THE DEVELOPMENT OF THE SORUS IN SOME SPECIES OF NEPHROLEPIS, TOGETHER WITH OBSERVATIONS ON POINTS OF ANATOMICAL INTEREST.

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Thesis
submitted by
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CONTENTS.

THE DEVELOPMENT OF THE SORUS IN SOME SPECIES OF NEPHROLEPIS, TOGETHER WITH OBSERVATIONS ON POINTS OF ANATOMICAL INTEREST.

Hooker in his "Species Filicum" (Vol. IV) describes six species of Nephrolepis, viz. N. tuberosa (Pr.), N. exaltata (Schott), N. acuta (Pr.), N. obliterata (Hook), N. floccigera (Moore) and N. davallioides (Kze.), the nomenclature being upheld by Christensen (Index Filicum) in only two cases, viz. N. exaltata and N. floccigera.

Hooker's N. acuta, N. davallioides, N. obliterata and N. tuberosa being referred respectively to N. biserrata, N. acuminata, Arthropteris, and N. cordifolia. In the "Synopsis Filicum" (Hooker), seven species are described, viz. N. cordifolia, N. exaltata, N. acuta, N. ramosa, N. altescandens, N. floccigera, and N. davallioides, of which three species, N. cordifolia, N. exaltata, and N. floccigera are upheld by Christensen. Of these seven species described by Hooker in the "Synopsis Filicum", N. exaltata, N. acuta, N. floccigera and N. davallioides are also described in the "Species Filicum". Of the others, N. cordifolia and N. ramosa, are respectively the N. tuberosa and N. obliterata of the "Species Filicum", while N. altescandens is described in the "Species Filicum" under Polypodium Colla.

The distribution of the genus is given as being general throughout/

throughout the tropics, and stretching a little to North and South of the tropical zones.

The plant consists of an upright scaly stock which gives rise to numerous stolons or runners, from which in turn spring numerous fibrous roots.

The leaves of the different species differ greatly in size and shape, but all are simply pinnate and have open venation. Of two of the species examined, N. biserrata had leaves more than three feet long with individual pinnae 7-10 inches long and half an inch broad, whereas in N. cordifolia, the length of the mature frond did not exceed two feet, while the size of an individual pinna was about one inch.

Nephrolepis forms the 27th group in Christensen's "Index Filicum". He upholds 17 species, viz.

N. abrupta, N. acuminata, N. acutifolia, N. barbata, N. biserrata, N. cordifolia, N. dicksonioides, N. duffii, N. exaltata, N. floccigera, N. hirsutula, N. Kuroiwae, N. Lauterbachii, N. lindsayae, N. pectinata, N. radicans and N. rivularis.

Professor Bower divides the Davallioid ferns into three sections,("The Filicales", Vol. III. P. 37).

I. Primitive individuality of the sorus retained (except in some species of Nephrolepis): position more or less marginal. Dermal scales.

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(1) Humata (Cav.) 14 species. Leaves once or more pinnate, venation free, Sori intra-marginal, edges of indusium free.

(2) Davallia (Smith) 67 species.

Leaves variously pinnate, venation free. Inner indusium with edges fused to leaf surface.

(3) Nephrolepis. (Schott).

Leaves once pinnate, venation free. Sori marginal or variously intra-marginal, marginal coenosori, in some species.

II. Individuality of sori retained: position intra-marginal. Inner indusium partially or completely abortive.

(4) Arthropteris.

III. Distinguished by relatively condensed leaf structure, culminating in simple blades. Dermal scales. Venation mostly open, but reticulate in the most condensed types. Sori marginal, fused in varying degree to form coenosori.

(5) Tapeinidium.

(6) Diellia.

(7) Odontosoria.

(8) Lindsaya.

(9) Dictyoxiphium.

This then places Nephrolepis in near relationship to/

to Davallia which has been examined developmentally by Professor Bower, who as a criterion of comparison places particular emphasis on the position of the sorus relative to the margin of the leaf.

The mature sori of the Davallias are situated on a vein-ending, and are slightly intra-marginal, the lower indusial flap being fused with the leaf surface.

On working out the development of the sorus in Davallia pentaphylla, however, Professor Bower found that the sorus though intra-marginal at maturity, is marginal at its initiation. The first sign of soral development is a flattening of the margin of the leaf, the indusial flaps arising as superficial outgrowths some distance back from the flattened margin.

The receptacle lies between the indusial flaps, in a marginal position. The upper indusial flap, which gives the appearance in the mature state, of being an extension of the leaf surface, arises at first by marginal segmentation. Later growth is not marginal but intercalary. Such conclusions were used by Professor Bower to link up Davallia with Lindsaya, Saccaloma, Dicksonia and Thyrsopteris, all of which have a sorus of marginal origin. Such ferns were shown to be intermediate between the gradate and the mixed soral types. (Bower, "Studies in Phylogeny of the/

the Filicales", pp. 453 - 462).

The development of the sorus in this genus has also been worked out by Von Goebel for Davallia dissecta ("Organographie" p.1143, Fig. 1134). Professor Bower in his paper mentioned above, in describing the origin of the sorus for the Davallias, states that such difficulties as are presented by the Davallias, become still more insistent in the case of Nephrolepis where the final position of the sorus is still more definitely superficial.

Considering their close relationship to the Davallias it was thought not unlikely that a study of the development of the sorus of Nephrolepis would lead to similar results to those found for Davallia. With this end in view, therefore, material was obtained from various sources including Royal Botanic Gardens, Kew, Royal Botanic Gardens, Edinburgh, Botanic Gardens, Glasgow, and Brooklyn Botanic Gardens, U.S.A. I would therefore take this opportunity of thanking the Directors of those various gardens, for their courtesy in providing me with the material for my work.

Considerable difficulty was found in getting material which would show the earliest stages in the development of the sorus, a great majority of the fronds being sterile; and of the fertile ones, many seemed to lose their tips at an early stage. The material of Nephrolepis biserrata (Sw/

(Sw) Schott, obtained from Kew Gardens under the name of N. acuta was however sufficient to allow of a fairly complete study of the soral development, and for this reason, more stress has been laid on this species than on the others where the material at my disposal was less complete. As it so happens, this was the species on which Professor Bower made his observations (Bower, "Studies in the Phylogeny of the Filicales", P. 46).

Other observations have been made by the writer, on
N. acuminata (Houtt) Kuhn. (= N. davallioides, Kze)
N. exaltata (L) Schott.
N. cordifolia (L) Pr. and N. Bostoniensis. (?).
Christ in his "Die Färnkraüter" p. 287-291 describes the position of the mature sorus of three of these species as follows: N. biserrata,- intra-marginal, but nearer to the margin than to the costa.
N. acuminata (davallioides) Marginal with almost equal indusial flaps.
N. cordifolia, deeply intra-marginal.

The question which presented itself was whether all types, irrespective of the final position of the sorus, would be marginal in origin, or whether there would be a difference in origin corresponding to the difference in final position.

Fig./

Fig. I.c. shows a stage in the development of the sorus of Nephrolepis biserrata, comparable to the stage figured by Professor Bower in his "Studies on the Phylogeny of the Filicales" plate XXIV, fig. 25.

Professor Bower suggests that on the analogy of such types as Davallia, the lip (l) might be considered equivalent to the body marked (l) in his figure of Davallia ("Studies on the Phylogeny of the Filicales", III, Pl.XXXIV, Fig. 24) and which is often called the "indusium", the hollow behind it being the receptacle, and the apparent expansion of the leaf blade (u) being really a greater development of the second "upper" lip, as shown for Davallia (loc. cit). There is of course a much greater development of the "upper" lip in Nephrolepis, and as Professor Bower points out, this development seems to arise by a marginal segmentation, not by intercalary growth, as in Davallia. He adds that it is still to be shown whether this segmentation is developmentally continuous with that at the margin of the pinna before the development of the sorus began. If this were the case then it would point to a phyletic slide of the originally marginal sorus, to the lower surface of the pinna.

In order to make a complete examination of the earliest development of the sorus, the still circinately coiled/

coiled apices of several fertile fronds of Nephrolepis biserrata were first fixed with chrom acetic fixing fluid, then embedded in paraffin wax, and serial sections cut, with the microtome. In this way large numbers of sections were obtained, and although it is obvious that many of the young pinnae would not be cut in the proper direction for showing the early development of the sorus, still it was possible to get quite a number which were. The difficulty of finding suitable sections and of interpreting them, was increased by the great development of hairs in the apical region. Large numbers of slides were examined and from these, figures were drawn illustrating as completely as possible, the various stages in the development of the sorus.

In no instance was there any sign of a broadening out of the margin of the pinna, such as was shown by Professor Bower to be the case in Davallia, before the development further back of the indusial flaps. Here the first sign of soral development is an upgrowth of tissue at a point which is distinctly intra-marginal, being usually situated at a distance of five or six cells back from the marginal cell (m) of the pinna (Fig. I.a).

This upgrowth of tissue develops later into the indusium, which, curving inwards towards the leaf surface/

surface, encloses a hollow receptacle.

There seems no doubt that the original marginal segmentation of the pinna is uninterrupted, and that the "apparent" extension of the leaf-blade is the further continuous development of the original leaf margin, not one of secondary superficial origin (Fig. I.B). There are here seven cells between the marginal cell and the indusium. A later stage in the development is shown in Fig. I.C. where the leaf blade has developed considerably, the indusium now lagging behind in its development, there being still only two cells in the forward projecting part of the indusium, while there are now eleven cells between the marginal cell and the cells forming the indusium.

It will be seen later that in the four species examined, the point of origin of the superficial sorus is practically constant for all four species, the cell which shows the first sign of enlargement being most frequently the sixth one back from the marginal cell. This is in distinction to what Professor Bower has described in the case of Blechnum, where intermediate stages in the phyletic slide of the sorus from the margin to the under surface of the pinna are found.

In the genus Blechnum though the indusial flap appears marginal in origin, Professor Bower has shown in/

in his figures ("Studies" Blechnum, Plate XXII Fig. 3 a-e) that the actual cell which gives rise to the indusial flap may be a cell adjoining the marginal cell or may even coincide with it, there being considerable variety of detail in the nearness of origin to, or even coincidence of, the indusium, with the marginal cell itself.

Such conditions as these suggest the first stages of a phyletic slide of the sorus from the margin to the under surface of the leaf.

Nephrolepis therefore appears to have gone still further, having in all cases examined, shown a distinct, if slight, intra-marginal origin of the sorus.

The outline of the pinna in all the species examined, as seen in transverse section, is somewhat peculiar, in that from a very early stage in its development, two large ridges of tissue are obvious on the upper, adaxial, surface, and to right and left of the midrib. There is a single vascular strand in the midrib, and there is only a very slight projection downwards, the abaxial surface of the pinna being almost flat (Fig. 3. G). There is no incurving of the margin of the pinna, the sporangia being protected entirely by the indusium.

The/

The indusium in each species is distinct in form, that of Nephrolepis biserrata being the most massive, and having a tendency to become recurved at maturity (Fig. 4 A). Nephrolepis cordifolia has an indusium of a much more slender type (Fig. 4 B), while Nephrolepis acuminata (Fig. 4 C) is intermediate, and has the added distinction of having a flatter receptacle than in the case of N. biserrata and N. cordifolia.

In all cases the indusium has attained to considerable size before any sign of sporangial development is evident. The first cell to show any signs of development is usually situated in an approximately median position on the receptacle. A single superficial cell enlarges, its nucleus becoming larger than those of the surrounding cells, which may also become somewhat crushed by its development. The position of such a cell is shown in Fig. I D. while Fig. 2 C. shows the further development of such a cell. This figure also gives detail of a young sporangial cell, such as is outlined in Fig. I D.

The fact that the first sporangium usually arises in a median position is suggestive of a basipetal sequence, but the final condition is in all/

all cases definitely a mixed one. (Fig. 2 A.) Here the sporangia are numbered in order of succession. The vein ending is also shown. It consists of a number of tracheids, and ends beneath the sorus. This is taken to be a sign of a marginal ancestry, types which are phyletically superficial having veins which do not end at the sorus, but continue past it towards the margin of the pinna.

In most cases examined it was found that the second and third sporangia developed one on either side of the first formed, median, sporangium, but occasionally the third sporangium developed between the first and second. This latter condition is seen in Fig. I F. Here the oldest sporangium is nearest to the indusium, several cell divisions already having taken place. The periclinal divisions below the level of the epidermis pointing towards the possibility of a long slender stalk. The characteristic "protective" curve of the indusium is also shown, the sporangia arising in a hollow receptacle which the indusium, together with part of the leaf blade, almost entirely encloses.

A further stage in the development of the sporangium is shown in Fig. 2 C. The older sporangium has a massive stalk, there being at this early stage little/

little difference in width between stalk and head region. The stalk is three rowed, no instance of a stalk with just a single row of cells having been observed in any of the species examined. A tetrahedral cell has been cut off at the centre of the head region, thus differentiating wall from sporogenous tissue. From the tetrahedral cell, a narrow cell has been cut off. This gives the initiation of the tapetal, or nutritive layer. The younger sporangium, towards the left of figure, shows division of the large nucleus, but no cell wall has been laid down. The fact that the indusium is only one cell in thickness throughout the greater part of its length is also shown. Near to its point of insertion on the leaf however, it becomes more massive.

A still further development of the sporangium is shown in Fig. 2 B. Here the stalk has become considerably elongated, while further development has also taken place in the head region. A central mass of spore mother cells has been formed, while the disintegrated remains of the tapetum are seen lying within the wall of the capsule. The younger sporangium shows a stalk only three cells in length, the individual cells being less elongated than those of/

of the older sporangium. Tetrahedral cell and tapetal layer are also differentiated. At a later stage, the spore mother cells previously seen as a coherent mass at the centre of the capsule, round themselves off, become separated from one another, and undergo the tetrad division which regularly precedes spore formation in the ferns. Such a stage is seen in Fig. 2 D. where the nucleus of each spore mother cell is seen to have divided. The remains of the tapetal layer are here also seen.

The fully mature sporangium consists of a much elongated stalk consisting of three rows of cells, and a head region, or capsule, which varies slightly in shape even within the one species. Some capsules examined were slightly elongated (Fig. 3 B.) while others were broader (Fig. 3 A). All were alike in having a vertical annulus, a unicellular series of indurated cells, which were regularly thirteen in number. The sequence of these cells was interrupted at the stalk and again at the stomium. In all cases there was a distinct stomium with hypostomium and epistomium. The stomium consists of two cells which are smaller then the cells of the epi - and hypo - stomium. They are thickened only along their inner walls and for some distance along the radial walls.

In/

In this Nephrolepis biserrata differs from the other species examined, where the cells of the stomium were found to be thickened on all walls.

The epi-stomium consists usually of three cells, and the hypo-stomium of from one to three cells (Fig. 3 A.) but occasional sporangia show as many as five much enlarged cells in the hypo-stomium (Fig. 3 B.). On one face of the sporangium the number of tabular cells may vary from eight to thirteen. No number outside of these being observed.

The opening mechanism of the capsule is seen in Fig. 3 C. where rupture of the capsule has taken place, and the bent back position of the annulus is clearly shown. The shrinkage of the outer tangential wall of the individual cells of the annulus is evident. The mass of spores which has remained attached to the bent back portion of the capsule is indicated by a dotted line. These spores would be forcibly ejected when the sudden flick back of the sporangium took place.

The spores of Nephrolepis biserrata show the somewhat unusual phenomenon of being of two distinct sizes. Both sizes of spores are oval in shape, but the smaller ones appear to be concave on one side. Both have spiney outer coats (Fig. 3 D.) This phenomenon of difference of spore size in one species has/

has been observed by Professor McLean Thompson, in Platyzoma, (Thompson, "A Further Contribution to the Knowledge of Platyzoma Microphyllum", Trans. Roy. Soc. Edin. Vol. LII Pt. 1.) and also in Nothochlaena affinis, (Thompson, "The Anatomy of Certain Rare and Primitive Ferns", Trans. Roy. Soc. Edin. Vol. LII Pt. II.). In both of these cases, however, three sizes of spores, a large, a medium, and a small, were observed. These were contained in sporangia of two sizes, the large sporangia containing small numbers of large spores, and the small sporangia containing large numbers of small spores. An intermediate size of spore was present in both types of sporangia. Dr. Thompson points out that such marked differences in size of sporangia and spores, are unknown outside of heterosporous plants. In homosporous Leptosporangiate ferns, differences in sporangial size in any one species are rare, and when any such variations do occur, the spore output per sporangium may be affected but uniformity of spore size and form is retained as in Stromatopteris. Heterospory is seen in Equisetum but here there is no difference in sporangial or spore size. It is only on germination that the difference becomes evident.

Dr. Thompson points out that there is no a priori reason/

reason why differences in the size of sporangia and spores should not accompany true homospory, as the difference in size might quite possibly be the result of difference of nutrition, but he suggests that it seems more likely that for Platyzoma it is a case of heterospory.

In the case of Nephrolepis biserrata, although there is marked difference in size of spore, there is no marked difference in size of sporangia. It therefore seems more than probable that the difference in spore size is here merely caused by difference in nutrition. This view is strengthened by the fact that the difference in size of spore was only observed in one species out of the many examined.

A number of spore counts were carried out, a single sporangium being immersed in a drop of glycerine by means of a capillary tube.

The following are the results for N. biserrata:-
57, 58, 62, 48, 47, 40, 54, 63, 61, 64, 48, 48.
This suggests that in the majority of cases the typical number is 64, with 48 as typical number in the remaining sporangia.

In order to study the anatomy of the stem, a young plant was separated from the larger parent plant to which it was attached by an underground stolon. The young plant was freed as far as possible from adhering/

adhering soil, and a sketch made of it, as shown in Fig. 5 A. Only the younger fronds have been included, together with the bases of the petioles of the older fronds. The short upright stock was dark brown in colour and was covered with scales. A single scale is shown in Fig. 6 A. It is composed of relatively thick walled cells, a number of glandular cells are seen round the edges of the scale.

The stock at its broadest point would be about half an inch in diameter, and from this it tapered off towards the apex and towards the base.

The whole stock was deeply ridged (vide Fig. 5 A). The auricled base of the upper part of each pinna is also shown in this diagram. The lower half of each pinna is rounded. The venation is open, each pinna having a distinct mid-rib, from which a series of secondary veins arise. These usually bifurcate, and in fertile pinnae the sorus is situated on the end of the upper branch of the vein. In some cases the lower fork of the vein may again branch, but neither of these secondary bifurcations bear sori (Fig. 3, E, F.) Stolons arise nearer to the apex of the stock than even the youngest fronds.

In a plant of N. biserrata obtained from Kew, aereal/

aereal stolons were seen to grow along the surface of the soil till they came into contact with the sides of the plant pot, after which they grew vertically upwards, curved over the edge of the pot, and continued to grow horizontally outwards. In this plant though several old fronds were fertile when I received the plant from Kew, none of the new growth on two succeeding seasons was fertile. A similar condition was shown by a plant of N. cordifolia obtained from Edinburgh. This "unwillingness" to produce fertile fronds made it difficult to secure the necessary young material for showing the soral development. The petioles of the young fronds appeared to be covered with brown hairs. These in microscopic examination are shown to be hair-like scales, which only widen out, a short distance above their point of insertion in the petiole. (Fig.6.B.)

The stolons were pale green in colour for some distance back from the apex, after which the colour changed to yellow and finally to dark brown, the change in colour being due to the development of sclerenchymatous tissue. The stolons were covered with lanceolate scales (Fig. 6 C.). Such scales are only found in advanced types of ferns, and, as shown by Professor Bower, ("The Filicales" Vol. I. p. 201) these/

these may be used in certain families such as the Marattiaceae, to show a distinction between primitive and derivative genera, the primitive types possessing hairs only.

No glandular cells were observed on the scales of the stolon (Fig. 6 C).

It was thought possible that a careful examination of the origin of the stolons might yield some definite results as to their position of origin in relation to the leaf bases.

To this end another young plant was taken and the leaves and stolons cut back as closely as possible to their points of insertion on the stock, where there was any difficulty in deciding from external appearance whether a structure was a stolon or a leaf base, sections were cut - the stolons showing a protostelic structure, and the leaf bases a much divided leaf-trace (Fig. 5 B).

Similar work has been done by Professor Bower on the stolons of Plagiogyria, (Bower. "Phylogeny of the Filicales", Plagiogyria, P. 434).

Here the stolon was found to arise in relation to a leaf base, the stolon arising from the adaxial side of the leaf base. In some cases the leaf was found to develop to a considerable size, before being arrested in growth, while the stolon remained a relatively narrow structure/

structure. In other cases the relative sizes of leaf and stolon were reversed, the leaf being the smaller and the stolon the larger. In extreme cases the leaf apex appeared to be substituted by a stolon.

In view of the former cases, however, Professor Bower does not think this latter a possible interpretation.

The origin of stolons from an older stock of Plagiogyria was also examined by the same author, and here the leaf appeared to be completely replaced by the stolon, though insufficiency of material made it impossible to decide whether the actual leaf apex was ever involved.

The origin of stolons or runners in Lophosoria has also been examined by Professor Bower, who finds that they originate from buds situated in a median position at the base of the leaf which bears them and on the abaxial side. The material of Nephrolepis at my disposal would not allow of such a definite statement for the position of origin of the stolons, for though the position of certain stolons might have fitted into such a scheme, there were others which were not in relation to any leaf base, while in one case (shown to left of Fig. 5 B) two stolons arose in close relation to each other, at the base of a single leaf. (Note: In Fig./

Fig. 5 B. leaf bases are slightly shaded; stolons are unshaded.)

Here again, as in the young plant shown in Fig. 5 A, stolons are seen to arise nearer to the apex of the stem than do any leaves. The stolons are in most cases narrower than the leaf bases.

In Fig. 5 B, the points of origin of eight stolons are seen, while there are only six leaf bases.

The lack of correlation between origin of stolons and leaf bases is also evident.

THE OPERATION OF THE SIZE FACTOR.

While studying the origin of the stolons from the underground rhizome, one was struck with the fact that there was a regular increase in diameter of the individual stolon, as one passed from the base of the rhizome upwards. This fact suggested that a series of sections cut from stolons arising at successively higher levels on the rhizome, might yield some facts of interest bearing on the operation of the Size Factor.

The importance of this factor was first emphasized by Professor Bower in his presidential address to the Royal Society of Edinburgh in 1920. In this address Professor/

Professor Bower showed how the principle of similar structures has affected the internal morphology of the vascular system of plants.

To quote Professor Bower's own statement of the facts: "The stems and roots of most plants are approximately cylindrical. The same is the case as a rule for their conducting tracts also. The cylinder is one of the solid forms in which the proportion of external surface to bulk is exceptionally low, any deviation from the cylindrical form, either by external projections or by involutions, necessarily leads to an increase in the proportion of surface to bulk. The surface varies only as the square of the linear dimensions, but the bulk as the cube. It follows, therefore, that in carrying out any of these physiological functions of a living organism, which depend on surface, as do all those of the acquisition and interchange of material, the actual size of the part which exercises that function is a matter of the greatest moment. The larger the plant is the more dependent will it then be upon its form and detailed structure, not only for the stability but also for the performance of its functions of absorption and transit of liquids and gases. This will apply not only to the external surface, but also to those internal/

internal surfaces which limit one tissue tract from another."

In this paper special emphasis was laid upon the necessity for maintaining a large surface of contact between the stele and the surrounding tissues, emphasis being naturally laid upon the endodermis as a controlling barrier. Professor Bower pointed out that this necessity was met by corrugation and varying degrees of disintegration of the stele. In relation to this broad aspect of the subject it is of interest to note that the relatively large rhizomes of Nephrolepis are dictyostelic, the larger the rhizome the more complex the dictyostele. On the other hand, the small stolons are always protostelic, throughout their entire length, in which respect they differ from the larger stolons of Plagiogyria which are protostelic at their base, but become solenostelic and finally dictyostelic where they have leaves.

In a later paper ("The Relation of Size to the Elaboration of Form and Structure in the Vascular Tracts in Primitive Plants." Proc. Roy. Soc. Edin. Vol. XLIII, 1923) where modifications of the xylem independent of the shape of the endodermis are studied, Professor Bower suggests that there is a factor, possibly connected with the physiological interchange between the/

the two tissues.

It is this later observation which is of particular interest in relation to the condition found in the variously sized stolons of Nephrolepis. In all of these, as mentioned above, the stele is protostelic, so that modifications in relation to the variations of size must be internal to the stele, i.e. they must affect the relations existing between the various stelar tissues and, more particularly, the relationship between living and dead tissues. This latter relationship is of considerable physiological importance since it bears directly on problems of translocation of water and food-stuffs. It appears in fact to be necessary for the plant to maintain a large surface of contact between the dead elements of the xylem and the surrounding living cells.

This is simple in the case of the small stele where there are only a few xylem elements at the centre of the stele, but as the plant enlarges, if this solid core of xylem is not broken up in some way, the bulk of xylem will increase much more rapidly than the surface of contact between it and the surrounding living tissue, (the bulk increasing as the cube, the surface only as the square of the dimensions.)

It has been shown by previous investigators that the/

the shape of the xylem tract does infact become greatly modified, that it may even become highly disintegrated.

A series of sections were cut from the stolons of Nephrolepis biserrata, in each case at a distance of 1/8 of an inch from the point of insertion of the stolon on the rhizome.

It was found that though there was a marked increase in the diameter of the stolon, arising at successively higher levels on the rhizome, it did not always follow that there was as marked an increase in the diameter of the stele, the increase in the diameter of the stolon being mainly caused by distention of the cortex. The set of diagrams included in Fig. 7 show the relative sizes of stele and cortex, while those included in Fig. 8 show the stele only. The xylem is shown in solid black. The position of the endodermis is indicated by an unbroken line. Fig. 8 A. shows the stele of the smallest stolon. Here the xylem tract consists of a central group of large tracheids with a relatively small intermingling of parenchymatous cells. The condition approaches to that of a solid xylem core with radiating stellate projections. If on increase of size of the entire stele, the xylem tract increased in/

in such a way as to be but a magnified image of this earlier condition, then the surface of contact between the xylem and the surrounding living cells would decrease enormously. This, however, is not the case, as a glance at Fig. 8, B-E will show. All of these diagrams show an increase in the number of radiating plates of xylem, not an increase in thickness of those already present in the young state. The narrow plate of cells is a formation which gives a very high proportion of surface to bulk, and therefore of surface of contact between living and dead cells. The final condition as seen in diagram E is what has been termed a xylem sponge, disintegration of the xylem mass having become very great indeed. There is now in many cases no connection between the plates of cells towards the periphery of the xylem tract, and those at the centre. This complete breaking apart of the xylem tracts avoids the danger of the formation of too solid a xylem core which would necessarily result if all the peripheral plates had to be joined up to the xylem elements at the centre of the stele, and which would cause the xylem elements in the centre to be isolated from living tissue.

Thus it is evident that even in steles where the range/

range in size is not great, it is yet possible to follow out the effect of the Size Factor.

Some very detailed work on the effect of size on internal morphology has been carried out by Dr. Claude Wardlaw who worked first on the Psilotales, and Eligulate Lycopodiales (Wardlaw, "Distribution of the Xylem in the Vascular System of Psilotum, Tmesipteris and Lycopodium". Trans. Roy. Soc. Edin. Vol. LIII, part III). Later work was done by the same author on Selaginella ("Size in Relation to Internal Morphology. No. 2. The Vascular System of Selaginella". Trans. Roy. Soc. Edin. Vol. LIV. Part II).

Dr. Wardlaw found that the larger stele is never a magnified image of the smaller one, but that the xylem becomes increasingly disintegrated in passing from smaller to larger size. By accurate measurements it was shown how a high proportion of surface to bulk and therefore of surface of contact between living and dead tissue was maintained in the xylem of even the largest steles.

Additional facts of interest bearing on the operation of the Size Factor in the ferns have been brought forward by Dr. S. Williams in his paper "Some Points in the Anatomy of Dicksonia" (Proc. Roy. Soc. Edin/

Edin., Vol. XLV, part III). Dr. Williams shows how the massive inwardly projecting flanges at the margins of the leaf gaps in Dicksonia Barometz and Dicksonia antarctica are a means of increasing the surface of interchange between the stele and the surrounding tissue, while in Dicksonia squarrosa, where the diameter of the stele is small, the inwardly projecting flanges are correspondingly small.

Attention is drawn also to the different methods adopted by such ferns as Dicksonia antarctica and Cyathea medullaris in order to maintain an adequate ratio of surface to bulk in their steles. Dicksonia effects this by means of corrugation while Cyathea does so by curving of the meristeles and by formation of accessory strands.

The influence of the Size Factor is also shown in the form of the petiolar strand of Dicksonia. The strand is horse-shoe shaped at the base of the frond, and higher up where the strands coalesce, considerable corrugation is evident. This corrugation greatly increases the surface of contact between the vascular strand and the surrounding tissue. Similar cases have been described by Professor Bower for Metaxya and Thyrsopteris.

Dr. Williams shows how in Dicksonia antarctica and Dicksonia squarrosa, practically every tracheid in the bulky/

bulky xylem masses is in contact at some point or another with one or more living cells.

De Bary ("Comparative Anatomy" p. 344) states that the xylem masses in ferns are of two types, those in which the xylem is homogeneous, and those in which the tracheids are intermingled with parenchyma, and that the two types are distributed according to species and perhaps genera. Dr. Williams, however, has examined a number of the examples cited by De Bary in support of the above statement, and finds that in all cases, either the stele examined was a small one, or one in which practically all the tracheids were in contact with living tissue, whereas in almost all cases where the xylem mass becomes bulky there is an intermingling of parenchyma.

In support of this statement Dr. Williams quotes the findings of A. S. March ("The Anatomy of Xerophilous Species of Cheilanthes and Pellaea", Ann. of Bot. 1914, P. 677). Marsh shows how in Cheilanthes Fendleri and C. gracillima there is a narrow band of tracheids and no parenchyma. In C. lanuginosa there is a wider band of wood and some parenchyma, while C. persica and Pellaea andromedaefolia with their broad bands of wood have a larger intermingling of parenchyma.

Since/

Since these are all closely related forms, Marsh's findings are in agreement with those of Dr. Williams, who summarises the findings thus: that increase in size of stele in the vast majority of Ferns has been accompanied by

(a) adaptations to increase the surface of interchange between the stele and the surrounding tissues.

(b) Modifications of the xylem mass to ensure constant contact between the stele and living parenchymatous elements.

Any exceptions to these findings occur among ancient or primitive types.

It is thus evident that the results of the work of the various authors quoted above, all concur in their support of the importance of the Size Factor, first emphasised by Professor Bower (Loc. Cit.).

DETAILED ANATOMY OF STOLON.

A number of diagrams have been made, giving more detail of the general distribution of tissues in the stolon.

A sector taken from an underground stolon is shown in Fig. 5 D. Here there are six protoxylem groups. This number was not, however, found to be constant, as some stolons showed only five protoxylem groups while still/

still others showed more than six groups. In the largest stolons examined it was extremely difficult to distinguish the protoxylem groups.

Fig. 5 D. shows a narrow band of phloem surrounding the xylem, it is shaded with lines placed closely together while the broad pericycle which surrounds the phloem is shaded less closely. The endodermis is indicated by an unbroken black line. Outside of this is the inner sclerotic cortex (stippled). The middle cortex with relatively thin walled cells is lightly shaded, while the outer cortex is again stippled. This also is sclerotic. There is considerable storage of starch in the middle cortex.

The distribution of the tissues in the aereal stolon is shown in Fig. 5 E. Here there appearsto be regularly only four protoxylem groups. This difference in number of protoxylem groups in the aereal and underground stolons has been noted by Sahni. (Sahni, "The Vascular Anatomy of the Tubers of Nephrolepis", New Phytologist, Vol. XV). The above mentioned author follows the development of the stele as it passes from the solid protostelic stolon into the much enlarged tubers found in N. cordifolia. He shows how the solid protostele/

protostele divides up into a network of tangentially flattened strands. He shows also the close similarity of the transition, to those passed through by many fern rhizomes in passing from the protostelic to the dictyostelic condition.

A detailed drawing of a small part of the stele of an underground stolon is shown in Fig. 5 C. A protoxylem group is included together with a number of metaxylem elements with their living cells in intimate contact. A few large sieve tubes are also shown, together with a mass of somewhat crushed protophloem cells. The pericycle consisting of from two to three layers of cells, and the single layer of endodermal cells is also shown. The fact that the endodermis and the pericycle are derived by division from a single layer of cells is clearly shown, there being more or less regularly, one pericycle cell corresponding to each endodermal cell. This is a condition which is common for ferns in general. Additional radial divisions in the inner layers of the pericycle tend to veil this relationship between endodermis and pericycle, for these layers.

There is very great thickening of the innermost cortical layer, the thickening not being laid down evenly on all walls, but being deposited principally on the inner tangential wall. This thickening proceeds so far that in some of the cells there is practically no lumen/

lumen left. There is an elaborate system of pits in the walls of these highly thickened cells; these allow of intercommunication from cell to cell. The thickening on the walls of the second layer of cortical cells is laid down much more evenly on all walls.

A similar drawing from a younger stolon is shown in Fig. 5 F. All the tissues shown here, correspond to those described for Fig. 5 C. the only difference being that lignification has not yet gone beyond the protoxylem elements.

ANATOMY OF THE STEM.

In order to make as complete an examination as possible of the structure of the stem, hand sections were cut in series from the base upwards towards the apex. These showed the stem to be protostelic at its narrow basal region, and dictyostelic in the wider central portion (Fig. 9 A-N).

When dealing with the structure of the stolon reference was made to Professor Bower's statements regarding the influence of the Size Factor, and the disintegration of the xylem in the protostelic stolon was taken as an illustration of that part of the statement which deals with the changes which occur in individual/

individual tissues as a result of increase in size. Other changes, however, were shown to occur as a result of increase in size. These involve changes in the formation of the stele as a whole, having the effect of bringing about brought about in order to increase the surface of interchange between the stele and the surrounding tissues. In this connection Professor Bower says that increase in size in the ferns, carried out under certain structural restrictions, has been a decisive factor in leading to their extraordinary vascular development, while the ontogenetic development in plants which, like the ferns, have no secondary growth, provide the most cogent evidence of the effect of increase in size upon internal structure. The form of the stem of the young fern plant is that of a gradually enlarging cone (vide. Fig. 5 A), and in a series of sections taken from the base upwards, the changes in the stele, brought about by the influence of the Size Factor can be noted.

The accompanying set of diagrams illustrate this in the case of Nephrolepis biserrata (Fig. 9 A-N). The conducting tract at the base of the stem consists of a narrow protostele, there being a core of xylem, interspersed with parenchymatous cells, and surrounded by a pericycle of several layers, and an endodermis. There/

There is considerable storage of starch both in the parenchymatous cells of the stele and in the cortex, which is sclerotic (Fig. 9 A).

A little bit higher up in the stem a wide involution is developed in the stele, thus exposing a much larger endodermal surface to the cortical cells (Fig. 9 B). This involution gradually widens till the stele is more or less crescent shaped (Fig. 9 C). Here stolon traces are seen to be arising to right and left of the stele.

(Figs. 9 A and B show the complete section of the stem; Figs. C onwards show only the stelar region).

Fig. 9 D. shows two stolon traces arising from the larger meristele and running obliquely through the cortex. The stele now consists of two meristeles, one of which is considerably attenuated. It is from this larger meristele that the stolon traces arise, while leaf trace strands are separated off from the margins of both meristeles.

In Fig. 9 E. two leaf trace strands have separated to the right of the meristeles, while in Fig. 9 F the third strand is being abstricted off from the main stelar mass. This is shown completely severed in Fig. 9 G. The fourth strand arises from the margin of the larger meristele (Fig. 9 H.) Here the origin of a stolon trace is also seen.

The/

The two first formed leaf trace strands are now seen each to be dividing into two.

The trace as seen in Fig. 9.I. consists of five separate strands, one of which is in process of division. The leaf trace towards the left of diagram now shows four strands.

In Fig. 9 J. the complete right hand leaf trace is passing out through the cortex, six strands now being present. A stolon trace is also being given off from the main meristele.

In Fig. 9 K. the leaf trace is running obliquely through the cortex. The stolon trace whose origin was shown in Fig. 9 J. has passed out from the meristele and the endodermis has again formed round the meristele.

From these figures it appears that leaf traces are given off alternately to left and right of the two meristeles, while stolons arise from the larger meristele only.

This distinction of point of origin of leaf trace and stolon trace would appear to bear out the conclusion come to from external examination, regarding the origin of the stolons, where it appeared that the stolon did not replace the leaf, nor did it appear to have any constant relation to/

to the leaf base.

The general structure shown above for the stele of Nephrolepis is very similar to that figured by De Bary for Davallia dissecta, and reproduced by Professor Bower ("Filicales" Vol. III p. 17), the only difference being that in Davallia the two meristeles are more nearly equal in size than is the case in Nephrolepis. Both show much divided leaf traces, departing to left and right of the two meristeles. In the case of Nephrolepis, however, further disintegration of the stele occurs. Sections cut from a comparatively old stem showed an advanced distyostelic condition, there being in the sections examined, six meristeles in the ring.

Fig. 9 L-N are drawn from these sections of an older stem. They show the further disintegration of the stele.

The magnification for these last three figures is less than for Figs. A-K.

There was nothing peculiar about the anatomy of the individual meristeles which therefore need not be described.

THE PINNA TRACE.

Davie in his paper on "The Pinna Trace in Ferns" (Trans/

(Trans. Roy. Soc. Edin. Vol. L. part IV) distinguishes two types of pinna trace, - marginal and extra-marginal.

In the marginal type the leaf trace may be either simple or "broken", i.e. consisting of several strands, but in all cases the pinna trace is supplied from the margin of the leaf trace strand or strands. In the paper mentioned above, various modifications of the marginal type of pinna trace are described, a simple type being that in which the adaxial extremities of the xylem masses become extended on the adaxial side of the petiole, and a few tracheids are separated off from the margin of the petiolar strand, e.g. Asplenium obtusatum.

A more complicated type is seen in Loxoma Cunninghami, where the trace in the base of the petiole is curved in outline. Here an arched pinna trace is cut off.

A third type is described for Balantium culcita where the pinna trace cut off from the margin of the petiolar trace is a replica of the arched parent trace.

A fourth, and simplest type, is described for Anemia hirta where each hook, separated off consists of a small group of tracheids placed at right angles to the set composing the side of the leaf/

leaf trace.

The extra-marginal type differs from the marginal, in that the margins of the petiolar trace remain intact throughout the whole length of the petiole. The first extramarginal type mentioned by Davie is that of Didymochlaena truncatula, in which the formation of the pinna trace is described as follows.

"The two adaxial strands have their margins sharply recurved so that they are almost parallel to the adaxial surface of the petiole. To supply the basal pinna, the back of the hook is lengthened towards the adaxial corner of the petiole. Across the narrow space between the two strips of tracheidal tissue thus formed new tracheids spread. The original outline of the leaf-trace strand is thus re-formed, while a ring of tracheids is attached to the back of its hooked portion. The ring soon separates, to pass into the base of the pinna and divide up into a pinna trace resembling the leaf-trace".

It is therefore evident that in such a type of pinna trace supply, the actual margin of the petiolar trace (i.e. the "Leaf Trace" of Davie) from which it arises, remains intact throughout the process, and since the pinna trace goes off from the outside of the/

the parent strand, the term "extra-marginal" is applied to the method.

In a type such as that just described no gap is left in the parent trace. Such is not always the case. Davie cites Leptopteris hymenophylloides as an example in which a gap is left, and Hymenophyllum demissum as a type in which only a single tracheid remains between the end of the abaxial curve and the marginal set of tracheids, after the pinna trace has departed.

Blechnum orientale is taken as the most nearly marginal among the extra-marginal types, only one or two of the marginal tracheids remaining intact throughout.

As an example of a combination of the two types of pinna supply, Histiopteris incisa is taken. Here the hooked extremity of the petiolar trace is cut off in marginal fashion, but simultaneously the projecting corner of the arch beside it lengthens and a ring of vascular tissue is nipped off from it, as in extra-marginal types. The two strands then pass out towards the base of the pinna, and finally form a pinna trace exactly like the petiolar trace.

In types with broken petiolar traces, pinna strands/

strands may be given off both from the adaxial and the adjoining abaxial strand as in Leptochilus cuspidatus.

In a table drawn up to show the type of pinna trace typical for the various groups of ferns, the Aspidieae are shown to have the extra-marginal type. Of the Davallieae, a number show the extra-marginal type, but all species of Nephrolepis named, viz. N. Amerpohlii, N. Fosteri, N. Piersoni, and N. Scottii, are described as being marginal. No species of Nephrolepis is, however, figured in the paper.

Of the types of pinna trace formation described, that of Davallia solida approaches nearest to the condition found in Nephrolepis biserrata, except that, whereas Davallia solida is shown to have two large adaxial strands, and only one small median strand, Nephrolepis biserrata has two large adaxial strands and five smaller abaxial ones. In Davallia solida the pinna trace is binary, i.e. two separate strands are abstricted off from one of the adaxial strands, and these pass separately into the pinna. In Nephrolepis biserrata the pinna trace consists of a single group of tracheids cut off from the margin of one of the adaxial strands.

The detailed structure of one of the adaxial strands/

strands is shown in Fig. XI.A. This shows the strand to consist of a central group of large tracheids and a band of smaller elements drawn out towards the margin of the strand, and having a group of protoxylem elements at its extreme tip. There is a surrounding band of phloem, a pericycle consisting at parts of a single layer of cells, while at other parts there may be two or three layers. The whole is surrounded by an endodermis. The inner walls of the cortical layer abutting on the endodermis are considerably thickened.
Fig. XI.B. shows the band of tracheids being cut off from the margin of an adaxial strand. A layer of pericycle cells has formed, thus separating the tracheids of the pinna trace from the main group in the parent strand. The pinna trace leaves the parent strand as a small circular strand consisting of a central group of xylem elements surrounded by a band of phloem, with pericycle and complete endodermis. This trace passes outwards through the petiole and into the pinna.

Fig. XI.C. shows an abaxial strand with its group of tracheids situated somewhat to one side of the strand, there being a one sided development of phloem. As in the adaxial strand described above there/

there is a pericycle and complete endodermis. The marked thickening and pitting of the walls of the innermost layer of cortical cells is clearly seen, the lumena of some of the smaller cells being almost completely filled in.

A complete series of sections were made, passing from the base of the petiole upwards towards the tip of the frond. Several sections were taken at regular intervals below the level of the first pair of pinnae, and also between each subsequent pair. In all cases the origin of the pinna trace was found to be marginal, a few tracheids together with a surrounding band of phloem being separated off from the margin of one of the adaxial strands.

In the series of diagrams seen in Fig. X. a quite appreciable contraction of the petiolar trace towards the base of the petiole can be seen. This has been noted for other ferns by Sinott ("Evolution of Filicinean Leaf Trace", Ann. Bot. Vol.25.1. 1911). The above mentioned author suggests that the increase which occurs above this region is probably due to the fact that the petiole becomes free from surrounding bases of leaves etc. and that therefore the increased petiolar trace, means increased mechanical support.

Fig. X.C. shows the lateral extension of the xylem elements at the margin of the left hand adaxial/

adaxial strand, preparatory to cutting off the pinna trace for the first pinna, while Fig. X. D. shows the same condition for the next, opposite, pinna. The two pinna not being exactly opposite, their traces are not given off simultaneously.

In Fig. X. D. one of the abaxial strands has united with the adaxial strand which is in process of separating off a pinna trace. It has been suggested by Davie (Loc. Cit.) that this may be a means of reinforcing the adaxial strand by means of the addition of extra tracheids.

In the series of diagrams (Fig. X) the giving off of the single pinna trace, and its subsequent passage out through the cortex can be followed for each pinna, the details being the same in each case.

Passing from the base of the petiole towards the tip, there is a decrease in the number of strands in the trace, till between the seventh and eighth pair of pinnae the trace is seen to consist of the two adaxial strands and a single abaxial one. The two adaxial strands now fuse but separate again below the ninth pair of pinnae. They fuse again, finally between the ninth and tenth pair of pinnae, after which there is a continuous reduction in the size of the trace, the abaxial strand disappearing entirely between the twelfth

and/

and thirteenth pair. The trace now consists of a single strand consisting of a mass of tracheids surrounded by a band of phloem. Fig. 10.W. shows the pinna trace being separated off for the lower of the thirteenth pair of pinnae.

Thus we find that Nephrolepis biserrata has a single marginal pinna trace, consisting of a small group of tracheids abstricted off from the margin of an adaxial petiolar strand.

This marginal type of pinna trace was held by Davie to be more efficient than the extramarginal type, in that by this means each successive pinna can be supplied with a long strip of tracheids which may be equal in width to the whole margin of the unincurved petiolar trace, whereas in the extramarginal type, the tracheids must be cut off from the narrow back of the hooked trace, where the number of tracheids present is relatively small, which is an obvious disadvantage.

Nephrolepis then has developed the type of pinna supply held by Davie to be "the most improved type" and the one which has proved to be the most adaptable.

In the series of diagrams contained in Fig. X the influence of the "Size Factor" is again evident.

At the base of the petiole, where the diameter of the/

the petiole is large, there is a wide horse shoe shaped trace, consisting of numerous strands, whereas towards the apex of the frond, where the diameter is smaller, the trace is reduced to a single strand, situated at the centre of the rachis.

NEPHROLEPIS ACUMINATA.

The material of this species was kindly sent to me by the Director of Brooklyn Botanic Gardens and though the fronds had been carefully packed with moss, they were unfortunately not in the freshest possible condition when I received them. This was of course more noticeable in the younger, more delicate parts of the fronds, but the still uncurled tips with their covering of hairs, survived somewhat better, and these I was able to embed and cut.

Other fronds were sent dry, and these I treated with Orzeszko's mixture for recovering herbarium material. The formula used was:-

Sodium Carbonate	5 gm.
Glycerine	25 gm.
Water	70 c.c.

Even despite the utmost care, however, it was impossible to get more than a few isolated stages of the/

the development of the sorus, but fortunately these obtained were of the earliest, and for my purpose, the most important, stages.

Nephrolepis acuminata is described by Christ (loc. cit.) under the name N. Davallioides. The sori are almost marginal and are situated each on a separate little projection of the pinna. The upper and under lip of the indusium are almost equal in size. The indusium is reniform.

The tip of the frond is drawn out into a long slender structure with a single sorus to each simple "pinna". Further back from the apex the pinnae become increasingly larger till at the base they may be from six to seven inches long, by less than half an inch broad (Fig. XII D).

Fig. XII G. shows the transition from the type of "simple pinna" found near the apex, to the more complex type with numerous sori to each pinna. The hairy nature of the petiole can also be seen in this figure. In this species there is a distinct difference between fertile and sterile pinnae, the fertile pinnae being longer and narrower than the sterile ones. They are also deeply crenated. The sterile pinna is short and broad and has a serrated margin.

As in Nephrolepis biserrata the first sign of soral development/

development is the outgrowth of a mound of cells, at a point several cells distant from the marginal cell. This development is seen in Fig. XII A. and appears to arise at a point six cells distant from the marginal cell. No evidence could be found which might suggest the first soral development to be marginal. A few of the hairs which cover the entire apex, in all species examined, are included in Fig. XII A.

A further stage in the development is seen in Fig. XII B. where the sixth cell back from the marginal one is seen to have enlarged considerably, and to be growing towards the margin of the leaf. This developes later into the protective indusium as shown in Fig. XII C. where the indusium is now a massive structure enclosing a hollow receptacle.

From these figures it can be seen that despite the fact that in Nephrolepis biserrata and N. acuminata, there is a very distinct difference between the final position of the sorus, relative to the margin of the leaf, still there is little or no difference in their point of origin.

No stages in the development of the sporangium have been figured, the material not being in sufficiently fresh condition, but Fig. XII H. shows the mature sporangium which has a long slender stalk and a capsule with the usual vertical annulus consisting regularly of thirteen cells/

cells as in N. biserrata. The epi-stomium and hypo-stomium consist usually of three cells, while there are two cells in the stomium. The stomial cells are thickened on all walls. The individual stomial cells are larger than those of N. biserrata. The annulus is interrupted at the stalk. There are eight tabular cells on one face of the capsule. The sporangium viewed from the side is shaped like a bi-convex lens. (Fig. XII F).

The spores are somewhat irregular in outline, seen from one aspect they appear to be approximately oval, while another view shows them to be convex on one side and concave on the other. (Fig. XII E). Along one side of the spore there is a distinct band of thickening. The surface of the spore is rough, there being an irregular grooving all over it. A series of spore counts were made. These gave the following results:- 60, 56, 59, 63, 60, 55. Probable number, 64.

NEPHROLEPIS EXALTATA.

This species is described by Hooker as having sori which are intra-marginal. The mature frond may be 1½ - 2 feet long, with individual pinnae 1-3 inches/

inches long. The apex of the fertile frond is seen in Fig. XIII A.

The earliest stages in the development of the sorus were not obtained, but a fairly early stage is shown in Fig. XIII C. At this stage there are seven cells between the marginal cell and the cell which is growing out to form the indusium.

Here again, as in N. biserrata the first cell to grow out to form a sporangium is situated in a more or less median position on the receptacle. (Fig. XIII G).

The first division of the sporangium is shown in Fig. XIII H. It is oblique and has its insertion below the level of the epidermis. The mature sporangium differs very little from the sporangia of the other species examined. The stalk is long and three rowed. The annulus is vertical and consists of thirteen cells. It is interrupted at the stalk. There is an epi-stomium and hypostomium consisting each of three cells which may or may not be larger than the cells of the annulus. Fig.XIII B. shows a sporangium where the cells of the hypo- and epistomium do not differ appreciably in size from the cells of the annulus. The two stomial cells are slightly smaller than the cells of the hypo- and epi-stomium/

epi-stomium. They are thickened on the inner tangential walls, and along part of their radial walls. There are eleven cells on the face of the sporangium.

The sporangium shown in Fig. XIII D. shows the thirteen-celled annulus, but here the cells of the hypo - and Epi-stomium are larger than the cells of the annulus. The two stomial cells are still larger than the cells of the epi- and hypo-stomium. Rupture of the sporangium has taken place, the two stomial cells having been drawn apart.

Fig. XIII E. shows a sporangium lying so as to show the three rowed nature of the stalk.

The spores are ovoid and slightly grooved. There is here again the single longitudonal ridge of thickening. The spores are larger than the spores of any of the other species examined. (Fig. XIII. F)

The results of a series of spore counts were as follows:

62, 60, 57, 59, 56, 60.

Probable number - 64.

Large numbers of sections both of N. cordifolia and N. bostoniensis were cut but it was found impossible to get early stages of the development of the sorus for either species. A few diagrams of the pinnae of N. cordifolia/

cordifolia are included among the figures. These show their close arrangement on the rachis, the open venation and reniform indusium. The individual pinnae are distinctly auricled especially on the lower side (Fig. XIII I.J.K.). The spores are distinct in shape from those of the other species examined, being rounder, and having little circular markings all over their surface. There are also a number of deep ridges on the spore (Fig. XIII. L.).

The material of N. bostoniensis which was obtained from Kew showed one point of interest, in that a number of the sporangia of this species showed curious hair-like outgrowths from the capsule (Fig. XIII. M.N.). No outgrowths of any kind were observed on the sporangia of any other species.

COMPARATIVE DISCUSSION.

Professor Bower in his comparative study of the Davallioid Ferns ("The Filicales", Vol. III, Chap. XXXVII) has shown how it is possible to trace their origin from the more primitive Dicksonioid type, which are characterised by their creeping habit, highly branched frond, dermal hairs, sustained individuality of the marginal and gradate sorus, the superficial origin of the two lipped indusium/

indusium, the oblique annulus and robust sporangial stalk, internal solenostely, and undivided leaf trace. Such features with slight modifications can be traced through the Dennstaedtineae to which group Professor Bower assigns Davallia Dubia, with its solenostelic vascular system, and hairs, not scales, as dermal appendages. Davallia contigua, formerly ascribed to Davallia , is now included in the genus Prosaptia, and from a general examination of its characters, is placed in near relation to Polypodium obliquatum. The Davallias proper as represented by Davallia dissecta and D. pentaphylla, are shown to have a sorus which is marginal in origin, while in D. griffithiana a gradate sequence of sporangial development has been seen to precede the later mixed condition. The vascular system shows also, an advance on the Dicksonioid Dennstaedtioid solenostelic condition, there being a higher disintegration of the stele, especially in the leaf trace. The dermal appendages are scales, not hairs.

All these features show Davallia to be advanced, though still showing traces of its Dennstaedtioid ancestry.

In Davallia the sorus at maturity tends towards a superficial position, the margin of the lower indusium being/

being adherent to the surface of the blade with which the upper indusium is merged. The flattened receptacle bears a mass of sporangia of mixed ages, though still showing signs of basipetal sequence. The sporangia have long stalks consisting of one row of cells. All these are features of advance, and show the transition from a gradate to a fully Leptosporangiate state. The individuality of the sorus is maintained throughout the genus.

Professor Bower in dealing with the comparison of the Davallioid Ferns says: "Of the three modifications especially noted for the Davallioid Ferns, the first is passage of the receptacle from the original marginal position of the Schizaeoid and Dicksonioid Ferns to the superficial position which is more or less marked in the Davallioids. This is a change of advance and gradual steps in the change are illustrated by the condition seen in Thyrsopteris, Cibotium, Davallia, Lindsaya and Nephrolepis".

Of the latter Professor Bower says: "Until the fuller developmental details are to hand it must remain uncertain whether the receptacle itself has ever in this group of Ferns slid from the margin to the surface in point of initiation. In all the others the receptacle/

receptacle is actually marginal in origin but in all of them, in more or less degree the sorus shifts towards the under surface in course of individual development".

The results of the work reported in the foregoing paper are such as to prove that in fact the receptacle in Nephrolepis has slid from a marginal to a slightly superficial position, in point of initiation, and that the point of initiation is practically constant for all species examined irrespective of whether, as in N. acuminata, the final position of the sorus is only slightly intramarginal, or whether, as in N. biserrata, it is quite distinctly so. In Nephrolepis there has therefore been what Professor Bower has termed a "Phyletic slide" of the originally marginal sorus to the lower surface of the pinna. Thus at the very initiation of the sorus, added protection is assured for the developing sporangia; such protection is only insured to the Davallias by a later shifting of the originally marginal sorus.

All the other features described for Nephrolepis, such as the dictyostelic vascular system, the much divided leaf trace, the presence of dermal scales, not hairs, the mixed sorus showing signs of basipetal origin, the long slender stalk of the sporangium and its vertical annulus interrupted at the stalk, bear out the correctness of the position/

position in close relation to Davallia, to which it has previously been assigned, while the slightly superficial origin of the sorus places the genus Nephrolepis at a point on a phyletic scheme, slightly more distant from the Dicksonioid type from which both Nephrolepis and Davallia are derivitives.

The sorus in certain species of Nephrolepis shows another modification: that of the formation of coenosori. This occurs in N. dicksonioides and N. acutifolia.

The results of my examination of the development of the sorus in a number of species of Nephrolepis show very clearly, as recorded above, that the point of initiation of the sorus has moved from a marginal to a slightly superficial position. A further point of interest is that the point of initiation is practically constant for all the species examined, irrespective of the final position of the mature sorus, c.f. Fig. I.A (N. biserrata), Fig. XII. A (N. acuminata) and Fig. XIII.C. (N. exaltata), all of which show the origin of the sorus to be at a point 5 or 6 cells from the margin of the leaf.

It may be stated in conclusion, therefore, that the facts described in this memoir confirm Professor Bower's allocation of Nephrolepis to a position close to Davallia, but at a point more distant than the latter from their common/

common Dicksonioid source.

SUMMARY.

1. A number of species of Nephrolepis were examined in order to ascertain whether the sorus is marginal or superficial in origin. In all species examined it was found to be slightly superficial, the first signs of development taking place at a point five or six cells back from the marginal cell. This point of origin appears to be independent of the final position of the mature sorus.

2. A study of the vascular system of the stem showed it to be of an advanced dictyostelic nature. The leaf trace consisted of a number of separate strands.

3. A series of sections taken at intervals from the base of the petiole upwards, showed the method of pinna trace formation to be marginal throughout the entire length of the frond.

4. A short study of the Influence of the Size Factor was carried out on various sized stolons. These in all cases were protostelic, the effect of increase in size being/

being a greater disintegration of the xylem mass, to allow of more complete contact between living and dead cells.

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DESCRIPTION OF FIGURES.

Fig. I. N. biserrata.

A - F Vertical sections showing successive stages in development of sorus. A & C x 320. B,D,E.F x 450 (For full description see text.)

Fig. II. N. biserrata.

A. Vertical section showing mixed condition of mature sorus. x 73.

B, C, D, various stages in development of sporangia, the youngest sporangium being seen to left in C. B x 320, C x 320, D x 225.

Fig. III. N. biserrata.

A,B,C, mature sporangia, x 640. D large and small spores, x 640. E, F, parts of pinnae showing venation, and position of sorus at end of upper branch of vein. E shows a second branching of lower half of vein; neither of these second bifurcations bears a sorus, x 4.

G Transverse section of pinna showing ridges on adaxial side, x 30.

Fig. IV.

Vertical sections to show characteristic formation of indusium in A, (N. acuta), B. (N. cordifolia), and

C/

C. (N. acuminata). x 73.

Fig. V. N. biserrata.

A. Young plant showing ridged, upright, rhizome. The origin of numerous stolons and leaves can be seen. Fibrous roots arise from the stolons, x ½.

B. Rhizome, with leaves and stolons cut back to within short distance of their point of origin on the stock. Leaf bases shaded, stolons unshaded, x 2.

C. Transverse section of stele of underground stolon (full description in text) x 450.

D, E. T. S. underground, and aereal stolons the former showing six protoxylem groups, the latter only four, x 45.

F. T, S. stele of underground stolon in which lignification is incomplete, x 450.

Fig. VI. N. biserrata.

A, B, C, scales from rhizome, petiole, and aereal stolon, respectively, x 40.

Fig. VII. N. biserrata.

A - E, diagrams to show relative size of stele and cortex in stolons of various sizes, (steles in solid black.) x 40.

Fig. VIII. N. biserrata.

A - E. T - S. steles from stolons shown in Fig.VII. These/

These show the disintegration of the xylem tract, (shown in solid black), brought about by increase in size, x 225.

Fig. IX. N. biserrata.

A - N. T. sections of rhizome taken at intervals from base upwards. These show transition from protostelic to dictyostelic condition, A - K, x 10. L, M, N, sections from older rhizome x 6.(Full description in text.)

Fig. X. N. biserrata.

A - X transverse sections of petiole taken at regular intervals from base upwards. (Full description in text.) x 10.

Fig. XI. N. biserrata.

A. T.S. adaxial strand of petiolar trace, x 120.

B. T.S. adaxial strand showing pinna trace being cut off in marginal fashion x 120.

C. T.S. Abaxial strand of petiolar trace x 320.

Fig. XII. N. acuminata.

A,B,C vertical sections showing various stages in development of sorus, x 320.

D. Apex of frond x $\frac{1}{2}$.

E. Spores x 450.

F/

F, H different views of mature sporangia x 450.

G. Small portion of frond near apex showing position of sori. x 1.

XIII. N. exaltata, etc.

A. Apex of frond x 1.

B, D, E. Mature sporangia x 450.

C. Vertical section showing early development of sorus. x 320

G, H. Early development of sporangia. x 320

I, J, pinnae of N. cordifolia. I x 1 1/3. J x 2/3.

K portion of pinna to show venation and position of sorus x 2.

L. Spores x 450.

M, N. Sporangia of N. bostoniensis showing unusual development of hairs x 450.