten days the bent tips of the stolons in each case showed evident signs of re-adjusting themselves to their former directions of growth; and in pot 2, some new secondary stolons which had developed during this period on portions of the primary stolon distal to the bend, grew vertically downwards as expected.

Case 2 may at first seem inexplicable, and it was the one most frequently met with, but perhaps it can be interpreted in the following way. If it were not for the proximity of the moist table on which the pot was placed, the stolons would probably tend to grow approximately in a horizontal direction, till they become too long, when their weight would come into play. The presence of the moist substratum, however, calls forth a *positive hydrotropic response*. The oblique position taken up by the stolons would thus be a compromise between two tendencies, the horizontal and the vertical.

No marked geotropic response seems to be exhibited by the stolons. The case of the vertically-growing stolons in the hanging plant mentioned above is probably to be explained, mainly at least, by the weight of the long stolons. Any geotropism, if present, must be weak. According to Lachmann,¹ the stolons produced on the underground region of the principal axis are geotropically less sensitive than the roots of most ferns. Sperlich who in 1906² expressed the belief that the subterranean stolons of *Nephrolepis* are positively geotropic, in 1908³ withdrew this view in favour of positive hydrotropism.

In the later paper just cited (p. 356) Sperlich raises the question whether *Nephrolepis* stolons are also sensitive to contact stimuli. The curious way in which the stolons pass close over the edges of the pots (see p. 267) is rather suggestive, but *Nephrolepis volubilis* affords a case which reminds one strongly of the tendrils of higher plants (Text-figs. 1 and 2). In Text-fig. 1, a portion of the long primary stolon (*p*) is shown bearing several lateral plants (*x*), while surrounding the points of origin of these lateral plants are seen the close coils of the tendril-like stolons, two of which are

¹ Lachmann, Contributions, etc., p. 150.

² Sperlich, Flora, 1906.

³ Sperlich, Flora, 1908, p. 354.

shown (natural size) in Text-fig. 2. It will be seen that the direction of coiling does not show any regularity. When young, these stolons are comparatively soft and pliable (one such young stolon is visible in Text-fig. 1, *y*), but the older ones, after coiling round supports become wiry on account of the very thick-walled cortex. These structures are undoubtedly of great help in supporting the primary stolon during its growth upwards among bushes and trees. The primary stolon itself may be seen to be loosely twining in Text-fig. 1.

Attention has already been drawn on p. 253 to the extraordinary habit of *N. volubilis*. The primary stolon makes it possible for the lateral plants to reach a very considerable height on trees, and though these lateral plants appear to be devoid of roots it is possible that these may develop when the plants are artificially severed from the stolon on which they are borne. From the large number of scars of fallen lateral plants on the primary stolon the surmise may perhaps be ventured that the lateral plants may be shed from the stolon after they have formed their leaves at the expense of the mother-plant.

Sperlich's¹ view regarding the origin of epiphytism in *Nephrolepis* is peculiarly borne out by the plant under consideration. He regards the possession of stolons by *Nephrolepis* as having probably been the initial stage in the gradual emancipation of the plant from the soil. This would be an analogous case to that of many phanerogamic epiphytes which according to A. F. W. Schimper have evolved from lianes rooted in the soil. The occurrence, within the genus, of a facultative epiphyte like *N. cordifolia* may not, perhaps, be quite without significance in this relation.

VI. THEORETICAL CONSIDERATIONS.

We may pass now to some of the considerations of theoretical interest attaching to the genus *Nephrolepis*. Of these, the one that has aroused the most prominent interest of investigators is undoubtedly the morphological nature of the stolons, which was responsible for the Lachmann-Trécul controversy,² the former author holding that they were cauline structures while the latter contended that they were roots. This question would seem to have

¹ Flora, 1908, pp. 357-8 and 360.

² Various papers in the Comptes Rendus, of which only the following need be mentioned: Lachmann, vol. CI, 1885, p. 603; Trécul, vol. CI, 1885, p. 920; Trécul, vol. CVIII, 1889, p. 1081. See also Lachmann, Contributions, etc., 1889.

been closed long since, till Velenovsky in 1905¹ propounded his view that the stolons of *Nephrolepis* belong to a new morphological category which he called "Achsenträger" (shoot-bearer). This term, as applied to these organs has been severely criticized by Sperlich, and Velenovsky has recently attempted to defend his position.² Nevertheless, there seems little room for a new morphological category for the reception of a structure whose cauline nature is decided beyond question (p. 255, footnote). It will suffice here to summarize in the form of a table the several views that have been put forward by various authors regarding the nature of the stolons.³

Root.	Shoot.	Combining Root & Shoot Characters.	An Organ <i>sui generis</i> .
Brongniart 1839	—	—	—
—	Kunze 1849	—	—
—	Hofmeister 1857	—	—
—	Russow 1873	—	—
Trécul 1885	Lachmann 1885-9	De Bary 1887	—
—	Goebel 1889	—	—
—	Poirault 1893	—	—
—	Sperlich 1906, 1908	—	Velenovsky 1905
—	Heinricher 1907	—	—

We have seen that the outstanding feature of the stem-anatomy of the species of *Nephrolepis* examined is the presence, near the apex, of a primitive type of dictyostele (not far removed from a solenostele), while in the leaf-trace we pass from the simple arc-like condition (*N. ramosa*) to the compound (double in *N. altescandens*, triple in *N. volubilis*).

So far as anatomical characters can be a guide to phylogenetic position, *Nephrolepis* would seem to occupy a place in that more or less coherent but intricate plexus of forms which illustrates, on the one hand, the transition from the solenostele to the dictyostele (with concomitant elaboration of the leaf-trace), and on the other, the "phyletic shift" of the sorus from the margin of the frond to its under surface. In the latter respect *Nephrolepis* is evidently well advanced towards the superficial type of sorus. For the location of the genus within this plexus of forms more data from

¹ Vergleichende Morphologie der Pflanzen, 1905, vol. I, p. 233, Prag.

² l.c., vol. IV, 1913, p. 32.

³ The references up to 1888 will be found in Lachmann, Contributions, etc., of the later ones the following may be mentioned: Goebel, Pflanzenbiologische Schilderungen, vol. I, 1889, p. 203, footnote; Poirault, Ann. Sci. Nat. Bot., 7, sér. t. 18, p. 160.

the anatomy of the mother-plant are necessary than are at present available.

The foregoing sketch of the range in habit and structure exhibited by the species of *Nephrolepis* may perhaps justify the following view regarding their relative positions within the genus. That a well-marked tendency towards the epiphytic habit is exhibited by most of the species of the genus is abundantly clear from what has preceded. Starting from a hypothetical solenostelic form with a short erect stock bearing leaves with simple leaf-traces, the epiphytic tendency may be considered to have found expression in two ways, and to have led to the gradual evolution of two main types of habit. On the one hand, the stem itself became a scandent rhizome bearing distant leaves, and forms like *N. ramosa* and *N. altescandens* were evolved. On the other hand, a much more specialized and highly efficient organ, the stolon (which is probably to be taken as a highly modified branch of the stem) was evolved for the purpose, with conspicuously successful results (*N. volubilis*, *N. cordifolia*).

The leaf-trace, along each of these two lines of progress, followed a course of elaboration of its own, from the simple (*N. ramosa*) to the compound (*N. altescandens*), along the first of these lines. Sufficient data are not available to enable one to delineate accurately the course of elaboration through which the leaf-trace passed in the stoloniferous forms. However, there is an indication (a faint one it must be admitted) that the evolution of the leaf-trace was less gradual in this series, for in *N. cordifolia* the simple arc-like trace described by Chandler¹ in one of the earlier-formed leaves of the sporeling soon gives place first to a double and then to a triple trace in the later leaves.

In this relation a detailed study of the sporelings of different species of *Nephrolepis*, on the lines of Chandler's work, would probably throw considerable light on the question. That a study of the lateral plants, (which are more easily obtainable) will not enlighten us to any great extent on this point is evident from the fact that, the lateral plant which, as already stated on p. 253, is produced under conditions favourable to rapid growth, no longer exhibits the earlier stages in the evolution of the leaf-trace.

If the conjecture put forward on the page just referred to has any justification, we have before us a remarkable case where exceptionally favourable physiological conditions are potent to the

¹ Chandler, l.c., p. 391

extent of eliminating from the ontogeny of a plant morphological features which probably marked important stages in its phylogenetic history.

From a study of the anatomy of *N. ramosa* we concluded on p. 266 that, in respect of the great similarity of structure respectively in the rhizome, branch, and the leaf at its origin, that plant formed a rather striking parallel to the case of the Hymenophyllaceæ. Although *N. ramosa* belongs to a phyletically much higher group of ferns, the above-mentioned feature in its anatomy may possibly go in support of the view, so strikingly borne out by the vascular structure in the Hymenophyllaceæ, that the strands of the stem and of the leaf are primitively identical structures.¹

Finally, the extensive development of protostelic structure exhibited by the stolons of *Nephrolepis* cannot pass unnoticed. The main axis of the plant has acquired extraordinary powers of branching, and into its branches a large portion of its energies is diverted. It seems unreasonable to regard the stolon, possessing as it does such a primitive vascular organisation, as an indication of primitiveness of the genus. Much more likely seems the view that it is a highly specialized organ whose structure may in some way be connected with the conducting functions imposed upon it.

In conclusion, I wish to express my thanks to Mr. Brooks not only for handing me the material of *N. volubilis* used in this research, but also for much help throughout the progress of the work. I have also to thank Mr. Boodle for valuable suggestions, and Professor Seward and Mr. Tansley for their kind interest in this investigation. I am also much indebted to Professor Seward for revising the manuscript.

VII. SUMMARY.

Nephrolepis volubilis, J.Sm., a highly specialized member of the genus, is described. The stolons arising directly on the mother-plant (primary stolons) are smooth cylindrical organs (natural size photograph, Text-fig. 2) which scale forest trees up to 16 metres and enable lateral plants, borne on them at intervals, to reach heights far above the mother-plant which is rooted in the soil.

Two to four shorter stolons which are wiry and irregularly coiled appear on each lateral plant, and seem to be contact-sensitive. They are climbing organs.

¹ Tansley, NEW PHYTOLOGIST, 1907, p. 115.

The stolons possess a single axial polyarch exarch protostele. Where a stolon branches the two steles run parallel to each other for some distance, enclosed in the same cortical envelope, before they become free. This "adnate tendency" is also shown by the stolons of several other species examined. The structure of the stolons is remarkably uniform in the different species.

In the endodermis of *N. volubilis* (stolon) peculiar strut-like bodies were found traversing the cells in the radial direction (Pl. IV, fig. 2). These may serve a mechanical function.

In the lateral plants the basal protostele becomes soon modified into a primitive form of dictyostele at the apex. The first leaf has a compound leaf-trace.

There are no roots on the lateral plants, but it may be that after the lateral plants have formed their leaves at the expense of the mother-plant, they are shed, and strike root on the ground. This is suggested by numerous scars on the primary stolon.

The primary stolons of several species of *Nephrolepis* (p. 268) are probably positively hydrotropic.

In *N. ramosa* and *N. altescandens*, two closely allied species without stolons but with scandent rhizomes the internode possesses the simplest type of dictyostele imaginable (viz., two strands separated by two leaf-gaps as seen in cross-section). In *N. ramosa* the vascular structure at the base of the branch and leaf-traces is almost identical, and recalls the condition in the Hymenophyllaceæ, which has been previously used in support of the view that stem-stele and leaf-strand are primitively identical structures.

In *N. altescandens* the leaf-trace arises as two separate strands, in *N. ramosa* as a simple C-shaped strand.

Sperlich's view regarding the origin of epiphytism in the genus (p. 269) is well borne out by a study of *N. volubilis*. He regards the appearance of the stolon as having been the initial stage in the gradual emancipation of the plant from the soil.

Velenovsky's adoption of a new morphological category, the "Achsenträger" (shoot-bearer), to include the stolons of *Nephrolepis*, has no justification in view of the evident cauline nature of these organs.

The primitive organisation of the stolon is not indicative of primitiveness of the genus. More probably it is an organ highly specialized for the conducting functions entrusted to it.

Possibly because of the exceptionally favourable physiological conditions in which it is placed (connected by the stolon to the

absorbing system of the mother-plant) the lateral plant of *N. cordifolia* (and perhaps of other species) in its ontogeny omits some of the earlier stages in stelar evolution which are shown by the sporeling (see pp. 260 and 263).

THE BOTANY SCHOOL,
CAMBRIDGE,
September, 1915.

EXPLANATION OF PLATE IV.

ILLUSTRATING MR. SAHNI'S PAPER ON THE ANATOMY OF *NEPHROLEPIS*.

(The figures are all from photographs).

1. *N. volubilis*. Transverse section of mature primary stolon, showing on the left the strand of a secondary stolon. Small-celled lignified outer cortex. Innermost cortical walls extremely thick, containing phlobaphene, seen as a black ring round the stele. Protophloem, a continuous wavy layer passing round the eight protoxylems. Phloem filling the bays in the xylem-cylinder, and separated from the tracheides by parenchyma. \times abt. 24.

2. *N. volubilis*. Part of transverse section of *young* primary stolon. Thin-walled inner cortex with triangular inter-spaces. The phlobaphene-containing walls comparatively thin. In three of the endodermal cells the "struts" (p. 256) are seen, two having become free by their inner ends. *s*, sieve-tubes; *t*, metaxylem tracheides which are yet thin-walled, only the protoxylem elements being lignified. \times abt. 130.

3. *N. volubilis*. Transverse section of petiole. Small dorsal strand and larger ventro-laterals. In all the xylem is crescentic, with phloem in the bays. Cortex as in Fig. 1. \times 50.

4. *N. volubilis*. Vertical longitudinal section of chalk-gland, showing the "spoon" shape. Regularly arranged epidermal cells in saucer-shaped depression. The gland is made up of swollen reticulate tracheides with parenchymatous cells between. The large black bodies may be resinous, but some of them are nuclei.

5. *N. Duffii*. Transverse section of forking stolon, with a root-strand above the strands of the arms of the fork. Each of the latter has four protoxylems with phloem in the bays. The root-strand has been given off from the strand on the right one of whose protoxylems is stunted. \times abt. 45.

6. *N. ramosa* (dried material from Kew Herbarium). Transverse section of rhizome showing *two meristemes in dorso-ventral plane*, with leaf-gaps, one of which is subtended by the arc-like trace. Sclerenchyma (black) surrounds each meristeme, one of which has its xylem interrupted (see p. 265, footnote). \times 45.

7. *N. altescandens* (dried material from Kew Herbarium) Transverse section of rhizome at a point where a leaf-trace (left) and a branch-trace (right) *happen* to arise at the same time. Leaf-trace consists of two separate strands constricted off from cauline meristemes. The attenuated portion of the xylem on the right will pass out as the C-shaped branch-trace. \times 40.

8. *N. altescandens*. Transverse section of rachis, showing arc-like strand with its adaxial ends turned outwards. On the right is a pinna-trace. *s*, a peltate ramental scale; *h*, hairs. \times 40.

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