

THE
NEW PHYTOLOGIST.

VOL. XVI, Nos. 1 & 2.

JAN. & FEB., 1917.

[PUBLISHED MARCH 19TH, 1917.]

OBSERVATIONS ON THE EVOLUTION OF
BRANCHING IN THE FILICALES.*

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[WITH ONE FIGURE IN THE TEXT].

I. INTRODUCTION.

THE starting point of this paper was an attempt to see how far our conception of the branch as a potential individual¹ finds support from the recapitulation by the branch of the sequence of structural changes undergone by the main axis during its ontogeny. In this connexion a previous statement by the late Professor Gwynne-Vaughan² was particularly suggestive, namely, that "the ontogeny of the vascular system of the plant as a whole is very frequently repeated, although more or less imperfectly, in the development of its lateral branches"—a statement which is substantiated by the researches of Stenzel³ on several species of *Aspidium*, *Alsophila excelsa*, *Blechnum* and *Struthiopteris germanica*, and of Mettenius⁴ on various other dictyostelic Ferns; by those of Gwynne-Vaughan himself (*loc. cit.*) on a number of solenostelic and dictyostelic Ferns, and, more recently, by those of Professors Lang⁵ and Bower⁶ respectively on the Ophioglossaceæ,

*Dissertation presented for the Sudbury-Hardyman Prize, 1917, at Emmanuel College, Cambridge.

¹ Braun, Alex., *Betrachtungen ü. d. Erscheinung d. Verjüngung in der Natur.*, 1851, p. 25.

² Gwynne-Vaughan, *Annals of Botany*, 1903, pp. 724-5.

³ Stenzel, *Verhandlungen der K. Leop. Carol. Akad. der Naturforscher*, 1861, p. 16.

⁴ Mettenius, *Abhandlungen der kgl. sächs. Ges.* 1861, Vol. IX. Ueber den Bau von *Angiopteris*, p. 499.

⁵ Lang, W. H., *Annals of Botany*, 1913, Vol. XXVII, i. p. 203 and 1915, Vol. XXIX, p. 1.

⁶ Bower, F. O., *Annals of Botany*. 1910, p. 423; 1912, p. 269; 1913, p. 443; 1914, p. 363; 1915, p. 495.

and on the Cyatheaceæ and Ferns of Cyatheoid affinity besides some other forms.

On taking a bird's-eye view of the subject it was observed that many of the forms fell into a rather striking series illustrating progressive stages in the specialization of the branch for the purpose of vegetative propagation. This progression appeared to be as clear and unmistakable in respect of the vascular structure, as in respect of the external appearance of the branch: the two lines in fact ran parallel to each other and rendered more or less mutual support.

But the interpretation of the series in terms of a phylogenetic relationship between its different stages seemed to be a difficult question, for, as will be seen, the different genera did not *necessarily* stand towards each other in relations corresponding to those subsisting between the respective forms of branching exhibited by them.

II. TYPES OF FILICINEAN BRANCHES AND THEIR VASCULAR SYSTEM.

It is well-known that in many species of *Nephrolepis* thin cylindrical stolons arise from among the crowded leaf-bases and, spreading in all directions from the main stock, grow out to varying lengths, and serve as efficient organs of vegetative reproduction by bearing so-called lateral plants at intervals. Under suitable conditions the growth of the stolons is so rapid that in a single season the mother plant may become surrounded by a small colony of young plants which eventually become independent, but even before doing so may, in turn, produce stolons themselves. Sperlich¹ sees in the production of these stolons the beginning of an attempt towards the attainment of an epiphytic habit; and to what a degree this attempt has been successful is well seen in *Nephrolepis volubilis*. Attention was drawn in a previous communication² to the extraordinary habit of this interesting Malayan Fern. The mother-plant is rooted in the soil, but the stolons are of such a great length that they carry the lateral plants borne on them high up among the neighbouring trees. It is a case, in short, of a terrestrial plant producing an epiphytic progeny. The epiphytic tendency so strikingly shown by the genus *Nephrolepis* may possibly be connected with a more effective vegetative propagation which would be ensured by the favourable position of the lateral plants.

¹ Sperlich, A., *Flora*, 1908, p. 357.

² Sahni, B., *NEW PHYTOLOGIST*, 1915, p. 251.

The morphological nature of the stolons of *Nephrolepis* has in the past been a matter of controversy,¹ but even a superficial comparison with other Ferns which are known to possess more or less specialized lateral branches to the stem will convince one of their true nature; to Kunze (1849), to Hofmeister (1857) and to Mettenius (1861) they were so apparent as specialized shoots that the possibility of their being of a different nature did not even present itself to them.

It is, in fact, possible to trace the origin of the highly specialized condition in *Nephrolepis volubilis* downwards through a series of transitional stages found in other Ferns, to that in which the stem divides at the apex into two approximately equivalent branches. This mode of branching is very common among forms with a creeping rhizome (*Polypodium* spp., *Davallia* spp.), and a forking of the stem is occasionally seen even in some erect or semi-erect forms, e.g., in *Plagiogyria semicordata*.² But in many other Ferns, chiefly of erect or semi-erect habit, there seems to be a tendency on the part of the branches to become modified to serve as organs of vegetative reproduction. They undergo a marked elongation in their proximal portion, which may be underground and bears only reduced scale-like leaves, and which in its modified form may be called a stolon. The stolon takes a horizontal or oblique course for a longer or shorter distance away from the mother axis before it passes over distally into the leafy crown. It evidently serves to remove the leafy end of the branch away from the mother axis before the former can strike root and assert its individuality as a separate plant. Velenovský³ records in *Struthiopteris germanica* underground stolons as long as three metres; rather similar stolons have recently been described by Professor Bower in *Thyrsopteris elegans*, *Plagiogyria*, etc., while Stenzel long ago drew attention to the specialized branches of *Alsophila excelsa*. The genus *Nephrolepis* indicates a further advance in specialization, since the stolons are normally entirely leafless. Moreover, whereas further branching of the stolon is rare in the previously mentioned forms (so that usually

¹ For references see the paper just cited, p. 269.

Among Ferns, structures which in appearance as well as in function most closely correspond to the stolons of *Nephrolepis* are the so-called Ausläuferblätter (runner-leaves, leaf-runners) of *Asplenium obtusilobum* Hk., *A. Mannii* Hk., etc., described by Professor Goebel (Biologisches Centralblatt XXII, 1902, p. 385) and more recently by Dr. Kupper (Flora, 1906, p. 337). There can, however, be no question of a homology between the two: the Ausläuferblätter, as Professor Goebel showed, are morphologically leaves.

² Bower, *loc. cit.*, 1910, p. 426.

³ Velenovský, *Vergleichende Morphologie*, Prag, 1905, Vol. I, p. 232.

each stolon bears only one crown of leaves), in *Nephrolepis* the stolon has extensive powers of branching. The apex of the stolon does not itself produce a leafy crown, but during its continued growth produces a large number of secondary growing points, many of which sprout into "lateral plants"¹ while the rest of them remain dormant. In view of the enormous length of the stolons, which ensures a corresponding increase in the number of lateral plants, and in the epiphytic habit of the latter, *N. volubilis* would seem to represent a further stage in the specialization of the filicinean branch.

Turning now to the question from the point of view of the vascular anatomy, we find a series more or less parallel to the one we have based upon the external features. For our comparison we shall refer to Fig. 1, p. 5 which represents in a purely diagrammatic way the vascular relations of the branch to the stock in a number of Ferns whose mature structure ranges from protostely to an advanced type of dictyostely. In the figure the branches are supposed to have come off in all cases at right angles to the main axis, so that they can be drawn as seen in longitudinal section while the main axis is seen in transverse section. In the branch the protostelic portion is shown as a single black band arising from the main axis; the solenostelic portion is shown as two bands which are parallel except towards their proximal ends, where the solenostele is seen to contract. In the solenostelic portions (whether of the main axis or of the branch), the leaf-gaps are not indicated, for the sake of better distinction from the reticulate portions, which are represented by interrupted bands. The leaf-traces have been omitted altogether, and no attempt has been made to draw the diagrams to scale.

Some of the diagrams would require further explanation in view of the facts that the branch very frequently arises in close association with a leaf, in an "axillary" or "infra-axillary" position, and that its vascular supply appears actually to originate from the trace of the related leaf, as in some Hymenophyllaceæ, species of *Zygopteris*, in *Cibotium*, *Plagiogyria*, *Lophosoria*, *Metaxya*, *Cheiropleuria* and *Botrychium Lunaria*. Without entering here into the question of the morphology of the organ in *Zygopteris* termed by Dr. Scott the "undivided trace," it may be stated that the view here adopted regards the branch as arising from the main axis, but with

¹ Thus with respect to the mother plant the lateral plants are usually branches of the second order. If, however, the apex of the main stolon is arrested, it is replaced by one of the neighbouring secondary growing points.

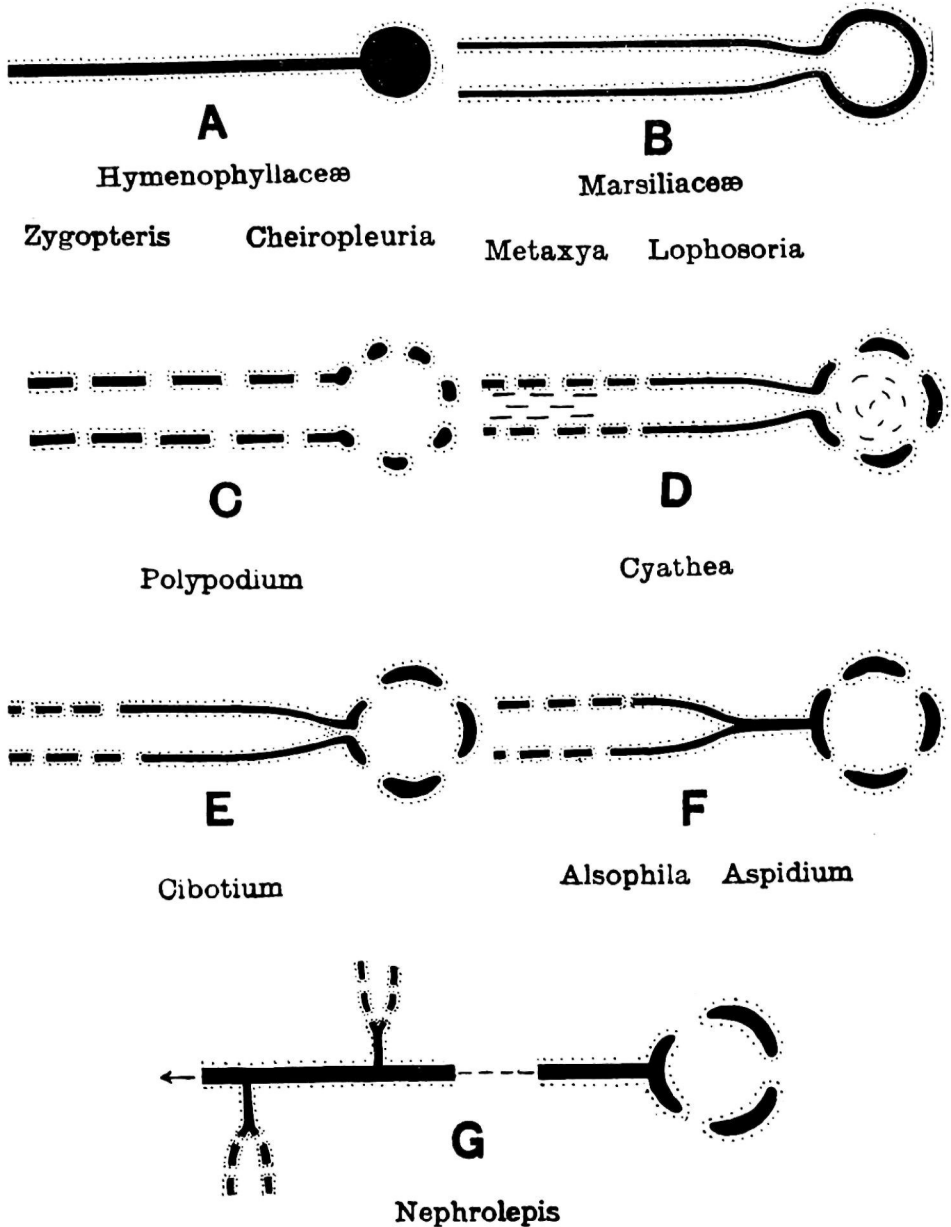


Fig. 1. Diagrams to illustrate the vascular relations between branch and main axis. Xylem black, phloem dotted. The thinner lines in D represent the medullary strands. Further explanation in the text, p. 4-9.

the proximal portion of its strand "adherent" to the trace of the associated leaf, which belongs to the main axis.¹ The strand under discussion would thus have a composite nature, and we may extend

¹ A view which we owe originally to Dr. Scott, (Annals of Botany, 1912, Vol. XXVI, i. p. 59) but which was rejected by him in preference to the leaf-trace theory. The question is further dealt with on p. 19 of the present paper

this view to all cases discussed in this paper, in which a branch arises in close vascular connexion with a leaf. In accordance with this view the plane of section in Fig. 1, A, B, D, E must be supposed to have passed, at the base of the branch, longitudinally through the ramular portion of this composite trace, the foliar portion of the latter being proximal or distal to the plane of section according as the branch is adaxial (Hymenophyllaceæ, *Zygopteris*, *Plagiogyria*, *Botrychium*) or abaxial to the leaf (*Cibotium*, *Lophosoria*, *Metaxya*, *Cheiropleuria*).

In the protostelic forms the branch always receives, as would be expected, a single solid strand which usually remains protostelic throughout its length (Hymenophyllaceæ,¹ *Zygopteris*, *Cheiropleuria*, Fig. 1, A). The branching may be either distinctly lateral, as in *Cheiropleuria* and the Hymenophyllaceæ, or a forking of the axis, as in *Zygopteris* (*Ankyropteris*) *corrugata*,² *Diplolabis Ræmeri*, *Metaclepsydropsis duplex*,³ *Botrychioxylon paradoxum*.⁴

In the solenostelic forms we find that the vascular system of the branch frequently appears to arise as a diverticulum of an associated leaf-trace, (*Lophosoria*, *Metaxya*) but, as explained above, may be regarded as being fused along one side of the base of the latter. In a number of solenostelic forms investigated by Gwynne-Vaughan, the branch at its base has a gutter-shaped strand, which, however, rapidly closes up into a complete cylinder (several species of *Hypolepis*, *Polypodium punctatum*, *Dicksonia adiantoides*). In the Marsiliaceæ with a tubular stele in the main axis the branch receives also a tubular strand, the pith of the branch being continuous through a gap with that of the main axis.⁵ According to Professor Seward,⁶ in *Matonia pectinata* the rhizome divides by forking, and sends into each branch a solenostele, as well as a portion of the accessory medullary system.

The branching of *Helminthostachys* has recently been described in detail by Professor Lang (*loc. cit.* 1915), and although the plant does not possess a typical solenostele it may be considered here. The branches arise from dormant axillary buds which are stimulated

¹ See, however, p. 14 below, in reference to *Hymenophyllum lineare*.

² Scott, Studies in Fossil Botany, 1908, p. 318.

³ Gordon, Trans. Roy. Soc. Edinb., Vol. XLVII, Part IV, p. 720 and Vol. XLVIII, Part I, p. 173.

⁴ Scott, Trans. Linn. Soc., 2nd ser. Botany, Vol. VII, Part XVII, 1912, p. 383.

⁵ De Bary, Comparative Anatomy, English Translation, 1884, p. 313.

⁶ Seward, Phil. Trans., 1899, Vol. CXCI, p. 187.

to activity when the growth of the apex of the main rhizome is arrested. The attachment of the branch stele is directly to the main stele, a short but variable distance in front of the related leaf-trace. There is some variation also in the behaviour of the vascular system of the branch, but in general it may be said that the branch supply originates as a single strand which rapidly becomes curved and then closes up into a xylem tube enclosing a "mixed" central xylem. The parenchyma sooner or later replaces the central tracheides altogether, forming a definite pith.

It is when we come to the Ferns with reticulate steles, however that we find the greatest diversity in the mode of origin of the branch vascular supply. In a large number of cases the vascular system of the branch takes its origin as a single protostelic strand although the main axis in that region is dictyostelic (several spp. of *Aspidium*, *Alsophila excelsa*, Fig. 1, F, *Struthiopteris germanica* and *Nephrolepis*). The protostele arises from one of the cauline strands, and persists for a varying distance outwards before it expands in a funnel-like manner into a solenostele, this giving place sooner or later to a dictyostele. In *Nephrolepis* the protostelic stage is enormously long, being met with throughout the length of the stolon; in this genus, moreover, the main protostele does not itself expand into a solenostele, but gives rise to secondary protosteles which enter the bases of the lateral plants. There each expands first into an extremely short funnel-like portion immediately succeeded by a dictyostele (Fig. 1, G). The branch supply in *Struthiopteris germanica* originates, according to Stenzel, as an abaxially grooved strand which, traced distally, is seen to close up into a complete tube. This tube further on becomes perforated by the leaf-gaps, so that from this point onwards the branch has a stele exactly like that of the main axis. Secondary branches are recorded by Stenzel in this species.

In *Aspidium* and *Alsophila excelsa* the protostelic stage is very short, being in the latter species succeeded by the solenostele near the point of exit of the branch-stele from the cortex of the main stem. Stenzel describes in the same plant one case in which the protostelic region was altogether unrepresented, the funnel-like expansion being sessile on the large cauline strand.

A more interesting condition is recorded by Professor Bower (*loc. cit.*, 1913, p. 454 and pl. 33, fig. 13) in the stolon of *Cibotium Barometz*, the stele of which at its base contracted to the *Lindsaya*-stage, so that its phloem was continuous, through a gap in the

xylem, with the internal phloem of the main stele.

The branch stele in *Adiantum trapeziforme*, which has a dictyostelic adult stem, is at its base a completely closed tube, having its pith continuous with that of the main axis (Gwynne-Vaughan, *loc. cit.*, p. 724). In some of the Cyatheæ we meet with a similar condition, which may be somewhat complicated by the presence of a medullary system of strands, both in the main axis and in the branch. The branch may either develop its medullary system independently of that in the main axis, or the two may be continuous through the gap at the base of the branch. The latter condition is described by Stenzel in a Fern erroneously called by him *Diplazium giganteum*.¹ In *Hemitelia setosa* (Klf.) Mett. Professor Bower records a branching stolon—the main stolon corresponded with the mother axis in its advanced type of Cyatheoid structure, while the secondary stolon was solenostelic, though it still possessed a weak medullary system.

In some material of a Malayan species of *Drymoglossum*, for which I am indebted to Mr. F. T. Brooks, the branch possessed at its base a C-shaped strand with its gap adaxial. This strand almost immediately broke up into two, which divided further so as to form a reticulate stele exactly like that in the main axis.

Lastly, we may mention the comprehensive genus *Polypodium*, among a large number of other Ferns with highly dissected steles and creeping rhizomes. In a great many of these the branch at its very base is dictyostelic, and in external appearance does not differ from the main axis, except perhaps in size. Thus Klein² describes in *Polypodium Heraclium* side branches which are attached to the main axis by a narrow base; the dictyostele in such branches is correspondingly contracted at its insertion on that of the main axis, and the first one or more leaves of the branch may fail to attain their normal stature. In *P. quercifolium* the same author describes both branches growing out from a contracted base and possessing a miniature dictyostele which increases in diameter with the branch itself; and others which are from the very start identical in structure with the main axis. These latter cases are not far removed from dichotomy in the wider sense. Here we may refer also to the Osmundaceæ, in which dichotomy of the rhizome has been described

¹ The genus *Diplazium* is generally placed in the proximity of *Asplenium* and *Scolopendrium*, but the description of the stem and petiole of Stenzel's Fern points unmistakably towards the typical Cyatheaceous structure.

² Klein, L., Nova Acta Leop.-Carol. Deutschen Akad. d. Naturf., Bd. XLII No. 7, p. 335 ff., 1881.

by Faull.¹ Immediately beyond the bifurcation either each branch may possess a complete ring of separate xylem strands (*Osmunda Claytoniana*), or the two rings may be interrupted by ramular gaps on the sides facing each other (*O. cinnamomea*, *O. regalis*, *Todea barbara*).

We have now reviewed the vascular relations between branch and main axis in a large number of Ferns selected from nearly all the great families in which the branching of the stem has been described and ranging in stelar structure from the simplest to the most complex type. The results may be briefly summarized as follows:—

I. In Ferns with a *protostelic* main axis the branch is also as a rule protostelic throughout its length (Hymenophyllaceæ, *Zygopteris*, *Cheiropleuria*) Fig. 1, A.

II. Ferns possessing a *tubular stele* in the main axis have in their branches either a tubular stele throughout their length (Marsiliaceæ, *Lophosoria*, *Metaxya*, *Hypolepis*, *Pteris incisa*, var. *integrifolia*, etc., Fig. 1, B) or at the base a solid strand which soon becomes converted into a tube (*Helminthostachys*).

III. In Ferns which have a *reticulate stele* in the main axis the vascular system of the branch may either

(a) be from the very base a reticulate stele, which may or may not be attenuated towards its insertion to the main stele (*Osmundaceæ*, *Polypodium* spp., Fig. 1, C) or

(b) it may start at the solenostelic stage, also often contracted at the base (*Adiantum trapeziforme*, *Cyathea*, etc., Fig. 1, D) or

(c) it may possess at its base the *Lindsaya*-type of structure (*Cibotium Barometz*, Fig. 1, E) or, lastly

(d) it may begin with a thin protostelic strand which is of variable length (*Alsophila excelsa*, *Aspidium cristatum*, *A. spinulosum*, *Struthiopteris germanica*, *Nephrolepis*).

When the main axis contains a medullary system of strands the branch may either develop its medullary system independently of it, or the two may be continuous through the gap at the base of the branch (several *Cyatheæ*, *Polybotrya Meyeriana*, *Matonia*).

In each case except (a), the branch, during its growth, passes successively through morphologically higher and higher stages, till it acquires the type of stele characteristic of the adult main axis in that species.

¹ Faull, Bot. Gaz., Vol. XXXII, 1901, p. 398.

III. THEORETICAL CONSIDERATIONS.

a. The Primitive Branch.

Although the branching of Ferns has long been a subject of detailed investigation, and nearly all the different forms of the vascular relations between stem and branch described above have been known since the publication of De Bary's "Comparative Anatomy," it has not hitherto been suggested that these relations can be arranged in such a regular series as that shown in Fig. 1, and the interpretation of the series in terms of the phylogeny of the filicinean branch has consequently not been attempted. Gwynne-Vaughan was the first to suggest that the ontogeny of the vascular system of the main axis is often more or less imperfectly repeated in the development of the branch; and subsequent work, chiefly that of Professor Bower, has added considerably to the data on which that suggestion was originally founded. It still remains to be seen which of the two conditions is the more primitive for the branch—is it that in which this repetition is more perfect, in which the branch, starting life with a thin protostelic strand, gradually "works its way up" to the morphological level of the main axis; or that in which it is from the very beginning at or near that level? These two conditions are represented by the two ends of the series C—F; the ends are connected by means of stages morphologically intermediate between them; and the problem before us is to decide whether the series is a descending or an ascending series.

It is evident that this problem is inseparably connected with the wider and much debated question of the primitiveness or otherwise of dichotomous as opposed to monopodial branching, and that the answer to the first will give the clue to the second.

Before proceeding to our discussion, the conclusion arrived at may be stated at once, namely, that the forms of branching depicted in Fig. 1, C—F, constitute an ascending series. In our discussion we shall give particular attention to the branching of the higher Ferns (those with reticulate steles), as affording a more complete illustration of the parallelism in structure between stem and branch, and a greater variety in the behaviour of the branch vascular system.

Naturally, the most direct way to attack the problem would be to enquire into the circumstances which lead to the production of the respective forms of branching. Let us conceive of the growing stem of a dictyostelic Fern which is about to branch, and ask

ourselves what are the conditions necessary to ensure the production of a branch fundamentally similar in structure to the original axis. Evidently a fundamental similarity of growth-conditions for the two resulting growing points is the essential provision; granted this the two growing points will inevitably produce two essentially similar (dictyostelic) branches, and according to the degree of similarity in the growth conditions the form of branching will more or less closely resemble a dichotomy. However, when the conditions are fairly unequal the resulting branches may no longer be to one another as the two arms of a fork. One of the arms may "tend to push the other aside and approximate to a continuation of the original axis."¹ In time the one comes to be known as the "main axis" "giving off" the other as a branch, though both may in their vascular structure be dictyostelic. The dichotomy may pass insensibly into the monopodial type of branching.

We have only to go a few steps further to arrive at the other extreme of our series, Fig. 1, F. It is a common occurrence for one of the products of division of the growing apex to become dormant *almost immediately* after its formation, while the other continues its growth as the main apex of the plant. This state of affairs is undoubtedly more specialized than, and easily derived from, that in which the two apices continue to grow side by side both utilizing to about the same degree the conducting system in their rear. One of the apices has been sacrificed to the better nourishment of the other, by passing over into a state of temporary inertia, and provision is thereby also made for a resumption of activity in case the main apex meets with an accident or otherwise becomes checked in its growth.²

¹ Tansley, "Lectures on the Evolution of the Filicinean Vascular System," *NEW PHYTOLOGIST*, 1907, p. 29.

² Such dormant buds, which trace their origin to the growing point, have to be distinguished from so-called adventitious buds, which appear in no constant position and as the result of a secondary meristematic activity in tissues already more or less mature. The former may conveniently be termed "primary" buds in contrast to the adventitious or "secondary" buds. The ultimate distinction, however, is only developmental, and even that criterion would be difficult to apply in the case of adventitious buds arising near enough to the growing point, but the latter condition appears not to have been recorded. According to Sadebeck's observations (Schenk's *Handbuch* I, 1881, p. 266) the adventitious buds in Ferns appear to be confined to the leaves. Sadebeck mentions as an exception to this statement the buds in the Ophioglossaceæ. Professor Lang, however, concludes from his detailed researches that the buds on the stem, at least, of *Botrychium Lunaria* and *Helminthostachys* are "part of the primary construction of the plant," and not adventitious as Farmer and Freeman (*Annals of Botany*, 1899, Vol. XIII, p. 423) had previously stated.

From several other sources similar conclusions have come to light regarding the buds found in relation to the branching of Ferns. Thus, Hofmeister's view (*Beiträge* etc. II, *Abhandlungen der Kgl. Sächs. Ges. der*

Such primary dormant buds are commonly seen on Fern stems, and as we have seen, very frequently in the proximity of leaf-bases. In accordance with the insignificant demands that they make on the food resources of the plant so long as they are in a dormant condition, a single thread-like strand is seen to connect them to the main vascular system, although the latter may be solenostelic or even dictyostelic. But when a plant has reached a certain development the surplus energy is diverted into these side channels. In response to the increased flow of food and water the thin strand at the base of the young branch is succeeded distally by a stouter and more efficient conducting system. If the adult stem has a protostele in the main axis, the branch usually retains a protostele; if the main axis is soleno- or dictyostelic the vascular system of the branch expands accordingly. A branch of a dictyostelic Fern, for example, produced in these conditions, would correspond to what we find in *Alsophila excelsa*, *Aspidium cristatum*, *A. spinulosum* (Fig. 1, F).

At this point the question may reasonably be asked, why is it that in the case of a soleno- or dictyostelic Fern the dormant bud does not always establish a diminutive soleno- or dictyostelic connexion with the main axis, rather than a protostelic one? We must remember that we have hitherto dealt only with buds which became dormant almost immediately after their origin. This is not always the case, however. The dormant stage may be delayed for a longer or shorter period after the division of the main growing point,¹ so that for a time the products of division have a more or less equal share of the food resources, and naturally develop a similar vascular system. This is, in fact, what happens in *Polypodium vulgare* according to Klein's observations,² and Stenzel's figures of the same species (*loc. cit.*, 1861, pl. V) show the reticulate stele of the main axis giving off similar steles to the branches. Klein's observations on *P. Heraclaeum* and *P. quercifolium*³ are further examples of the same phenomenon.

Wiss. V, 1857, Math.-Phys., Klasse III, p. 651) that the stolons of *Nephrolepis* arise from adventitious buds was shown to be incorrect by Sperlich in 1906 (Flora, p. 469). Further, Sadebeck's statement (in Engler u. Prantl, Nat. Pflanzenfam. I, 4, 1st part, p. 44) that the branching of Ferns with dorsiventral rhizomes is due to lateral buds traceable to the main apex, is in support of the general view expressed in 1861 by Stenzel (*loc. cit.*, p. 34) that the branching of the Fern stem has no relation to adventitious buds. Pringsheim appears to have been the first to express this opinion (Bot. Ztg., 1853, p. 609), which was in 1855 adopted by Irmisch (see Hofmeister in Pringsheim's Jahrb., Vol. III, 1863, p. 279). If this is true, as seems probable, there is no doubt also that the buds in *Cheivopleuria*, *Lophosoria* and other Ferns investigated by Professor Bower, are of primary origin.

¹ Schoute, Ann. Buit., 1906, p. 88.

² Klein, L., Bot. Ztg., 1884, p. 585.

³ Klein, Nova Acta, 1881, Bd. XLII, pp. 353, 366.

Thus the development of a thread-like or reticulate branch-stele, as the case may be, from a reticulate main stele, would seem to depend upon whether the rudiment of the branch became dormant soon after its first origin or whether it was allowed for some time to grow side by side with the apex of the main axis before it became quiescent. The extremely minute size of the branch-initial in the former case might explain the thread-like character of the stele—a kind of stele which would result if the contraction of a reticulate stele be carried far enough. In this connexion it is rather illuminating to notice that even when a reticulate main stele gives off a similar branch stele, the latter is often rather suddenly constricted at the base, though still reticulate. This constriction is obviously due to the fact that the branch-bud was at an early stage pushed aside, though not at once reduced to dormancy, by the main growing point so that the development of the two was unequal at first.

We have tried to analyse the biological conditions governing the two extreme modes of branching shown in Fig. 1, C, F. More difficult seems an explanation of the intermediate stages, D, E, where from a dictyostelic main axis arise branches which at their insertion are respectively at the solenostelic and the *Lindsaya*-stages. We lack the support of observed facts, and no definite statement can be made till further work has been carried out. At the same time, there seems to be nothing against our explaining these cases on the same principle as above, namely, that the formation of the type of vascular cylinder is determined by the size of the bud at the commencement of its activity, this size being more or less fixed for the given species and controlled by the biological conditions.

That the conditions of nutrition exercise a far-reaching influence on the development of the vascular system is only an expression of the general principle that these conditions are all-important for the development of the whole plant—a principle which is the foundation stone of the science of experimental morphology. We shall consider a few examples which appear to be particularly instructive in connexion with the problem before us.

In his study of *Matonia pectinata* Mr. Tansley¹ described some plants which were found in a deeply shaded rock-crevice. To quote his own words, “they were, no doubt, plants of some age which had been unable to attain anything like their full growth owing to

¹ Tansley and Lulham, *Annals of Botany*, Vol. XIX, 1905, p. 490.

want of soil and light. Their vascular system is of interest, since it leads up from that of the . . . young plants to that of the typical adults." In some plants of *Helminthostachys zeylanica* Professor Lang¹ found that the rhizome, which had already attained the adult type of structure (with tubular xylem), subsequently reverted to the juvenile (protostelic) condition by passing through a series of changes involving a diminution in size of the whole rhizome. Professor Lang legitimately explains the phenomenon as due to growth under less favourable conditions of nutrition. It is of interest to find the same view expressed by Professor Bower in his paper on the origin of medullation in the Pteridophyta.² He remarks that in the Ophioglossaceæ the young plant may at first either have a solid xylem cylinder, or there may be a small pith from the very beginning; and he relates the latter condition to a more efficient nutrition of the young plant.

In their development such young plants are directly comparable with the different types of branches described above, whose steles at the base are medullate or non-medullate according as their rudiments entered at once on a vigorous life, or, on the other hand, became dormant while still relatively minute, and subsequently had to work up from a small beginning. In striking consonance with this idea is Professor Lang's conclusion (*loc. cit.*, 1915, p. 34) that "the simpler type of stele characteristic of normal young stages in the ontogeny of *Helminthostachys* is to be associated with small size and less efficient nutrition." This conclusion may well be extended to all vascular plants developing from a small beginning. As the flow of food increases the axis grows in thickness, and its stele undergoes a corresponding dilatation; we have here a phenomenon similar in essentials to that seen in the tubers of *Nephrolepis*³ though less pronounced in degree.

I regret that when I wrote the paper just cited I was not aware of the papers referred to in the footnote.⁴ Of these the last-mentioned requires special attention. The author describes, in *Hymenophyllum lineare*, sessile or stalked tuberous bodies produced as side-branches from the rhizome. From the description and the

¹ Lang, *Annals of Botany*, 1915, p. 33.

² Bower, *Annals of Botany*, 1911, p. 550.

³ Sahni, B., *NEW PHYTOLOGIST*, 1916, p. 72.

⁴ Senn., *Verh. natf. Ges. Basel*. Bd. XXI, p. 115, Die Knollen von *Poly-podium Brunei* Werckle; Christ und Giesenhagen, *Flora*, 1899, p. 79.
Giesenhagen, *Berichte d. deutschen bot. Ges.*, 1909, p. 331 and Pl. XV, fig. 8.

figure given it appears that a thin protostelic strand branches off from the main stele and, on entering the base of the tuber, expands and acquires a pith. It is not said whether it becomes converted into a reticulate stele. Seeing that the adult rhizome of *Hymenophyllum* never possesses a medullate stele, the appearance of such a structure in the tuber carries a peculiar theoretical interest, not only as supporting the hypothesis offered in my paper on the tubers of *Nephrolepis*, but also as showing that under the influence of physiological factors an organ may, so to say, break loose from the morphological check which may be said to have been imposed upon it by the phylogenetic position of the plant.

To take an instance from the animal world, the governing influence of the conditions of nutrition on growth is well illustrated by the rather startling results which Gudernatsch¹ has recently obtained by feeding tadpoles respectively on the thymus and thyroid glands of various mammals. While young tadpoles fed on thyroid cease further growth in size, prematurely pass on to the changes of metamorphosis, and become dwarf frogs, those fed on thymus grow into giant tadpoles, and if they are kept long enough under this influence, the metamorphosis is altogether suppressed.

If the line of argument traced above is sound, we have in it a strong support for the view that in the Ferns at least the primitive type of branching was the dichotomous, and that the monopodial type was derived from it by the gradual suppression of the growing point of one of the arms of the fork, which in the extreme cases became dormant immediately after its origin. The impetus for the departure from dichotomy probably originated in the need for a more effective nourishment of one of the branches. This need was supplied at the expense of the other branch, whose further development was postponed till a surplus of nutrition was available. The most important line along which the latter branch has evolved is, as we have seen, specialization for vegetative propagation. As of secondary importance may be mentioned the modification of the branch to serve as a climbing organ, so well seen in *Nephrolepis*, as well as its transformation into a tuber for the storage of food and water (*N. tuberosa*, *Polypodium Brunei*).

Further, if the sequence of events has been as we have conjectured, we arrive at the interesting theoretical conclusion that the evolution of the filicinean branch has mainly consisted in the

¹ Gudernatsch, Zentralblatt für Physiologie, 1912, Vol. XXVI, p. 323.

intercalation, at its base, of a series of stages each morphologically less complex than the preceding; that, in short, the process has been one of retrogressive evolution in a basipetal direction. The appearance of relatively simple types of vascular structure at the base of a highly evolved branch, such as that in *Alsophila*, *Nephrolepis*, etc., must be regarded as a cœnogenetic feature, and not as strictly primitive.

In our attempt to trace the evolution of branching in Ferns we must constantly keep in view one fact, which was pointed out in the introduction to this paper. This was, that many Ferns of a relatively high order of evolution, such as *Polypodium* and *Pteridium*, commonly branch dichotomously, while on the other hand, relatively primitive types such as the Ophioglossaceæ may show a monopodial type of branching. Thus we do not find that there is a necessary parallelism between the evolution of the modes of branching on the one hand, and the evolution of the plants themselves on the other. We are driven to the conclusion that these two lines must have been independent of each other.

b. The Branch as a Potential Individual.

If, as we have suggested above, the evolution of the branch has in the main been guided by the need for vegetative propagation—and, of course, the phenomenon of branching in itself primarily implies an amplification of the plant-body—it is of interest to find that the further the branch recedes from its ancestral form, the more nearly does it approximate to our conception of it as a potential individual. For the sake of an ampler illustration we shall again confine ourselves to the branching of the dictyostelic series C—F, Fig. 1. We see here that the stele of the branch of *Alsophila excelsa*, in virtue of its origin from a relatively minute dormant bud, has necessarily to pass, during its growth, from a fine thread-like beginning, through gradually expanding solenostelic stages, before it finally attains the adult type of structure. Stenzel's description of the branch stele of *Alsophila* corresponds in the broad features with Gwynne-Vaughan's description of the ontogeny of the main stele. In sharp contrast stands the branch of *Polypodium* which, having at its disposal from the very beginning the ample food resources of the plant, has been able at the outset to develop a dictyostelic vascular system. A striking illustration of the same phenomenon was recorded in this journal,¹ where it was suggested that probably because of the more favourable physiological conditions in which it

¹ Sahni, B., NEW PHYTOLOGIST, 1915, pp. 263, 271.

begins its development the lateral plant of *Nephrolepis cordifolia* in its ontogeny omits some of the earlier stages in stelar evolution, which are passed through normally by the sporeling. It would be agreed that, inasmuch as it passes through a series of stages parallel to that passed through by the main axis during its ontogeny, the lateral branch of *Alsophila excelsa* more nearly corresponds to our idea of an individual, than does the branch of *Polypodium*.

We have taken as one criterion of individuality the degree to which the ontogeny of the branch resembles that of the corresponding main axis. Hence in a case like *Alsophila excelsa*, where this resemblance is rather close, the structure of the branch should be susceptible of the same phylogenetic interpretation in the light of the recapitulation theory, as the structure of the developing main axis. And this view should hold in spite of the probability that the the simpler structure of the branch at the base is of relatively recent origin, because the *ontogeny* of the branch still resembles the ontogeny of the main axis.

The specialization of the branch has, however, gone further than the stage of *Alsophila excelsa*. The branch in *Nephrolepis* (Fig. 1, G) has been subjected to physiological conditions very different to those affecting the main axis. The result is that a portion of the branch, the stolon, has assumed an appearance and structure so widely different from that of the leaf-bearing stock, that anything short of an organic connexion between the two would not have convinced one that they both belong to the same plant. The apex of the primary stolon is endowed with the power of long-continued growth, and of producing a large number of lateral dormant buds, each the beginning of a potential individual.

c. The Relation Between Branch and Leaf.

We may pass now to another aspect of the evolution of the filicinean branch, namely, the relation of the branch to the leaf, which is so conspicuous a feature in relatively wide circles of affinity. We know that this relation existed in some of the most ancient known branching Ferns, the Zygoteridæ, and it is seen to-day in the Ophioglossaceæ Hymenophyllaceæ, Cyatheæ, and sporadically among Ferns of a still higher order.

It is to be noticed that the relative positions of branch and leaf vary in different groups of Ferns. The branch (or the rudiment of it which may fail to develop) is sometimes adaxial (Ophioglossaceæ, Hymenophyllaceæ) sometimes abaxial (Cyatheæ) to the

leaf, while in other cases it may apparently arise from the petiole of the related leaf, some distance from its base, either on the adaxial or the abaxial face.

Moreover, although in a general way the relative positions are fairly constant for each group taken by itself, this constancy tends to be discounted when we consider the vascular relations of the branch and leaf. In those Hymenophyllaceæ in which "axillary branches" are generally found it sometimes happens that the branch-trace is inserted on the main stele independently of the leaf-trace. Boodle¹ records one such case in *Trichomanes radicans*, and I have myself seen other cases in herbarium specimens. Mettenius² also draws attention to the varying position of the branch bud in the Hymenophyllaceæ. We have already referred to Professor Lang's statement (see p. 1) that the branch-trace in *Helminthostachys zeylanica* is inserted directly on the main axis, some distance in front of the trace of the subtending leaf. In the closely allied species *Botrychium Lunaria*, however, the same author found that whereas usually the chief vascular connexion of the branch was with the adaxial face of the leaf-trace, in some cases the attachment was deeper in the axil and more closely related to the stele of the main rhizome. Within the Zygopterideæ also we meet both with "axillary branches" having a vascular connexion with the trace of the subtending leaf, and with branches having their steles directly inserted on that of the main axis.

Nor do we find that the numerical relation of one branch to one leaf is obligatory, more than one branch to a leaf having been recorded not only in several species of *Hypolepis*, but also in *Cyathea mexicana*, *Dicksonia (Cibotium) Barometz*, *Polypodium grandiens*, *Cystopteris montana* and other Ferns.

Finally, considering the Ferns hitherto unmentioned we cannot detect in the great majority of them any relation whatever between the positions of branch and leaf.

Thus if we view the Ferns *as a whole* it may be said that the branch does not hold any regular position with respect to the leaf; and the question arises whether the primitive condition was that in which leaf and branch were separate, or that in which they were produced in relation to each other. From his detailed study of *Botrychium Lunaria* and *Helminthostachys zeylanica* Professor Lang has concluded that the regular presence of axillary buds in these species is in favour of this relation being "part of the

¹ Boodle, Annals of Botany, 1900, p. 473.

² Mettenius, Abhandlungen der Kgl. Sächs. Ges., 1861. Ueber Seitenknospen bei Farnen, p. 615.

primary construction of these plants" (*loc. cit.*, 1915, p. 47). With this condition as a starting point he has postulated a gradual retreat of the branch from its subtending leaf, as well as a stronger development of the branch, to arrive at the dichotomous type of branching now known to be so common in the *Zygopteridæ*.

While it is agreed that in the *ontogeny* the axillary buds in the *Ophioglossaceæ* (and elsewhere) are laid down at the growing point of the axis, and are not adventitious, it seems difficult to admit that the production, by the growing point, of a branch rudiment regularly in connexion with each leaf rudiment, was the *primitive* state of affairs. The latter condition naturally suggests itself as being a specialized case of that in which there was no such regularity; and I venture to suggest that the origin of this relation, which is admittedly very ancient, may perhaps be traced to some possible biological advantage accruing from it. One of these was probably the protection of the young bud during its period of dormancy. However, while the protection afforded to the branch initial by its axillary position is obvious in such cases as *Zygopteris*, the *Hymenophyllaceæ*, and the *Ophioglossaceæ*, some other explanation must be sought for cases where the bud is abaxial to the leaf.

In his well-known recent paper on *Zygopteris Grayi* Dr. Scott discussed the morphology of the organ conveniently termed by him the "undivided trace."¹ Of the two views discussed, the one that regards the associated leaf as the first leaf of the branch, may be dismissed at once, not only in view of the variation above mentioned, but also because the leaf is always orientated with regard to the main axis, whether the branch is adaxial or abaxial to the leaf.

From the form and structure of the undivided trace in the Shore specimen of *Zygopteris Grayi* Dr. Scott has been led to decide in favour of the second view, which regards the strand in question as being from its base upwards of a foliar, and not axial, nature. However, as he himself suggests, "we may . . . regard the axillary stele as 'adherent' to the adaxial side of the leaf-trace" (*loc. cit.*, p. 59), and this is the position here adopted. While it is true, as Dr. Scott remarks, that this way of looking upon the subject does not throw any new light on the facts, and the difference is ultimately one of words, from a comparative

¹ Scott, *Annals of Botany*, 1912, Vol. XXVI. (i), pp. 57—60. Since the branching of *Zygopteris Grayi* and the *Hymenophyllaceæ* is analogous to that in the other Ferns in which the branch is closely related to the leaf, the term "undivided trace" may be extended to the corresponding organ in these cases, whether the branch is adaxial or abaxial to the leaf,

study of the corresponding structures in the living Ferns it seems more natural and therefore preferable to regard the strand in all such cases as being of a dual nature. The relative importance of the leaf and branch portions of the strand are subject to variation. In the figured Williamson specimens of *Zyopteris Grayi* the axial characters predominate, while in Dr. Scott's specimen the leaf-trace characters are more prominent, though still there is, in the latter specimen, a fairly well-developed adaxial bulge with its median strand of "mixed" internal xylem, destined to supply the branch. A similar variation in the relative importance of leaf and branch has been noticed by Professor Bower in *Plagiogyria* (*loc. cit.*, 1910, p. 434).

Professor Bower's account of the branching of *Cheiropleuria bicuspis*¹ is particularly illuminating in connection with this question. When the leaf has no branch in connection with it, its trace arises as a small tangentially flattened strand which divides into two before entering the petiole. When there is a branch connected with the leaf, a very much larger circular strand is given off from the main stele. Evidently this strand cannot correctly be described as the leaf trace, for at the proper level two small strands come off from its inner-face, and these constitute the divided part of the leaf-trace, while the bulk of the original strand passes into the "infra-axillary" branch. Since the leaf belongs properly to the main axis, the basal undivided portion of its trace must be regarded as being adherent to the inner face of the ramular portion of the "undivided trace."

The branching of *Pteridium aquilinum* still remains a puzzling case, in spite of the fact that this is such a common Fern, and has so frequently been investigated since the time of Hofmeister. No completely satisfactory interpretation can be given of the morphology of the vascular system of branch and leaf in this species, by any of the views hitherto offered. The more recent observations are those of Velenovsky,² Bayer,³ and Mr. Tansley,⁴ but only the last-mentioned author has taken account of all the different forms of branching observed in this species. It appears, however, that the only way to arrive at a definite solution, namely, a study of the development of the plant, has still to be carried out.

Mr. Tansley also described in *Pteris incisa* var. *integrifolia*, a

¹ Bower, *Annals of Botany*, 1915, Fig. 7, p. 505.

² Velenovsky. *Sitzungsber. Böhm. Ges. Prag.*, 1890 (Review in German, *Bot. Centralblatt*, Vol. 46, 1891, p. 32),

³ As referred to in Velenovsky, *Vergleichende Morphologie*, 1905, Vol. 1.

⁴ Tansley and Lulham. *New Phytologist*, 1904, p. 1.

dichotomy of the rhizome with a petiole coming off exactly at the angle and forming a direct continuation of the axis behind the angle. As he pointed out, this case finds the closest analogy in *Hypolepis tenuifolia*, the chief difference being that the branching in the latter plant is monopodial, with the leaf more closely related to the side-branch.

Finally, the formation of new plants from adventitious buds which are usually confined to the leaves, may also be included under branching. In accordance with their origin from minute initials, these plants are connected to the parent leaf by a thread, like strand which rapidly dilates and becomes elaborated into the adult type of stele. This method of branching is probably the most recently evolved, but evidently on account of its success as a means of rapid propagation, it has already been established in a very large number of Ferns, in some cases to the detriment of the usual method of reproduction by spores.

Just as the relation of adventitious buds to primary buds is obscure, it would be difficult to relate this latest mode of branching to the usual method, in which the branch always springs from a bud originally laid down at the growing apex of the mother axis.

IV. SUMMARY AND CONCLUSIONS.

The most important direction in which the evolution of the filicinean branch system has progressed is specialization for vegetative propagation. This is only an elaboration of the fundamental idea involved in branching, namely, the amplification of the plant-body. Subsidiary efforts have been made in the direction of (a) epiphytism (*Nephrolepis volubilis*), (b) food or water storage (*Nephrolepis tuberosa*, *Polypodium Brunei*, *Hymenophyllum Ulei* and *H. lineare*.¹)

On taking a bird's-eye view of the branching of Ferns it is observed that the different forms may be arranged in a series beginning with those in which the rhizome divides into two more or less equal branches, and ending with forms in which the proximal part of one of the branches attains a great length and bears either reduced leaves (*Struthiopteris*, etc.) or none at all (*Nephrolepis*). This portion, which has been called a stolon, serves to remove the leafy apex of the branch away from the mother-axis, and to feed it before it establishes an independent root-system. In the extreme case (*Nephrolepis*) the stolon is capable of producing a large number of lateral branches each of which is a potential

¹ Giesenhagen (Berichte, 1909, pp. 331,333) considers the tuberous bodies in *Hymenophyllum Ulei* and *H. lineare* as insect-galls, but Christ (Geographie der Farne, 1910, p. 99) regards them as water-storing organs.

individual. The local reduction or absence of leaves in the latter group of forms allows of no doubt that the mode of branching they possess is a highly specialized one, and it is most natural to derive it from the dichotomous type illustrated by the former group: the two extremes are connected by an unbroken series of transitions (Fig. 1 C—G, p. 5).

This conclusion is corroborated by a study of the branching of Ferns from the point of view of their vascular anatomy. This affords a series of transitions parallel to the above, while independent grounds are given for the view that the latter ends of these series represent the derivative, the former the primitive condition. For a *résumé* of our knowledge of the vascular relations of branch and stem throughout those Filicales in which branching has been described, the reader is referred to p. 9 and Fig. 1, p. 5.

When the growing apex of a Fern stem divides in preparation for branching, the resulting growing points may either both continue their growth simultaneously, or, as very commonly happens, one of them may almost immediately become dormant, while the other continues its growth in the direction of the original axis. A third possibility is that the dormancy of one of the growing points may be delayed for a variable period of time during which the two have been growing together as in the first case. Of these three conditions the second will be generally admitted to be derived from the first, since it involves a sacrifice of one of the branches for the good of the other; while the third condition may be considered to be intermediate between the other two.

An inquiry into the circumstances under which the different forms of branching occur shows that the dichotomous types correspond to the first of the cases mentioned above, while in the extreme monopodial types the branches arise from buds which become dormant immediately after their origin, when they were still minute. The intermediate types probably correspond with the third case.

There is no necessary parallelism between the evolution of the modes of branching on the one hand, and the evolution of the plants themselves on the other: the two processes must therefore have been independent of each other. Dichotomy still persists among the higher Ferns, while some of the most primitive Ferns (*Ophioglossaceæ*) show an advanced monopodial type of branching.

The monopodial type of branching has been derived from the dichotomous by a process of retrogressive evolution in the basipetal direction, involving the successive intercalation, at the base of the

branch, of a series of stages, each morphologically less complex than the preceding. This process naturally finds its full illustration in forms with reticulate steles. The basal protostele of the specialized branch is therefore a cœnogenetic feature, not strictly primitive.

The departure from dichotomy was entered upon at a very early period in the history of the Filicales.

We may look upon the simpler organization of the specialized branch in its proximal region as a sudden drop to a morphologically lower and more stable level in consequence of a loss of physiological conditions necessary for the production of the morphologically higher condition. The alleged retrospective nature of traumatic structures may perhaps also be regarded in the same light.

Viewing the group of Filicales as a whole it may be said that the branches do not hold any regular position with respect to the leaves. In those cases where the branches arise in some relation to leaves, this association is, in its evolutionary origin, a secondary phenomenon attributable to possible biological advantages, one of which may be the protection of the young bud. Significant in this connection is the fact that in some plants possessing so-called axillary branches (Hymenophyllaceæ, Ophioglossaceæ) while the stele of the branch is sometimes inserted on that of the main axis independently of the subtending leaf-trace, it is sometimes confluent with the latter at the base. The view here adopted is that in all such cases the portion of the strand common to leaf and branch, conveniently termed by Dr. Scott the "undivided trace," is of a dual nature; we owe this view originally to Dr. Scott, but he rejected it in favour of the foliar view. Professor Bower's description of *Cheiropleuria* strongly supports the former view.

The formation of new individuals from adventitious buds on the leaves is the most recently evolved method of branching in Ferns, but it is difficult to relate it to the usual method, in which the branches always spring from buds laid down at the growing apex of the mother-axis.

My hearty thanks are due to Mr. Tansley, not only for valuable suggestions regarding the literature, but also for much helpful advice and criticism during the preparation of the manuscript of this paper. I have pleasure also in heartily thanking Professor Seward for references to literature.

THE BOTANY SCHOOL, CAMBRIDGE,
December, 1916.

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