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SIZE IN RELATION TO INTERNAL MORPHOLOGY.

NO. I.—DISTRIBUTION OF THE XYLEM IN THE VASCULAR SYSTEM OF PSILOTUM, TMESIPTERIS, AND LYCOPODIUM.

BY

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[With Eighteen Figures in Text.]

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XXV.—Size in Relation to Internal Morphology. No. I.—Distribution of the Xylem in the Vascular System of Psilotum, Tmesipteris, and Lycopodium. By Claude W. Wardlaw, B.Sc., Assistant in Botany, Glasgow University. *Communicated by* Professor F. O. Bower, F.R.S., President. (With Eighteen Figures in Text.)

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In his Presidential Address to the Royal Society of Edinburgh in October 1920, Professor Bower (2) called attention to the question of Size in relation to stelar morphology, and advanced evidence (with particular reference to the Filicales) to show how the principle of similar structures has affected the internal morphology of the vascular system of plants. In dealing with the application of this principle he remarks that "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 those 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 those 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 its 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 surfaces which limit one tissue tract from another." In illustration of this, examples were taken from the stems, tubers, and petioles of the Filicales, and the size-factor was also found applicable to the large prop-roots of palms, such as *Areca* and *Verschaffeltia*.

In this paper attention was specially drawn to the endodermis as a controlling barrier both morphological and physiological. But in his second contribution on this subject (3), where he deals with modifications in the form of the xylem independent of the shape of the endodermis, he remarks: "The facts suggest that there must be also a factor, perhaps connected with the physiological interchange between the xylem and the surrounding phloem, which depends also upon the area of their surface of contact." This is remarkably like a statement from an entirely different source. I refer to the Presidential Address of Professor Dixon (8) at Hull in 1922. With reference to the bast he says: "Its distribution and conformation are such that, while it possesses a very small cross-section, it appears with the other living elements of the vascular bundles, medullary rays, wood parenchyma, etc., to present a maximum surface to the tracheæ. This large surface may find explanation in the necessity of interchange between the living cells and the dead conduits. The colloidal contents of the former render this process slow, hence the necessity for the large surface of interchange to enable sufficient quantities of organic substances to be abstracted from and introduced into the tracheæ to meet the needs of the plant."

It will be seen, then, that the problems relating to Size may be referred to two categories: (1) Those which deal with the distribution, accommodation, or rearrangement of systems of tissues; this would include all cases which relate to the stele as a whole, *e.g.* the successive modifications in stelar form as illustrated by the Filicales. (2) Those which deal with the mutual relationships between tissues and between individual cells; this bears on some of the more intimate aspects of physiology, such as the transference of liquids from cell to cell, and from one kind of tissue to another, as, for instance, the intra-stelar relations of xylem and phloem.

This latter aspect of Size as a causal factor in morphology is far-reaching in its application, since it arises not only in relation to the conducting tracts, but also, as HABERLANDT (10) has indicated, to the distribution and form of the photosynthetic tissues, to the interlocking of cells whose mechanical structure depends on cohesion, and to absorbing organs such as haustoria. In all such cases a large proportion of surface to bulk is an advantage, and the form of the cells and organs concerned may in many instances be correlated with what HABERLANDT has described as the Principle of Maximum Exposure.

The present investigation was undertaken in order to determine, by actual measurements in specific instances, the nature and extent of the changes in shape of the xylem, in different parts of the same plant and in different species, and to see how far modifications in form are associated with actual increases in size. The families here to be discussed are the Psilotales and the living eligulate Lycopodiales.

Before passing on to the observations recorded it may be well at this point to consider briefly the nature of stelar constitution and function. Problems concerning the interchange of liquids and gases between different tissues are constantly before the physiologist, and in particular those dealing with the relationships between living and dead tissues of the conducting tracts. Anatomical investigations have served to demonstrate the important point that the dead-conducting elements of the xylem are always in contact with living tissues. This constant association of living and dead tissue would in itself suggest some important physiological relation between them. It is generally accepted that the passage of water into the vessels and tracheides is primarily effected by forces residing in the living tissues which surround the dead conduits, while the living cells are held as responsible for the control and transference of the solutions passing in and out of them.

A question intimately connected with this close relationship of living and dead tissue is that of the ascent of sap. Two lines of explanation have been suggested—the "vitalistic," and the "physical." In the former, as expounded by such investigators as WESTERMAIER, GODLEWSKI, JANSE, and SCHWENDENER, the cause of the ascent of sap is referred, in some way, to the living cells which always occur in close contact with the dead conduits; and on the other hand, physiologists who sought to explain the ascent of sap on purely "physical" lines were never able wholly to exclude the living elements from the process. A new aspect of the subject has been recently introduced by Professor DIXON (8). In his Presidential Address to the British Association at Hull in 1922, he suggested as a result of experimental investigation that the transport of organic substances needed in the distal-growing regions is effected through the tracheæ of the wood, and that the substances travel in the water filling these channels, the movement being effected by root-pressure, transpiration, etc. In view of the physical difficulties arising out of their anatomical construction, he does not regard the elements of the bast as suitable for the rapid transport of plastic substances, and remarks on the possibility of interchange between the living cells and the dead conduits as already quoted, referring in particular to the large surface of contact between the two tissues. Whether we adopt this attitude, or adhere to the older view that the plastic materials travel as a rule in the phloem, does not affect the principle underlying the present investigation. For without entering into the controversy as to the proportion, quantity, or quality of the plastic material associated with, or travelling in, the thin-walled elements of the phloem, wood parenchyma, medullary rays, etc., we do know that certain materials of carbohydrate and protein nature occur in these tissues. That these substances are translocated has been demonstrated by studies of their seasonal occurrence and distribution; the materials may travel up or down the stem, or they may be deposited under the control of the living protoplasts during periods of quiescence. This will require a close contact of thin-walled elements with the water-containing channels, and as transit by diffusion may be assumed to be directly proportional to the surface, it will be necessary to secure as large a surface of contact as possible between the living and dead tissues, and this is generally achieved. As we pass, however, from a conduit of small size to one of larger size, the problem is constantly changing. In seedlings and sporelings and in adult plants of small size the difficulty of maintaining an adequate interchange between living and dead tissues of the vascular strand does not arise, for in them the xylem consists of a small number of tracheides or wood-vessels, and these are closely invested on all sides by thin-walled living cells. This state of affairs is seen in the young unthickened roots of Angiosperms, and in the small steles of Pteridophytes. In the process of ontogenetic growth an increase in size takes place, and the latter brings in its train problems of physiological and constructional nature, both of which, as a rule, are solved by some adequate modification of structure. In fact, Size becomes an essential factor in stelar morphology and physiology.

If the form of the dead water-conducting tract remain unaltered as its bulk increases, it follows from the principle of similar structures that the proportion of surface to bulk of the dead tissue will decrease. In actual practice it is found that as the plant increases in size there is an accompanying increase in the amount of water-conducting tissue in the stele. With increase in the bulk of the dead-conducting tissue the relative area of surface abutting on living tissue will fall off, unless some rearrangement or modification of the form of the xylem takes place whereby a larger proportion of surface to bulk is assured. In the absence of some alteration of shape this reduction in the ratio of surface to bulk will become more and more accentuated with increasing size, till finally it may become a limiting factor. But any deviation from the cylindrical form, either by external projections or by involutions, necessarily leads to an increase in this proportion.

It will be shown by instances taken from plants with simple stelar structure, and having no secondary thickening, how as the size increases in the individual development the xylem tract is modified and may even be disintegrated. Thus the section of the larger region is not simply the magnified image of the smaller. The contours of the dead tracts of xylem are altered with increasing size, in ways that provide an increase in the proportion of surface abutting on the living cells to the bulk of the dead tissue. But no strict rule is observed; the details may vary in the genus, species, and even in the individual; in fact, it appears from comparison of the actual structures that the problems arising in relation to increasing size may be solved along several lines, by modifications differing in degree and even in kind, but all agree in providing an increased proportion of surface to bulk as the actual dimensions increase.

Stelar Morphology in the Psilotales.

Psilotum triquetrum, Sw. Figs. 1 and 2.

The eleven drawings (fig. 1) represent transverse sections taken successively from below upwards, from the rhizome and aerial stem of a single plant. They serve to illustrate the successive changes in shape of the xylem as the stele enlarges. In the sections 1–3 from the rhizome, the small monarch core of tracheides has a simple outline, and is surrounded by thin-walled elements of phloem and conjunctive parenchyma. In No. 4, with its greatly increased size of the xylem core, the compact, approximately cylindrical structure is lost, and disintegration has begun. Later it becomes fluted and irregularly stellate (Nos. 5 and 6), owing to the intrusion of the thin-walled conjunctive tissue that surrounds it. As the size increases further (Nos. 6, 7, 8) the xylem becomes still more deeply penetrated by the surrounding thin-walled living elements, and a central pith is formed. Near the base of the aerial stem, where the number of tracheides is greatly augmented, the pith widens out and forms an irregular star inside the xylem, so that rays of living cells penetrate the mass of xylem from the inside, in much the same way as they did from the outside, as shown in the sections lower down (No. 5). In the largest sections from the aerial stem the xylem is broken up into plates or groups of tracheides surrounding a central pith (No. 10). In the steles of some aerial stems the pith is sclerosed, sometimes wholly, sometimes only in part, and it was observed that where sclerosed tissue adjoins the tracheides these are less densely massed than where they are surrounded on all sides by living tissue.

This brief statement will serve to indicate the changes that take place in the stele of *Psilotum* as its size increases.

Tmesipteris.—In *Tmesipteris* a state of affairs is found comparable to that of *Psilotum.* The following description is based partly on personal observations, and partly on the published accounts of BERTRAND, SYKES, HOLLOWAY, and others, to which further reference will be made (see figs. 3 and 4).

The young rhizome has a centrally placed stele, consisting of a solid core of xylem, surrounded by thin-walled tissue. In the vascular cylinder of a rhizome of medium size, the living tissue begins to penetrate the compact central core of tracheides, and as the number and size of the latter increase, this process is continued so that the xylem is divided into two groups or plates. The position and configuration of the latter are constantly changing. They tend to join up laterally and to split apart at other points, suggesting on the one hand the necessity for continuity in the water-conducting tracts in the transverse direction, and on the other hand a need for surface-relation with the adjoining thin-walled living tissue. In this connection HOLLOWAY (13) remarks: "It would seem then, from a comparative study of the rhizomes of plants of different ages, that along with the increase in number of xylem elements in the central cylinder, there is a diminishing disposition on their part to cohere in one group, so that the original monarch condition becomes lost, and the xylem is disposed in separate plates or groups in the midst of the phloem, the tendency being in the oldest rhizomes for these groups to be arranged more or less in the form of a ring surrounding a central group of thin-walled (so-called) pith elements." In the stout aerial stems of *Tmesipteris* the stele is comparatively large, and the tracheides are disposed in four or five groups surrounding a central pith. HOLLOWAY (13) found in the young plants which he examined that the configuration of the vascular tissues is identical in both rhizome and aerial shoot, and that as the number of conducting elements increases the xylem tends to rearrange itself in groups surrounding a central pith.

Thus it will be seen that the anatomical investigations conducted on *Psilotum* and *Tmesipteris* have led to the recognition of the essential similarity of their steles, both in adult stems and in the general course of ontogenetic development, and in both it has been fully demonstrated that on passing from a stele of small size to one of larger size, the xylem becomes decentralised and disintegrated. Changes in form such as these lead the morphologist to seek some underlying principle, and to estimate the nature and extent of its

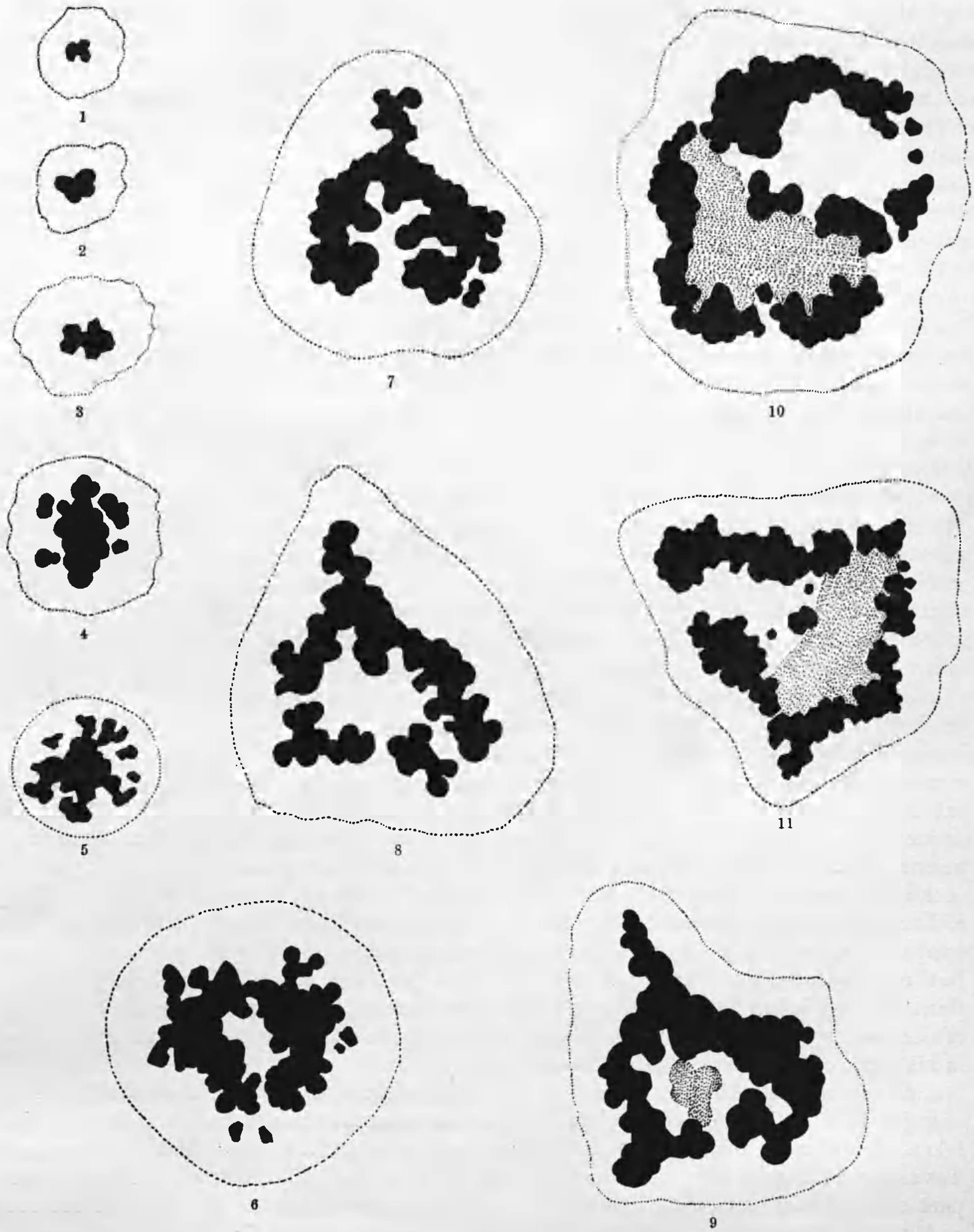

FIG. 1.—*Psilotum triquetrum*, Sw. Series of sections taken from the base of the rhizome into the stout aerial stem of the same plant.

1–4, small stele of rhizome; 5, stele with stellate structure; 6–9, formation of excentric pith; 10, large stele from aerial stem; 11, section taken above thickest part of stem, diameter of stele decreasing.

Xylem black, sclerotic tissue stippled, broken boundary line inner limit of endodermis. (× 93.)

application. In examining such steles it is not sufficient merely to note the form: we should also consider them as structures developed so as to meet successfully certain physiological and constructional needs. Little attention has been devoted to this aspect of the subject. BERTRAND (1) has described in great detail the anatomy of the rhizome of *Psilotum*, and regards it as consisting of branches and cladodes of different morphological value, and with each he tends to associate a definite type of stele. Miss FORD (9), however, points out that this is not necessarily the case, and refers the variability observed in the stele to other causes: "The structure of the stele depends, for the most part, on the size and development of the branch in question, and not on the position it occupies in regard to the main mass of the rhizome."

In view of the state of affairs found in the Filicales, it might be thought that the breaking up of the xylem is associated with the presence of leaf-gaps. This, however, does not seem to be the case. Miss SYKES (17) points out that it is the rule that the leaf-trace leaves no leaf-gap, and her anatomical investigation, as also that of HOLLOWAY (13), shows that there is disintegration in the xylem in stems of *Tmesipteris* which either have no leaves or small leaves without leaf-traces. Further, the study of ontogenetic development shows that the main modifications of the xylem are to be explained with reference to other causes than leaf-insertion. Moreover, in *Psilotum*, which is without leaves, we also find this process of disintegration, and even if we were to regard the plant as descended from some leafy ancestor retaining its foliar-gaps, this does not explain stellation in steles of medium size, or disintegration and decentralisation in large ones. HOLLOWAY finds that disintegration of the xylem occurs also in large rhizomes, and concludes that the formation of the pith is not necessarily associated with the aerial stem. He further observes that "this alteration in the xylem grouping is in nowise occasioned by any branching of the stele."

In the conclusion to her paper Miss FORD (9) suggests a physiological explanation of the large steles found in the aerial stems of *Psilotum*, those in which the xylem forms an interrupted ring surrounding a central pith. She suggests that the leaves of *Psilotum* represent reduced, and not primitive structures, that the size of the stele has been retained, but the demand for water conduction being less, tracheides which originally occupied the centre of the stem are no longer developed, and their place has been taken by ordinary parenchyma. It has been pointed out (3), however, that this explanation, though it probably does apply sometimes, cannot be used in the case of *Psilotum*, where the pith is decidedly of excentric origin. Discussion of the stele, then, has been largely morphological and comparative, and little attention has been devoted to the physiological and causal aspects. But recently attention has again been called to problems of stelar morphology in these plants (3), and it has been shown by a table of measurements that increase in the complexity of the xylem goes along with increase in size, a fact to which HOLLOWAY has also referred in his paper on the young plant of *Tmesipteris*.

Measurements.—In order to arrive at a more clear conception of the nature of these changes in the form of the xylem in *Psilotum*, measurements were made from sections taken at different levels from the rhizome and stem of the same plant. The material was sectioned transversely, from the thin basal region of the rhizome onwards to the thickest part of the aerial stem, and from the series thus obtained, outline drawings of the stele and of the xylem were made by camera lucida under a magnification of 140, some on paper with square-centimetre ruling for purposes of measurement, and duplicates on drawing paper for illustration. The latter series is shown in fig. 1 (Nos. 1–11); the xylem is represented by solid black, sclerotic tissue is stippled, and the outer broken line in each case represents, as far as could be determined, the inner limit of the endodermis. This series covers a considerable range in stelar size, the smaller sections being those from the basal region of the rhizome.

The measurements made from this series are stated in Table I. In each section the diameter of the stele, the area of the xylem, and the perimeter of the xylem were measured. The area of the xylem was determined from the outlines drawn on the paper with the square-centimetre ruling: the estimate in each case refers to the whole area irrespective of the size of the cavities of the tracheides. The perimeter in each case was obtained by measuring the boundary of the xylem in short lengths on strips of paper ruled off in cms. and mms. Here, and in the tables that follow, the perimeter is taken to connote the linear outer limit of the xylem as a whole, or where it is disintegrated, the sum of the limits of its several parts.*

The figures in Column II show that there is a fairly uniform increase in the diameter of the stele from ·17 mm. to ·75 mm. (No. 10), after which there is a decrease in diameter (No. 11) as the more distal regions of the stem are approached. In Column IV the area of the xylem in cross-section is stated in sq. cm., and in Column V its perimeter in cm., these measurements referring to the objects under a magnification of 140 diameters. The area of the xylem is taken as being proportional to its bulk, and the perimeter as proportional to its outer limiting surface. By dividing the figures in Column V by those in Column IV, the proportion of surface to bulk is obtained for the xylem in each section. These ratios are shown in Column VI, bulk being stated as unity in each case. Where the stele is small the proportion is relatively high, but as increase in size takes place, there is a diminution in this ratio. The figures in Column VII are purely theoretical, and show what the proportion of surface to bulk would be, in each section, if the xylem were in the form of a solid core of cylindrical shape. A comparison of the ratios in Columns VI and VII indicates the significance of the successive modifications in the form of the xylem. Column VII shows how, as the stele enlarges, if the xylem were to remain in cylindrical form, the ratio of surface to bulk would diminish rapidly, and in the largest section (No. 10) would fall to rather less than one-eighth that of the small section (No. 1), whereas the actual ratios for the living organism (Column VI) indicate that, by reason of the complicated contour of the xylem in large steles, the ratio diminishes much more slowly, and in the case of section No. 10 falls only to rather less than one-third that of section No. 1. In both cases the principle of similar structures has led to a decrease in the proportion of surface to bulk, as size increases, but in the actual plant this has been kept within limits by successive modifications in the form of the xylem. In the more distal branches the difficulty of maintaining an adequate proportion of surface to bulk is solved by the decrease in size as the apical region is approached. Here we have the converse of the upgrade sequence. This is illustrated by fig. 1 (No. 11), and by the measurements for section No. 11.

Discussion for *Psilotum*.

In the small stele the solid core of tracheides is intimately surrounded by thin-walled living cells, which control the passage of water into the dead conduits, which probably modify the nature of the substances travelling in them, and promote and control the various

* *Note on Measurement.*—In this connection the sources of error are many, and measurements such as these, for several reasons, can only be relatively accurate. Thus the figures will not show absolute values, but for the purpose on hand will serve for comparison, and will be sufficiently accurate to give some indication of the kind and extent of changes in shape.

TABLE I.

Psilotum triquetrum.

I. Number of Section.	II. Diameter Stele in mm.	Measurements used for Calculation obtained under Magnification of 140. III. Diameter Stele in cm.	IV. Area Xylem in sq. cm.	V. Perimeter Xylem in cm.	VI. Area Xylem : Perimeter Xylem. Ratio of Bulk to Surface.	VII. Ratio of Area to Perimeter in a Cylinder equivalent to the Core of Xylem.	VIII. Remarks.
1	·17	2·4	·27	2·5	1 : 9·26	1 : 6·82	Small protostele. Xylem solid.
2	·18	2·5	·52	3·8	1 : 7·31	1 : 4·91	Protostele. Xylem solid.
3	·24	3·4	·73	4·3	1 : 5·90	1 : 4·15	Xylem solid.
4	·29	4·1	3·56	19·2	1 : 5·40	1 : 1·88	Xylem solid, slightly fluted.
5	·26	3·7	4·36	22·8	1 : 5·23	1 : 1·70	Xylem irregularly stellate.
6	·53	7·4	10·85	39·5	1 : 3·64	1 : 1·08	Xylem irregularly stellate. Beginning of formation of excentric pith.
7	·56	7·8	13·31	41·5	1 : 3·12	1 : 0·97	Xylem with irregular excentric pith.
8	·61	8·5	15·33	49·0	1 : 3·20	1 : 0·91	Xylem triangular. Pith stellate.
9	·64	9·0	16·50	51·4	1 : 3·12	1 : 0·87	Xylem with irregular pith partly sclerosed.
10	·75	10·5	18·92	56·0	1 : 3·00	1 : 0·81	Xylem an interrupted cylinder with partly sclerosed pith.
11	·64	9·0	13·80	43·5	1 : 3·15	1 : 0·95	Xylem interrupted cylinder with partly sclerosed pith.

The actual diameters and perimeters will be obtained by dividing the figures in Columns III and V respectively by 140, and the actual areas by dividing the figures in Column IV by 140^2.

N.B.—The ratios in Columns VI and VII are the ratios of bulk to surface for *the magnified objects*; the actual ratios will be given by multiplying these figures by 140, *i.e.* in No. 11 the actual ratio of bulk to surface will be 1 : $3·15 \times 140$.

Column VII.—To calculate proportion of surface to bulk in equivalent cylinder.

A = cross-section of cylinder, which is known from Column IV The cylinder may be regarded as being 1 cm. in height. Its *bulk* will be $A \times 1$, and *surface* under consideration will be *perimeter* $\times 1$.

r = radius of cylinder.

Area of cross-section of cylinder $= \pi r^2 = A$.

$$\therefore\ r = \sqrt{\frac{A}{\pi}}.$$

$$\text{For unit bulk, surface of cylinder} = \frac{2\pi r \times 1}{\pi r^2 \times 1} = \frac{2}{r} = \frac{2}{\sqrt{\frac{A}{\pi}}}.$$

$$\text{Log surface} = \log 2 - \tfrac{1}{2}(\log A - \log \pi).$$

Example.—Section No. 1. A = ·27 sq. cm. bulk = $·27 \times 1$ cubic cm.

Log surface $= \log 2 - \frac{1}{2}(\log ·27 - \log 3·14)$.

Surface = 6·82 sq. cm.

Ratio of bulk to surface in equivalent cylinder = 1 : 6·82.

As these ratios are only intended for general comparison with one another, it has not been thought necessary to calculate in terms of specific surface. The ratios of bulk to surface for the magnified objects have been used because of their greater clearness.

interchanges between tracheides and cortex. If this is so, it follows that when the bulk of the xylem increases, that is when the individual tracheides increase in number and size, if the solid cylindrical structure is maintained, there will be a decrease in the proportional surface of interchange between the living tissue and the tracheides, since the cylinder is one of those solid forms in which the proportion of surface to bulk is very low. In very small cylinders, of course, this proportion is comparatively large, but as the diameter of the cylinder is increased, the proportion of surface to bulk falls off rapidly. In order to increase this proportion, some departure must be made from the cylindrical form. This may take place in many ways. A simple method consists in fluting or corrugating the periphery of the cylinder, and this process, when continued more deeply, produces the effect which we recognise as stellation. This is what we find in *Psilotum* (fig. 2 (3).) Stellation is only effective within limits, however, and the next stage recognised in the enlarging xylem is the invasion of the solid core of tracheides by living tissue, so that an excentric pith is formed. From the latter, rays of living tissue penetrate the denser masses of xylem, and in this way a comparatively large surface of interchange is established (fig. 2 (4).) With further increases in size the pith broadens out, and the xylem on its periphery is drawn out into elongated plates. It is to be noted in passing that the flattened solid is one in which the proportion of surface to bulk is large. These plates of xylem join up laterally, and are perforated at other points by living tissue, suggesting the need for continuity in the xylem in the transverse direction, and also the need for close contact with living tissue.

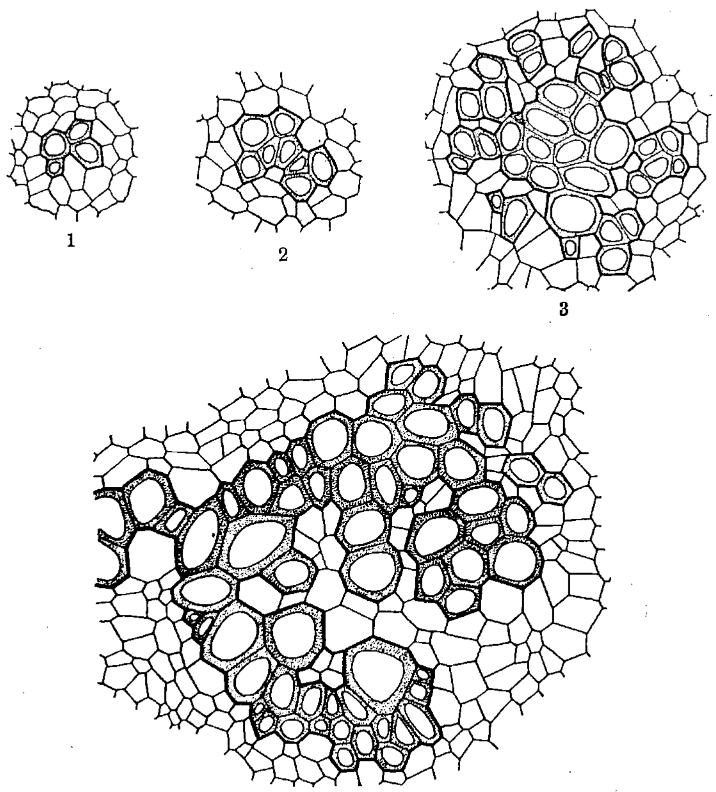

FIG. 2.—*Psilotum triquetrum*, Sw.
1, 2, Small stele in rhizome; 3, stele showing stellate xylem; 4, formation of excentric pith, showing how a large surface of contact is established between the dead conduits and living tissue. (× 154.)

These observations, studied in conjunction with related physiological activities, and with the measurements stated in Table I, indicate how the principle of similar structures is related to internal morphology, and it would appear that the form and structure of the xylem in large steles, and the successive modifications in form observed on passing from a stele of small size to one of large size, are to be referred, firstly, to the need for adequate contact between the tracheides and living tissue, and secondly, to the actual bulk of the xylem. In short, if suitable morphological changes did not accompany increase in bulk, Size might become a limiting factor of such a nature as to curtail or inhibit some of the vital physiological processes.

Tmesipteris.—What has been described for *Psilotum* is found to apply also to the stele of *Tmesipteris.* Fig. 3 (1–5) illustrates, in diagrammatic form, sections of the stele in rhizomes and stems of different thickness, after HOLLOWAY (13). It will be seen that as the size of the stele is increased the xylem becomes decentralised and disintegrated. The details relating to those steles are embodied in Table II. The relation of the living tissue to the xylem is

TABLE II.

Steles of Tmesipteris.

	Name. Figures from HOLLOWAY.	Part.	Diameter Stele in mm.	Remarks.
1.	*T. lanceolata.* Fig. 81	Rhizome of young plant	·09	Stele with solid xylem core.
2.	,, Fig. 82	Rhizome of medium grown plant	·17	Solid xylem core, showing beginning of formation of excentric pith.
3.	,, Fig. 83	Large rhizome	·28	Xylem divided into two plates by enlarging pith.
4.	,, Fig. 88	Aerial stem of adult plant	·42	Xylem divided into five groups of tracheides, forming ring round central pith.
5.	*T. tannensis.* Fig. 91. (Xerophytic form)	Base of aerial stem of adult plant	·30	Xylem divided into four groups of tracheides.

illustrated for two sections in fig. 4 (1, 2), and the larger section shows how a large surface for interchange between xylem and thin-walled tissue has been achieved by the formation of an excentric pith.

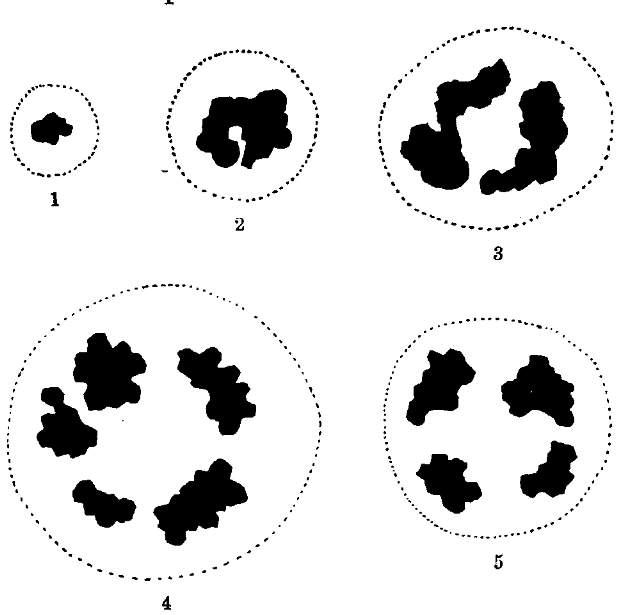

FIG. 3.—Steles of *Tmesipteris* (diagrammatic, after HOLLOWAY).

1, *T. lanceolata*, stele from small rhizome; 2, *T. lanceolata*, stele from medium grown rhizome; 3, *T. lanceolata*, stele from large rhizome; 4, *T. lanceolata*, stele from aerial stem of adult plant; 5, *T. tannensis* (xerophytic form), stele from base of aerial stem of adult plant. (×93.)

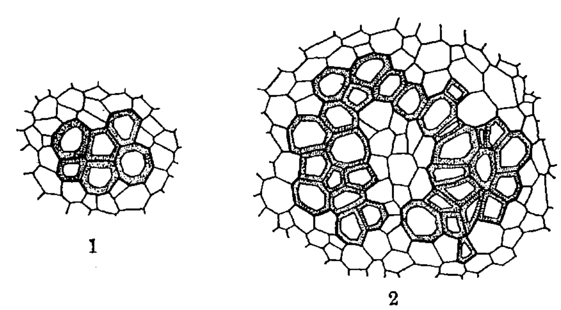

FIG. 4.—*Tmesipteris lanceolata.*

1, Small stele with compact xylem core; 2, larger stele showing penetration of the xylem core by living tissue. (×154.)

The vascular systems of two varieties of *Tmesipteris* have been described. These are *T. lanceolata* and *T. tannensis*; the former is the larger and grows in moist humus, the latter is smaller and xerophytic. The general arrangement of the vascular tissue is the same in both, but in the smaller xerophytic species, *T. tannensis*, the stele is not so large, and HOLLOWAY (13) has noted that "it does not show the same extent of development of vascular tissue with the consequent splitting up of the xylem into constantly changing groups." Evidence such as this points to the relation between stelar structure and size. With regard to the living tissue associated with the xylem, Miss SYKES (17) points out that in *Tmesipteris* the pith cells are elongated, pitted on their tangential walls, *i.e.* on the walls abutting on the tracheides, are often collenchymatous, and contain proteid masses like those found in the phloem. JENNINGS and HALL have referred to these elements as sieve parenchyma. In the case of *Psilotum* Miss FORD (9) discusses the nature of the tissue surrounding the xylem. She was unable to distinguish sieve-tubes, but noted that the tissue which invades the xylem is of the same general nature as that which surrounds it. Such evidence gives point to the physiological aspect of the question.

In the case of the Psilophytales it has been shown (3) that as the diameter of the stele increases, there is an increase in the complexity of the xylem. These facts point to the presence of a factor other than mere leaf-insertion. This factor imposes stellation of the xylem as a concomitant of increase in size. The evidence from the leafless stem of *Psilotum* confirms this view. This being so for the steles of the Psilotales and Psilophytales, it remains to see how far increase in size may have acted as a determining factor in the stelar morphology of Lycopods, and to find if there are any changes comparable to those recorded for the families mentioned above.

STELAR MORPHOLOGY IN THE LYCOPODIALES.

Since the publication of NÄGELI'S paper (15) in 1846 many investigations have been carried out on the curious and varied steles in the genus *Lycopodium*. It has long been known that the distribution of the vascular tissues in these plants is subject to considerable variation, not only in different species, but also in different individuals of the same species, and in the shoots and branches of different rank in individual plants. In his paper on the morphology and anatomy of the stem, JONES (14) gives a summary of the relevant publications until the year 1905. In *The Origin of a Land Flora* (1908) (5), Professor BOWER has correlated the facts relating to the genus known at that time, and in the recent publications of HOLLOWAY (12) many references are to be found relating to stelar problems in these plants.

For the present purpose it has not been thought necessary to discuss in detail the results obtained by these observers, but rather to present a brief account of the known facts relating to the stelar morphology bearing on the present proposition.

CRAMER (7) and JONES (14) have shown that there is no obligate relationship between the number of leaves and the number of protoxylems, and STRASBURGER (16) has shown that the stele is essentially cauline. On the smaller branches where the number of leaves is small, 4 to 6, in whorl or spiral, it is usual to find a corresponding number of protoxylems, but where the latter increase beyond 6, there is no definite numerical relation between the two. This coupled with other evidence would indicate that the axis in Lycopods is the dominating feature of the shoot, while the leaf has little influence on the morphology of the stele.

With reference to the outstanding characteristics of the stele, it has been said (5), "They stand apart from almost all other vascular plants in the presence in their mature axes of a stele having peripheral protoxylem, and often showing the solid xylem-core characteristic of the protostele" (*Land Flora*, p. 328). In the smaller species the stele is simple, and in cross-section the xylem is seen to be disposed in the form of a star having groups of protoxylem at the extremities of the arms, and with phloem and conjunctive tissue lying in the bays between the xylem plates. This condition is common to the steles of sporelings and to those of the finer distal branches in the larger species. In the mature stems of the latter the vascular cylinder shows a greater degree of differentiation, and the xylem is disposed in such a way as to form a more or less elaborate sponge, the interstices of which are occupied by phloem and conjunctive tissue. In epiphytic types such as *L. squarrosum* the stele is radial, and in cross-section the xylem appears as an interrupted meshwork of thin plates of tracheides. In the terrestrial types, mostly with characteristic dorsiventrality, the xylem consists of a number of more or less parallel plates, lying approximately in the horizontal plane. The xylem plates do not run up and down the stem unaltered. On the contrary, their disposition is constantly changing, two bands joining up at one point and separating at another. The distribution of the phloem is consequently affected, and for short distances it may appear in transverse sections to be isolated as a phloem "island" surrounded on all sides by curved plates of xylem. This applies to both radial and dorsiventral types, but is not so conspicuous in the latter. The dorsiventral stele with its parallel bands of xylem, at one time referred by STRASBURGER (16) to the fusion of phylogenetically distinct steles, has been shown by HOLLOWAY (11) and others to be but a specialisation from the radial type consequent on the branching being confined to one plane.

JONES has commented on the similarity between the stellate stele of the young stem of *Lycopodium* and those of the roots of Phanerogams, and he suggests that it is probably a primitive condition. The widespread occurrence of this structure, derived along a number of distinct lines of descent, may be taken as an indication of its efficiency. The departure from the stellate form in older stems, with the formation of a complex xylem sponge, and accompanied by a certain amount of disintegration, suggests many problems of causality. So far no adequate data have been put forward indicating the nature of the factors causing these changes. In the first place, since the distribution of the xylem is independent of leaf-insertion, why do we find the xylem disposed in the form of a star and not, for example, as a compact core of tracheides? And secondly, if the stellate structure of small steles is an efficient one, as we may assume it is, why is there a departure from it in larger steles? Here, as in the Psilotaceæ, we may consider it as probable that Size is a factor in the stelar morphology, and that "the complexity of vascular structure is closely related to actual dimensions" (4). The evidence presented below will indicate the actual relation between Size and vascular complexity in the genus *Lycopodium*. For this purpose, observations were made on the steles from branches and stems of different size from the same individual, various measurements were taken, and calculations based on these were made. For purposes of comparison, similar measurements were made for a number of species. The nature of these results will have an added significance when studied in conjunction with the problem of interchange between the living and dead conducting cells of the vascular strand.

Detailed measurements were made from the following :—

L. dichotomum, Jacq. ; *L. squarrosum*, Forst. ; *L. Phlegmaria*, Linn. ; *L. cernuum*, Linn. ; *L. clavatum*, Linn. ; *L. scariosum*, var. *Jussiæi*, Desv. In each case drawings were made by camera lucida, and the measurements of area and perimeter were obtained as described for *Psilotum*. To facilitate explanation the results are presented for the most part in tabular form.

Lycopodium scariosum, var. *Jussiæi*. Figs. 5 and 6. Table III.

This species will be dealt with first, as it provides a wide range in stelar size, and also because the anatomy of the sporeling has been adequately investigated (HOLLOWAY (11) and CHAMBERLAIN (6)).

The plant has a characteristic plagiotropic habit, creeping along the surface of the ground; the leaves borne on branches of limited growth show marked heterophylly. The stele in the adult stem is remarkably large, and the xylem, which forms an elaborate sponge, consists of a number of more or less parallel plates of tracheides, a condition typical of dorsiventral species. In the stem of the sporeling, however, the stele is small and simple, and in transverse section is seen to consist of a four-rayed star of xylem with phloem and conjunctive

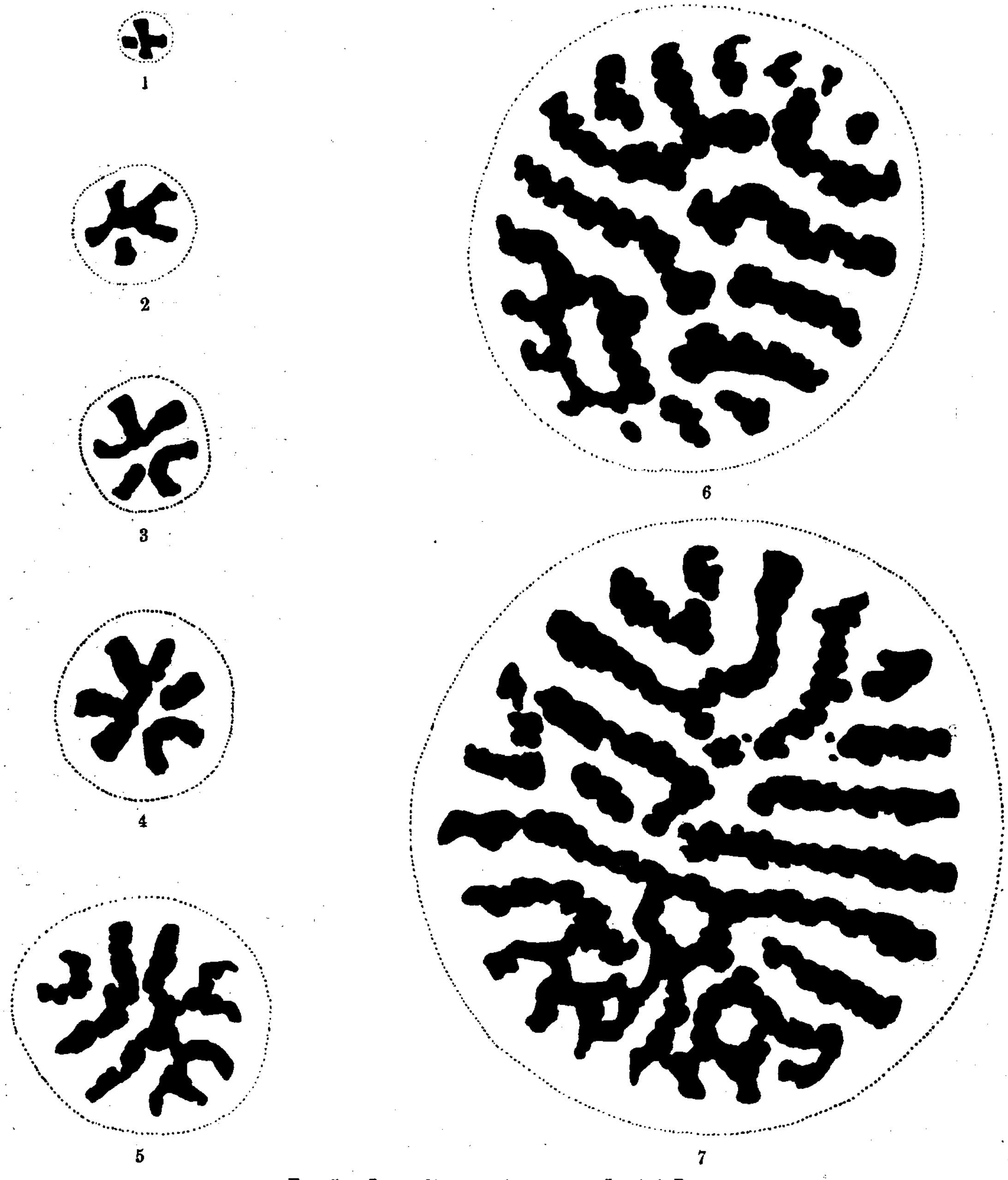

FIG. 5.—*Lycopodium scariosum*, var. *Jussiæi*, Desv.

1, Stele of sporeling (after HOLLOWAY); 2, section from fine distal branch; 3–7, sections from branches of different thickness. This series illustrates the increase in complexity of the xylem which accompanies increase in size. (× 73.)

tissue lying in the bays between the arms. Each arm consists of a thin plate of tracheides, usually one tracheide in thickness, with a small, broad group of protoxylem elements at the extremity. As the sporeling develops, the number of arms in the star increases, a four-rayed star passing into a five-rayed one, and the latter into a six-rayed one, and so on, until eight or nine arms are formed. These changes are associated with expansion of the stele. Holloway (11) describes the ontogenetic development, and figures the stele from a sporeling, $1\frac{1}{2}$ cms. high, and quite destitute of leaves. It is important to note that the stele has taken up a definite shape apart from interference by leaf-traces. Where the stele is large the stellate structure is not maintained. The star resolves itself into a series of parallel bands between which are masses of thin-walled tissue. The initiation of this new distribution of tissues is generally associated with branching, and the maintenance of this arrangement throughout the stele is related to the fact that the branches always pass off from the stem on the same plane. It has been shown generally for Lycopods by Holloway (11) that when branching takes place there is a departure from the radial construction, and the xylem is rearranged into bands parallel to the plane of branching. The xylem plates then divide and a segment of each passes off into the branch. This is followed by a return to the radial construction in orthotropic forms. In dorsiventral species, on the other hand, where the next branch passes off on the same plane, the parallel disposition of the xylem plates is maintained. The "parallel" type, then, is but a specialisation from the radial consequent on the branching being restricted to one plane. In larger stems increasing complexity of the xylem accompanies further increase in size, and the stele of an old stem is seen to consist of a large number of parallel bands of xylem between which are layers of phloem and conjunctive tissue. The result of these changes is that the xylem is always disposed in thin plates (one or two tracheides in thickness) in such a way that the dead conduits are at all points in close contact with thin-walled living tissue. This is the general sequence of events in ontogenetic development. In the fine distal branches the stele presents the same simple arrangements described for the sporeling, and on passing down into thicker branches changes comparable to those in the developing sporeling may be observed. For the most part the observations presented here were made from branches and shoots of different rank, and not from a succession of sporelings, and while it is not suggested that the physiological conditions present in the steles of ultimate branches are the same as those in the sporeling, in both the changes incident on increased bulk are of the same nature. This being so, a representative series of measurements may be obtained from branches of different thickness.

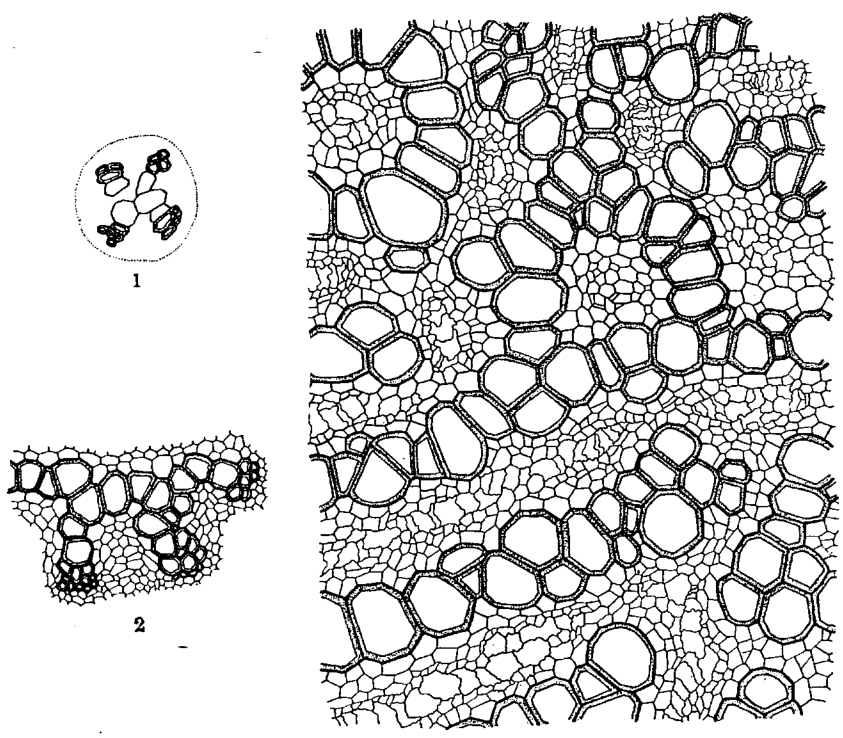

Fig. 6.—*Lycopodium scariosum*, var. *Jussiæi*, Desv.

1, Xylem in stele of sporeling (after Holloway); 2, xylem in stele from a distal branch; 3, xylem in a large stele.

The distribution of the xylem in all cases is such as to present the maximum surface of contact to the living tissues. (× 154.)

The diagrams in fig. 5 (1–7) indicate the range in stelar size and complexity for

L. scariosum, var. *Jussiæi*. No. 1 is from the sporeling plant, after HOLLOWAY (11), No. 2 is taken from a fine distal branch, and Nos. 3–7 are from successively larger branches and shoots, all being drawn to the same scale. In fig. 6 (1, 2, 3) the nature of some of these steles is illustrated in greater detail. All show one feature in common, namely, the large surface of xylem presented to the living tissue. Measurements and calculations based on fig. 5 (1–7) are embodied in Table III, along with descriptive notes. In making these

TABLE III.

Lycopodium scariosum, var. *Jussiæi*.

I. Number of Section.	II. Diameter Stele in mm.	Measurements used for Calculation (×110). III. Diameter Stele in cm.	IV. Area Xylem in sq. cm.	V. Perimeter Xylem in cm.	VI. Area : Perimeter = Proportion of Bulk to Surface.	VII. Ratio Area : Perimeter. The Xylem in each Stele is regarded as magnified to Area of that of No. 7, but maintaining its own Shape.	VIII. Ratio of Area to Perimeter in a Cylinder equivalent to the Core of Xylem.	IX. Remarks.
1	·11	1·2	·32	4·0	1 : 12·50	1 : ·96	1 : 6·27	Xylem radial; interrupted four-rayed star.
2	·26	2·9	1·53	11·1	1 : 7·25	1 : 1·22	1 : 2·86	Xylem radial; interrupted five-rayed star.
3	·29	3·2	2·20	14·6	1 : 6·64	1 : 1·34	1 : 2·39	Xylem radial; interrupted six-rayed star.
4	·39	4·3	3·38	20·7	1 : 6·12	1 : 1·54	1 : 1·93	Seven-rayed star, interrupted.
5	·53	5·8	8·31	45·6	1 : 5·49	1 : 2·16	1 : 1·23	Stele dorsiventral. Xylem in 3–4 parallel plates of tracheides.
6	·96	10·6	30·01	136·9	1 : 4·56	1 : 3·41	1 : 0·65	Stele dorsiventral. Xylem an elaborate sponge, with about 5 parallel plates.
7	1·27	14·0	53·70	240·5	1 : 4·48	1 : 4·48	1 : 0·48	Xylem, very elaborate sponge. Many parallel plates.

N.B.—In Tables III to VII the measurements were obtained under a magnification of 110 diameters. Those in Table I were obtained under a magnification of 140 diameters. It is not intended that comparison should be made between the ratios in Table I and those in Tables III to VII.

The actual ratios and dimensions will be obtained as described for Table I.

The figures in Column VII were obtained as follows:—

A = area of No. 1 = ·32 sq. cm.

A′ = area of No. 7 = 53·70 sq. cm.

$\sqrt{\frac{A'}{A}} = m$ = magnification required to increase area of No. 1 to area of No. 7.

If section No. 1 were magnified by m its area would be Am^2 and its perimeter (p) would be pm.

For unit area, the perimeter in the magnified section would be $\frac{p \times m}{A \times m \times m} = \frac{p}{A \times m}$.

But $\frac{p}{A} = 12·5$ and $m = \sqrt{\frac{53·70}{·32}}$.

$\therefore$ Perimeter in magnified section $= \frac{12·5}{\sqrt{\frac{53·70}{·32}}} = ·96$ cm.

measurements the same conditions were observed as in the case of *Psilotum*. The area and perimeter of the xylem were measured under a magnification of 110 diameters, and are stated in Columns IV and V in sq. cm. and cm. respectively. The diameter of the stele ranges from ·11 mm. in the sporeling to 1·27 mm. in the adult stem (Column II). The increasing dimensions are to be correlated with the advance in stelar complexity illustrated in fig. 5 and described in Column IX. The proportion of surface to bulk for the xylem was obtained for each section by dividing the figures in Column V by those in Column IV, bulk being stated as unity in each case. These ratios are stated in Column VI, and it will be seen that, despite the modifications in the form of the xylem in larger steles, the proportion of surface to bulk diminishes. This decrease is largely due to the fact that the individual tracheides in large steles are on the whole of greater diameter than those in smaller steles, and by the principle of similar structures have individually a smaller proportion of surface to bulk.

The significance of increasing complexity of the xylem with increasing size is demonstrated in Column VII. In saying that modification of form accompanies increase in size, it is realised that this may be regarded merely as the statement of a truism, but, as Professor BOWER has remarked (3), "it is quite possible to imagine it otherwise so that the larger organ would merely be the magnified image of the smaller." In Column VII the amount of xylem in each section is regarded as magnified so as to equal that of the largest section, No. 7, but the shape of the xylem still being regarded as unaltered; *i.e.*, in No. 1 the area of the xylem (Column IV) is taken as being magnified so as to equal 53·70 sq. cm. (the area of No. 7), but the tracheides remain grouped together in the form of a much enlarged interrupted four-rayed star. In the same way No. 2 is regarded as magnified so that its xylem in cross-section has an area equal to that of No. 7, but its form is that of a much enlarged five-rayed star. The same consideration has been applied to each section, and the calculations show what the proportion of surface to bulk would be in each case. If, in No. 1, the xylem were equal in quantity to that of No. 7, and if it consisted of a large four-rayed star, its proportion of surface to bulk would be very low—less than one-quarter that actually found in No. 7. In other words, the high degree of disintegration of the xylem in section No. 7 has given it more than four times as great a proportion of surface to bulk as it would have had if increase in size from the small stele of the sporeling had not been accompanied by suitable modifications in form, or if the larger stele had been but a magnified image of the smaller. The ascending numbers in Column VII, then, may be regarded as a numerical statement of the increased proportion of surface to bulk achieved by an increased complexity in form. Further, a comparison of the ratios in Columns VI and VII point to the fact that, whereas the simple starlike xylem gives a high proportion of surface to bulk where the stele is small, the disintegrated spongy structure is relatively more efficient for this purpose where the stele is large. In short, the large stele is not merely the magnified image of the small one, and the data advanced would point to the importance of size in its relation to those modifications of form which make for functional efficiency.

The figures stated in Column VIII indicate what the proportion of surface to bulk would be if the tracheides were concentrated into a solid core of cylindrical form, such as we find in the homogeneous protostele. In both columns (VI and VIII) there is a decrease in the proportion of surface to bulk as size increases; if the xylem were in the form of a solid cylindrical core the proportion of surface to bulk would fall from 6·27 in section No. 1 to 0·48 in section No. 7, or, in other words, the ratio in section No. 7 would only be $\frac{1}{13}$ that of section No. 1, whereas the actual ratio for the living organism only falls from 12·5 to 4·48; that is, the ratio in section No. 7 is rather more than $\frac{1}{3}$ that of section No. 1. These results are significant in two ways: firstly, they show how a large proportion of surface to bulk has been achieved throughout by the distribution of the xylem in thin plates, and secondly, they show how greatly the problem is intensified where the stele is of a large size.

Lycopodium clavatum, Linn., etc. Fig. 7.

The development of the stele in *L. clavatum* agrees closely with what has been described for *L. Jussiæi*. The plagiotropic habit of the plant is familiar, as is also the stele of the adult stem. The sporeling, as figured by JONES (14), has stellate xylem, with three to five groups of protoxylem, and in the course of ontogenetic development changes take place in every way comparable to those found in *L. Jussiæi*. A similar series may be observed on passing from the fine distal branches down into the main stem. The disposition of the xylem is always changing, the xylem, in fact, forming a sponge. This is not such a conspicuous feature as in some of the radial types, because the sponge is of a more attenuated nature.

The successive stages in the elaboration of the vascular system were followed out, and measurements and calculations based on these were made.

The results obtained fall into line with those recorded for *L. Jussiæi*, and the theoretical considerations indicate the relatively large proportion of surface to bulk achieved in the larger steles consequent on the successive modifications in the form of the xylem. The large surface of xylem in contact with thin-walled living tissue is illustrated for a small and a large stele in fig. 7.

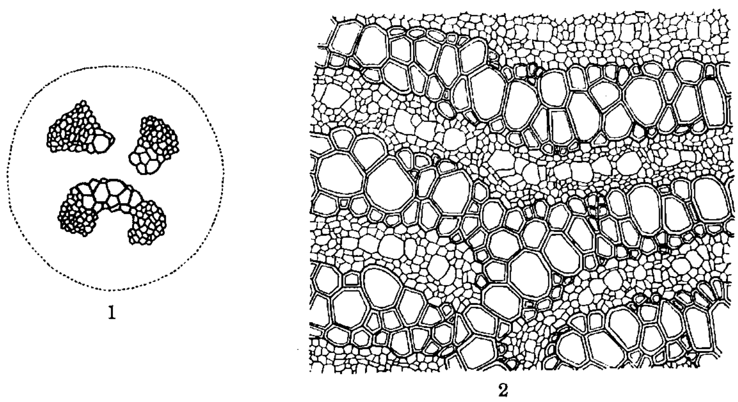

FIG. 7.—*Lycopodium clavatum*, Linn.
1, Xylem in small stele from a fine distal branch ; 2, xylem and associated living tissues in the stele of a thick horizontal stem. (× 154.)

There are many species included in the section *Clavatum*. These are characterised by the marked dorsiventrality of the shoot, and the stele in the adult stem consists as a rule of a dorsiventral sponge of xylem, with thin-walled tissues lying between the plates of tracheides. In the sporeling, however, and also in the smaller branches, the stele is radial and of simple construction.

Fig. 8 (1–7) illustrates small and large steles of *L. alpinum*, *annotinum*, *volubile*, and *densum*. In *L. volubile* the stele of the sporeling consists of two curved plates of protoxylem, embedded in thin-walled tissue. In the course of development these plates enlarge, divide, become stellate in disposition, and after a certain size has been reached, the xylem is rearranged into a series of parallel plates (HOLLOWAY (11)). The sporeling anatomy of *L. complanatum* has been investigated by Miss WIGGLESWORTH (18), who describes morphological changes similar to those found in *L. volubile* and *clavatum*. The same general features will probably be found to apply to other dorsiventral species.

Lycopodium squarrosum. Figs. 9 and 10. Table IV.

L. squarrosum is characterised by radial symmetry and orthotropic growth. At the base of the stem or in the young plant the stele is of the radial type and the xylem is stellate

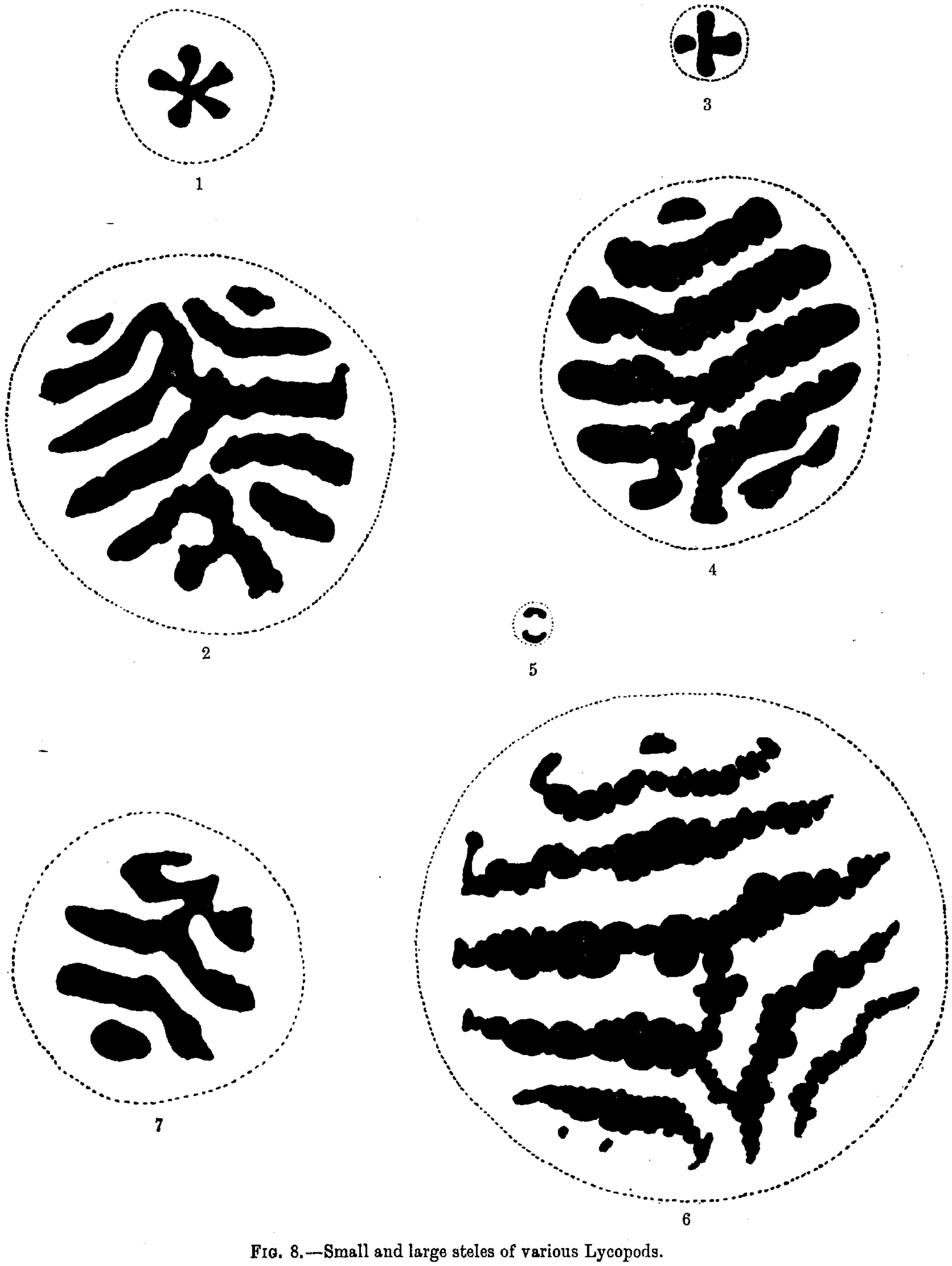

FIG. 8.—Small and large steles of various Lycopods.

1, 2, *L. alpinum*; 3, 4, *L. densum*; 5, 6, *L. volubile* (diagrammatic, after HOLLOWAY); 7, *L. annotinum*.

These figures show that with increase in size there is a departure from the simple stellate condition, found in small steles, and an advance in the complexity of the xylem. (× 73.)

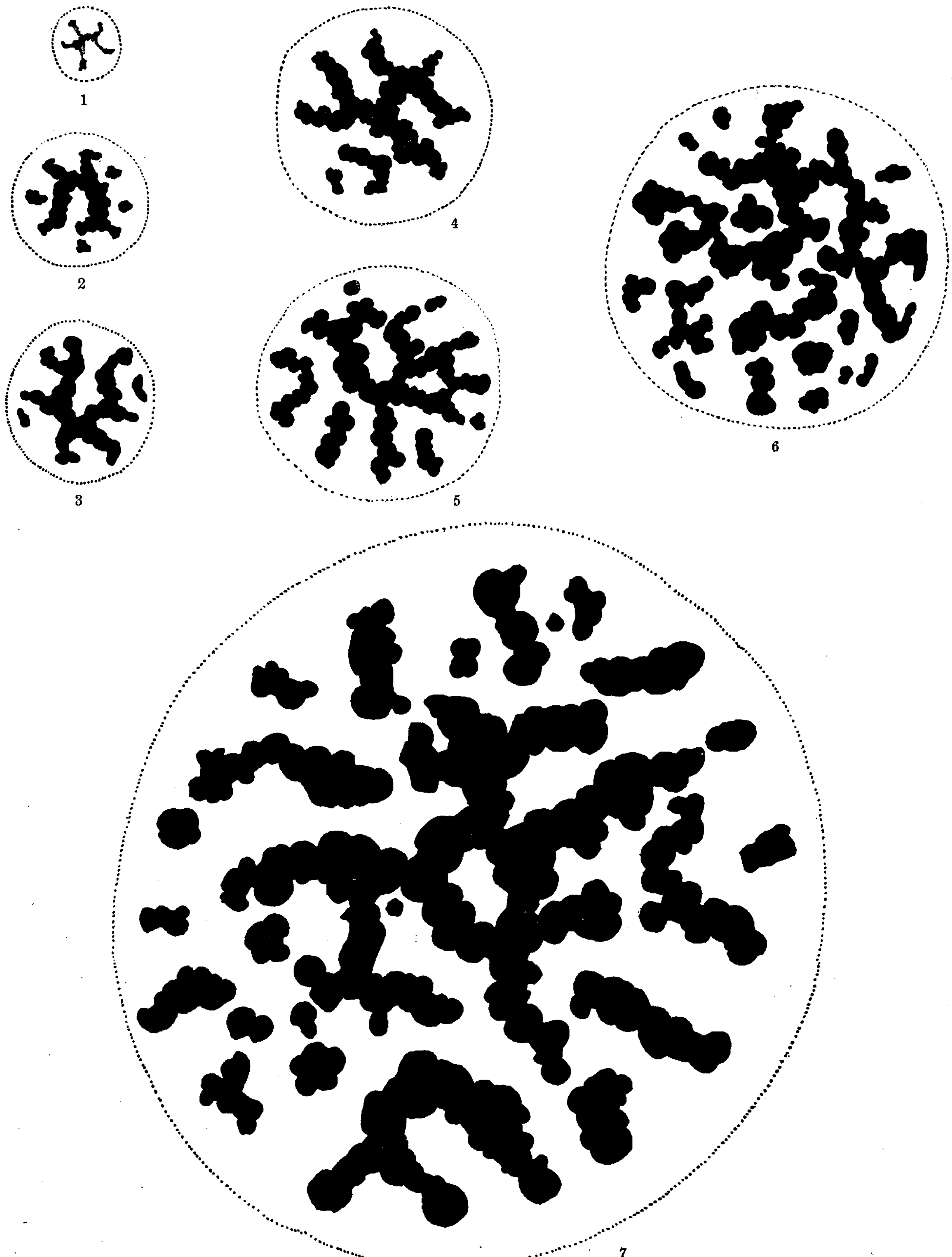

FIG. 9.—*Lycopodium squarrosum.* Series of sections from base of stem upwards showing the increase in complexity of xylem with increase in size. (× 73.)

in structure. With expansion of the stele the form of the xylem is modified and the number of rays in the star is increased. The stellate structure is by no means regular, the rays being sinuous and interrupted. In the larger steles the separate arms are linked up by cross-connections, so that the stele, in transverse section, has a meshlike structure, composed of thin plates of tracheides closely invested on all sides by thin-walled living tissue. In many sections islands of phloem are to be observed, completely surrounded by curved plates of xylem. The disposition of these plates is always changing, indicating the sponge-like nature of the xylem. These same general features are characteristic of many of the orthotropic terrestrial and epiphytic species, such as *L. selago*, *Phlegmaria*, *dichotomum*, etc.

In fig. 9, sections from *L. squarrosum* are shown, No. 1 being a very small stele from the base of the stem, Nos. 2 and 3 from the same stem, higher up, and the others from thicker stems.

The diameter of the stele, the area of the xylem, and the perimeter of the xylem were measured as before, and calculations based on these were made. These, with remarks on the nature of the xylem, are set out in Table IV. The general inference is that here again the

TABLE IV.

Lycopodium squarrosum.

I. Number of Section.	II. Diameter Stele in mm.	Measurements used for Calculation (× 110).			VI. Area : Perimeter = Ratio of Bulk to Surface.	VII. Ratio Area : Perimeter. The Xylem in each Stele is regarded as magnified to Area of Xylem in No. 7, but maintaining its own Shape.	VIII. Ratio of Area to Perimeter in a Cylinder equivalent to the Core of Xylem.	IX. Remarks.
		III. Diameter Stele in cm.	IV. Area Xylem in sq. cm.	V. Perimeter Xylem in cm.				
1	·17	1·9	Too small for practical measurement.		...	...	...	Small five-rayed star. Lignification not complete.
2	·32	3·5	2·05	16·5	1 : 8·05	1 : 1·20	1 : 2·48	Irregular interrupted eight-rayed star.
3	·35	3·9	3·45	24·9	1 : 7·22	1 : 1·39	1 : 1·91	Irregular interrupted nine-rayed star.
4	·53	5·8	5·73	31·8	1 : 5·55	1 : 1·38	1 : 1·48	Xylem an irregular star.
5	·58	6·4	9·80	53·8	1 : 5·49	1 : 1·79	1 : 1·13	Xylem a small sponge.
6	·82	9·0	21·70	110·5	1 : 5·09	1 : 2·47	1 : 0·76	Xylem a more elaborate sponge.
7	1·77	19·5	92·40	294·5	1 : 3·19	1 : 3·19	1 : 0·37	Stele large; xylem a very elaborate sponge.

complexity of the contour of the xylem is to be correlated with increase in size. The relation of the dead conducting tissue to the adjoining thin-walled living tissue is illustrated in greater detail in fig. 10 for sections of the stele at different levels. There is a marked increase in the size of the tracheides as the stele expands, a feature which explains to some extent the fall in the proportion of surface to bulk despite the modifications in the form of the xylem.

The steles of *L. Phlegmaria* and *L. dichotomum* are of the radial type, and their ontogenetic development is similar to that of *L. squarrosum.* In both, however, the stele is of much smaller size, the tracheides are smaller, the xylem shows a higher degree of

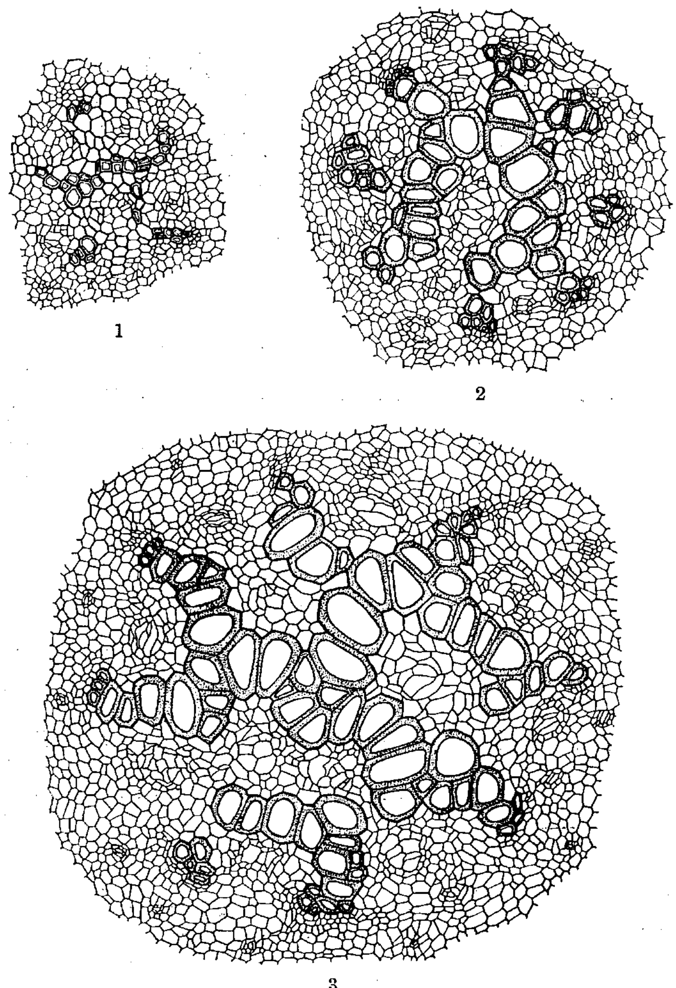

FIG. 10.—*Lycopodium squarrosum.*

1, Very small stele from base of stem, lignification not complete; 2, 3, sections from higher levels of the same stem. (× 154.)

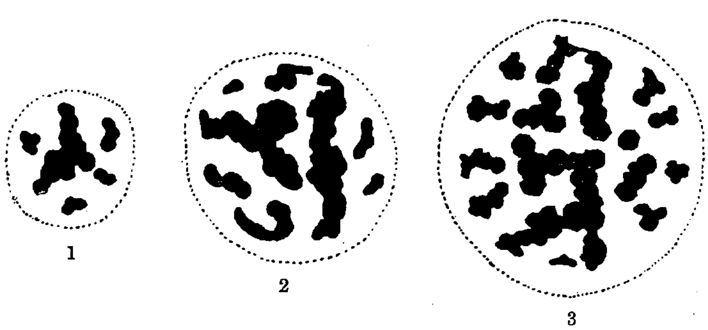

FIG. 11.—*Lycopodium Phlegmaria.* Distribution of the xylem in the stele at different levels. (× 73.)

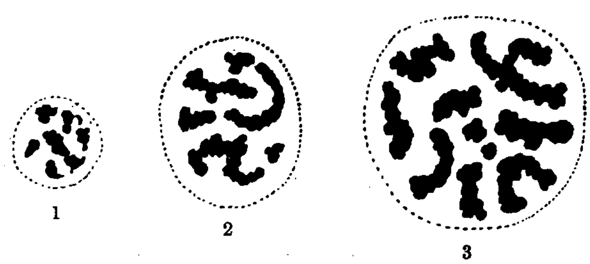

FIG. 12.—*Lycopodium dichotomum.* Three sections from branches of different thickness of the same plant.

1, Fine distal branch; 2, larger branch; 3, main stem. (× 73.)

disintegration, and has, as a result, a high proportion of surface to bulk. Three sections of *L. Phlegmaria* are shown in fig. 11, and three of *L. dichotomum* in fig. 12. Measurements

TABLE V.

Lycopodium Phlegmaria.

I. Number of Section.	II. Diameter Stele in mm.	Measurements used for Calculation (× 110). III. Diameter Stele in cm.	IV. Area Xylem in sq. cm.	V. Perimeter Xylem in cm.	VI. Area : Perimeter = Ratio of Bulk to Surface.	VII. Ratio Area : Perimeter. The Xylem in each Stele is regarded as magnified to Area of Xylem in No. 3, but maintaining its own Shape.	VIII. Ratio of Area to Perimeter in a Cylinder equivalent to the Core of Xylem.	IX. Remarks.
1	·23	2·5	1·23	11·8	1 : 9·59	1 : 4·34	1 : 3·20	Xylem, interrupted six-rayed star. Six groups of tracheides.
2	·36	4·0	3·71	29·6	1 : 8·00	1 : 6·29	1 : 1·84	Xylem sponge, disintegrated; eight groups of tracheides.
3	·45	5·0	6·00	50·3	1 : 8·38	1 : 8·38	1 : 1·43	Xylem sponge, very much disintegrated. Fifteen groups of tracheides.

TABLE VI.

Lycopodium dichotomum.

I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.
1	·15	1·6	·55	7·3	1 : 13·28	1 : 5·11	1 : 4·78	Interrupted five-rayed star.
2	·27	3·0	1·87	20·8	1 : 11·12	1 : 7·89	1 : 2·59	Xylem sponge, disintegration of plates.
3	·39	4·3	3·71	38 6	1 : 10·40	1 : 10·40	1 : 1·84	Elaborate sponge. Xylem much disintegrated.

were made as before, and these are stated in Tables V and VI. They bear out the general principle already demonstrated correlating size and complexity of structure in the vascular system. Comparing steles of equal diameter of *L. Phlegmaria* and *L. dichotomum*, we see that the tracheides in the former are on the whole larger than those in the latter (figs. 13 and 14). The

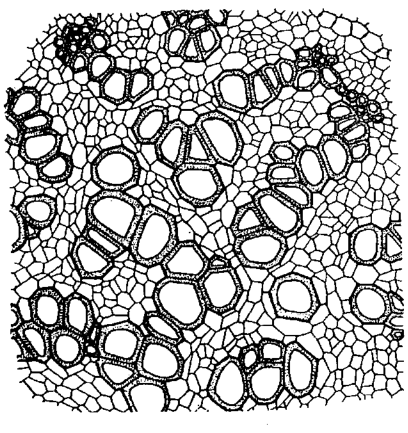

FIG. 13.—*Lycopodium Phlegmaria.* Distribution of the xylem in a stele of large size. (× 154.)

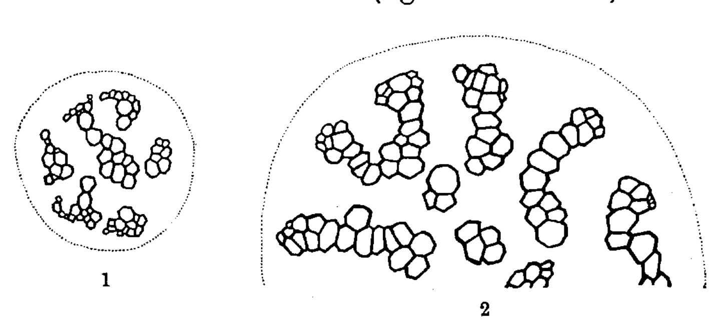

FIG. 14.—*Lycopodium dichotomum.* Distribution of the xylem in a small and large stele. (× 154.)

proportion of surface to bulk in *L. dichotomum* is as a result greater than that in *L. Phlegmaria.* The actual size of the tracheides, then, must be taken into consideration where a comparison is being drawn between steles of different species. Other species have been examined, *L. selago*, *carinatum*, *carolinianum*, and *serratum*, and in these the form and distribution of the xylem in the vascular strand is such as to provide a large surface of contact with the associated living tissues.

Lycopodium cernuum, etc. Figs. 15 and 16. Table VII.

Holloway (11, 12) has separated the *Cernuum* group (including *L. Drummondii*, *ramulosum*, and *laterale*) from the *Clavatum* and *Phlegmaria* sections of the genus for several reasons, one being the course of development in the stele. The early independence of the sporophyte is reflected in the prominent development of leaves in the young plant, and consequently the first formed vascular tissue is the leaf-trace system, and "for a considerable time in the development of the plant the indiscriminate arrangement of the leaf-traces in the stem determines the nature of the stelar arrangement" (Holloway (11)). When the plerome cylinder develops, the leaf-traces affix themselves to its periphery. "Transverse sections of stems of young plants show that there is no definite arrangement of the vascular tissues, the different xylem and phloem elements preserving no constant relative positions." In both young and old stems the disposition of the vascular tissues is very indefinite, the xylem forming curved plates very irregularly arranged, and showing a high degree of disintegration. In all stages, however, the tracheides are arranged in such a way as to present a very large surface of contact to the associated living tissues. Six steles of different size from branches and shoots of the same plant are shown in fig. 15, detailed drawings of some of these in fig. 16, and in Table VII various measurements made from fig. 15 (1–6). These illustrate the fact that disintegration of the xylem is correlated with increase in size, and

Table VII.

Lycopodium cernuum.

I. Number of Section.	II. Diameter Stele in mm.	Measurements used for Calculation (× 110). III. Diameter Stele in cm.	IV. Area Xylem in sq. cm.	V. Perimeter Xylem in cm.	VI. Area : Perimeter = Ratio of Bulk to Surface.	VII. Ratio Area : Perimeter. The Xylem in each Stele is regarded as magnified to Area of Xylem in No. 6, but maintaining its own Shape.	VIII. Ratio of Area to Perimeter in a Cylinder equivalent to the Core of Xylem.	IX. Remarks.
1	·13	1·4	·31	4·0	1 : 12·90	1 : ·78	1 : 6·36	Tracheides very small, disposed in three isolated groups.
2	·24	2·6	1·66	16·1	1 : 9·70	1 : 1·37	1 : 2·75	Tracheides larger, arranged in three parallel plates.
3	·48	5·3	7·75	48·8	1 : 6·30	1 : 1·92	1 : 1·27	Xylem irregularly disposed in curved interrupted plates.
4	·58	6·4	12·54	69·4	1 : 5·53	1 : 2·14	1 : 1·00	Larger number of irregularly disposed xylem plates.
5	·86	9·5	32·13	152·7	1 : 4·75	1 : 2·94	1 : 0·63	Large xylem sponge. In section many irregular xylem plates.
6	1·33	14·6	83·80	393·5	1 : 4·70	1 : 4·70	1 : 0·39	Very large xylem sponge. Tracheides large, disposed in curved plates. High degree of contact with living tissue.

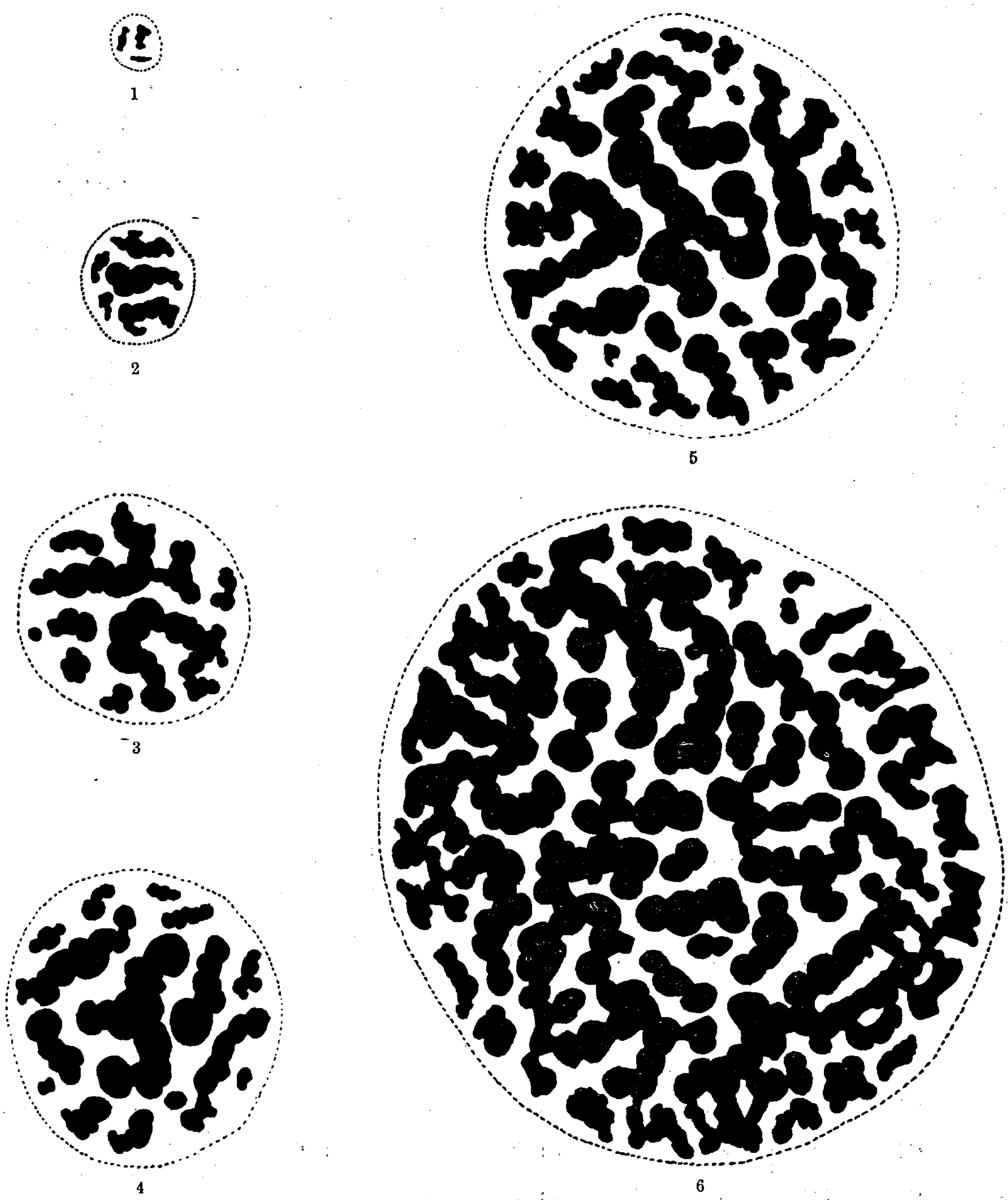

Fig. 15.—*Lycopodium cernuum.* Sections from branches and stems of the same plant showing that a high degree of disintegration of the xylem accompanies its increase in bulk.

1, Section from a very fine distal branch ; 2, section taken from same branch nearer main stem ; 3, 4, 5, sections from successively thicker branches ; 6, section from a thick stem. (× 73.)

that it is of such a nature as to make for a high proportion of surface to bulk. *L. laterale*, *Drummondii*, and *ramulosum* belong to the same type, and illustrate the fact that the same principles have been at work in the development of the vascular system.

Discussion for Lycopodium.

In the construction of the Lycopod stele one general feature has been demonstrated, namely, that the disposition of the xylem, whether in steles of small or large size, is such as to present a large surface of contact to the adjoining thin-walled tissue. Even in the sporeling the tracheides are grouped together into thin plates, which may be radially arranged or more irregularly disposed in the vascular strand. In contrast to the cylinder the flattened solid or plate-structure is one in which the proportion of surface to bulk is very large, and it may be assumed from the early appearance of these plates (instead, for example, of a solid core) that in Lycopods a high degree of interchange between the dead conduits and the associated living tissue is necessary. This being so in small steles, with increase in size the problem will become greatly intensified, and the satisfaction of the physiological requirements will depend very largely on suitable morphological changes. The nature of these modifications has been demonstrated in several instances, and the illustration and data advanced show that they are such that the tracheides continue to be disposed in thin plates, the tendency being to maintain, as far as possible, a high proportion of surface to bulk. The stellate condition has been recognised as the usual primitive state, since it occurs in simple types such as *L. selago*, and is also characteristic of an early state in ontogenetic development. Such a stele with plates of tracheides radiating from the centre presents a stellate appearance in section. With expansion of the stele there is an increase in the number of radiating plates, or, as seen in transverse section, an increase in the number of arms in the star. The fact that increase in bulk takes the form of an increase in the number of plates and not, as might quite well be expected, in a thickening of the existing ones, suggests that there is some factor involved which tends to maintain a large proportion of surface to bulk, since it is clear that this ratio would be reduced by any thickening of the xylem plates. Further, the increase in the number of radiating xylem plates does not go on indefinitely, but continues only until seven to nine are formed, after which there is a departure from the stellate condition. Why should this be so? As a rule each plate is

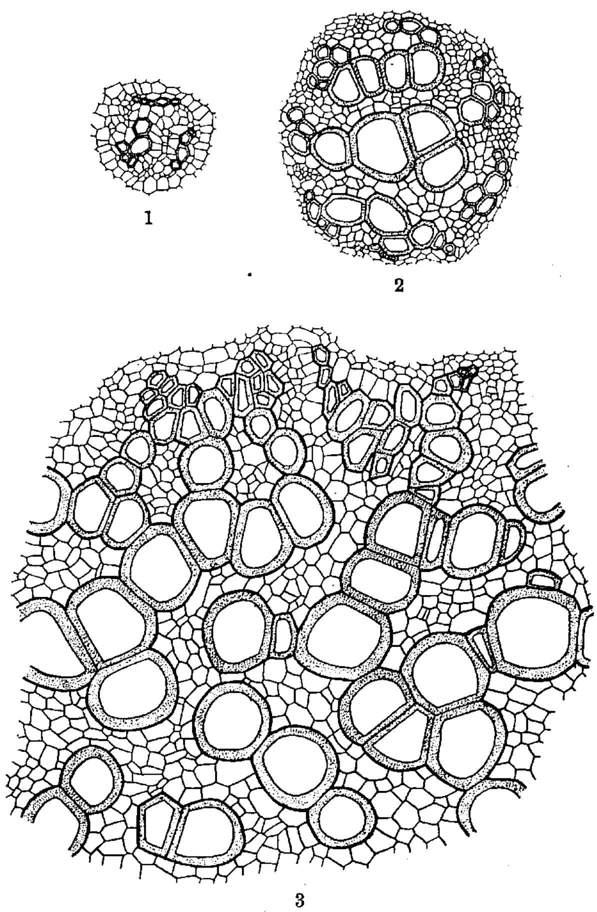

Fig. 16.—*Lycopodium cernuum.*

1, Section from a fine distal branch, showing irregularly disposed xylem; 2, section showing arrangement of tissues in a larger stele; 3, section showing the very high degree of contact between the tracheides and thin-walled tissues in a large stele. (× 154.)

wedge-shaped, with the thick end, composed of the larger metaxylem elements, towards the centre, and as a result of the convergence of the broad ends of the xylem plates some of the innermost tracheides will be cut off from contact with living tissue; with the addition of other radially disposed plates an ever-increasing number of tracheides would be isolated. Ultimately, a homogeneous solid xylem core would be formed, and the proportion of surface to bulk would thereby be greatly diminished. As a matter of fact this does not occur. It has been shown in the smaller steles where the stellate condition is found that the arms of the star are very often interrupted at the point of junction with other arms, and in the larger steles instead of there being an increase in the number of rays it has been shown that they become sinuous and interrupted, and are linked up by cross-connections of xylem disposed more or less tangentially. These changes give rise to the interrupted meshlike structure seen in section, and lead to that formation in the adult stele which has been described as the xylem sponge.

The tables show that in passing from steles of small size to larger ones, there is a decrease in the proportion of surface to bulk, despite disintegration and modifications in the form of the xylem. This is to be explained largely by the fact that the individual units, the tracheidal cavities, are, on the average, much larger in the large steles, and each tracheide has therefore a smaller proportion of surface to bulk.

Column VII, in each table, is significant in indicating what the proportions of surface to bulk would be if the large steles were merely magnified images of the smaller ones, *i.e.* if the simple stellate condition were retained throughout. The calculations show that the proportion would be very considerably reduced, and the column read as a whole, with its ascending ratios, points to the fact that the elaboration of form has not advanced indiscriminately, but has been governed by what HABERLANDT (10) has described as the *principle of maximum efficiency.*

The large proportion of surface to bulk achieved, especially in large steles, by the disposition of the xylem in thin plates is indicated by comparison of Columns VI and VIII, the xylem in the latter being regarded as compacted into a solid cylindrical core. These calculations show that, although the problem is one of lesser importance where size is small, it becomes increasingly accentuated with increasing size.

The conclusion arising out of the data advanced for the Lycopods and Psilotales is that size is a factor in stelar morphology. While this is so, it is also realised that other factors are at work in determining the form and constitution of the stele and of its component parts. The distribution of the tracheides, their size and construction, suggest many points of interest. The metaxylem elements have elongated pits, and not only do these occur where the tracheides adjoin, but they also occur where the tracheides abut on the thin-walled living tissue. Thus if fluids pass readily from one tracheide to another by means of these pits, their occurrence at the point of junction with living tissue would point to a similar necessity or facility for free interchange between the two tissues. Professor BOWER (2) has pointed out that although it is often useful to compare steles of different species and genera it is not always possible to do so, and remarks: "The ontogenetic evidence is more weighty than that from comparison." This is the case in Lycopods, and the observations made on stelar construction point to the fact that the reason is to be sought in the size of the tracheides themselves. By comparing steles of different species we find that, size for size, some show a greater degree of disintegration than others, *e.g.* by comparing the xylem in *L. dichotomum*, *Phlegmaria*, *squarrosum*, and *clavatum*, we see that *L. dichotomum* and *Phlegmaria* show a high degree of disintegration, whereas the xylem in steles of the same diameter from

L. squarrosum and *clavatum* are much less broken up. They all show the same general changes in the course of ontogenetic development, complexity and disintegration being more marked as size increases. The difference seems to be one of degree, since in some species these changes take place over a smaller range in size. Where this is the case it has been noted that the tracheides are relatively small. While we do not know what the relations between the xylem and thin-walled tissues are, it is clear that small tracheides and

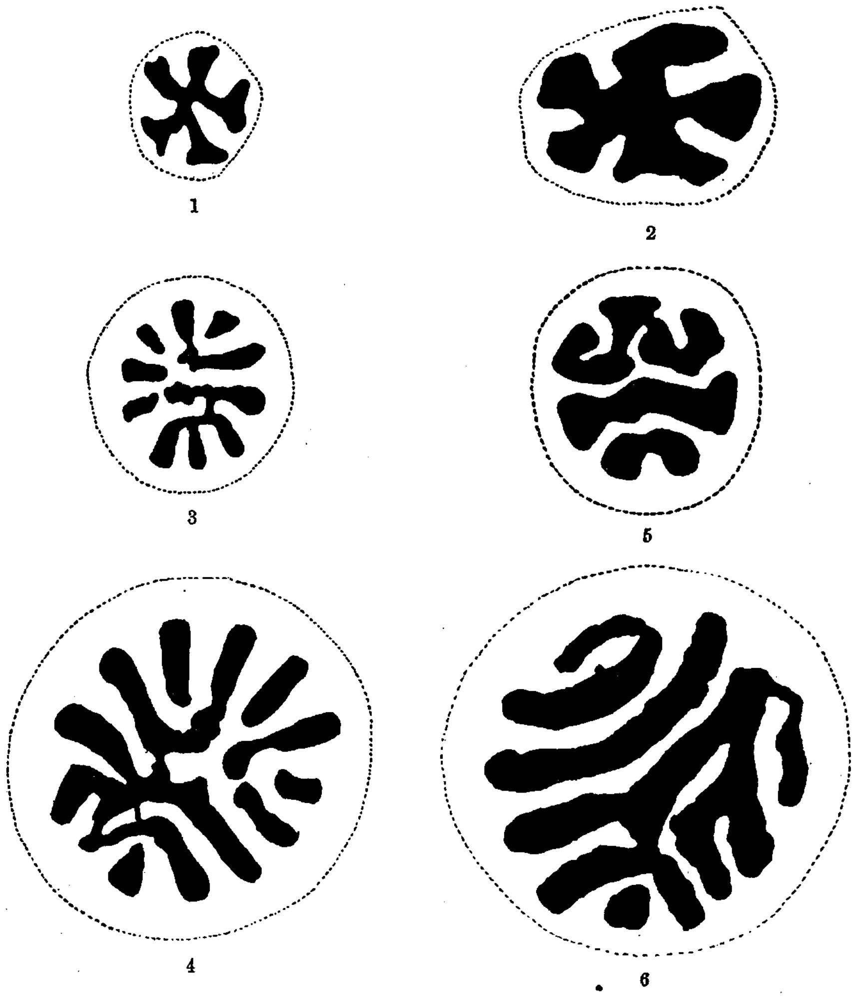

FIG. 17.—Sections from different plants of the same species which show that other factors, as well as the size-factor, are at work in determining the morphology of the stele.

1, 2, Steles from different plants of *L. selago*; 3, 4, two sections from the same plant of *L. clavatum*, based on a delicate plan of construction; 5, 6, two sections from another plant of *L. clavatum*, based on a rather coarser plan of construction. (× 73.)

disintegration would make for a greater surface of interchange than would larger tracheides and xylem less divided. In fact, we recognise that while some steles such as those of *L. dichotomum* and *Phlegmaria* are based on a delicate plan of construction, with small units, others such as *L. squarrosum* have much larger units, and are based on a coarser plan of construction.

Thus while it is not possible to compare all steles in the genus, when account is taken of the size of the tracheides a comparison between similar groups of species becomes possible, and from the latter it is seen that the larger the stele the greater is its complexity.

A general plasticity has been recognised in Lycopods, and some species may show a considerable range of xerophily. This is reflected in the vascular system, and is illustrated by fig. 17 (1–6); Nos. 1 and 2 are from different plants of *L. selago*. Each stele has xylem in the form of a five-rayed star, but No. 2 is of a much bulkier nature, and will have a lower proportion of surface to bulk. In the same way, Nos. 3 and 4 are from one plant of *L. clavatum*, and Nos. 5 and 6 from another. It will be seen that Nos. 3 and 4 are based on a more delicate plan of construction than Nos. 5 and 6, and will consequently have a much greater proportion of surface to bulk. These examples show that, while the size factor is seen at work in ontogenetic development, it may not always be obvious when steles from plants grown under different conditions are compared.

In dealing with this plasticity HOLLOWAY (12) has made some interesting observations,

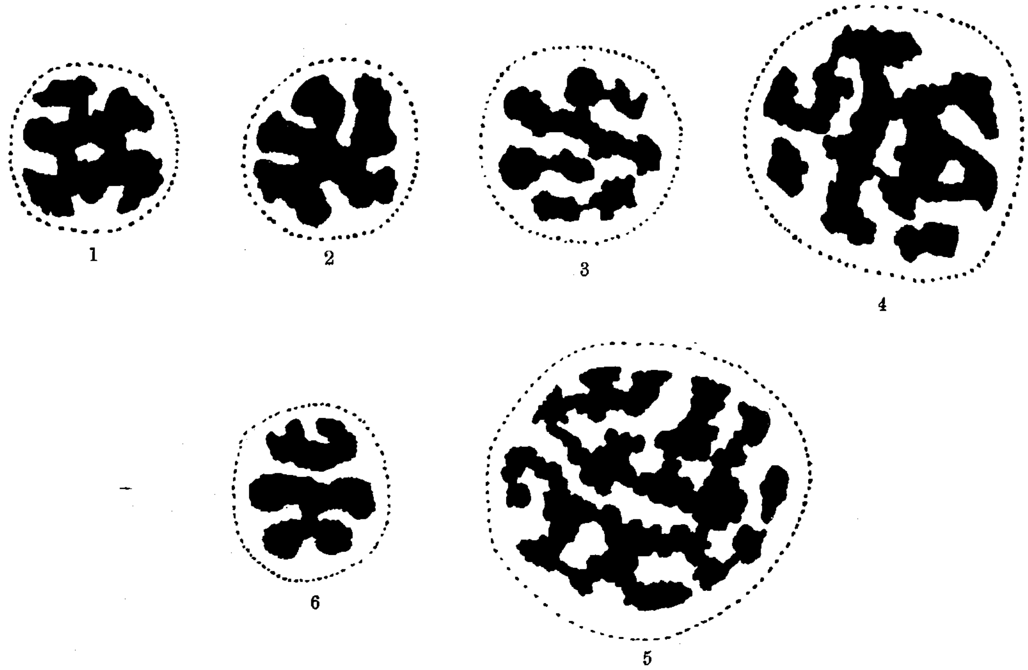

FIG. 18.—Series of steles linking up *L. selago* and *L. Billardieri*.

1, *L. selago*; 2, *L. varium*. Macquarie Island variety; 3, *L. varium*. Campbell Island variety; 4, *L. varium*. Otira Gorge variety; 5. *L. Billardieri*. Typical epiphytic form; 6, *L. Billardieri*, var. *gracile*. Small delicate type. (Diagrammatic, after HOLLOWAY.) (× 67.)

and indicates the lines along which comparison of steles from different species becomes possible. He shows that a chain of forms links up the two species *L. selago* and *L. Billardieri*, and that "the stelar anatomy is identical throughout the whole chain of forms, what modifications there are being dependent simply upon the size of the plant." This is illustrated by fig. 18 (1–6). *L. selago* is the smallest of the three, and the xylem is usually a simple star, or extended across to form parallel plates. When the stele is of larger size there is an increase in complexity, and a phloem island may be recognised. The latter bears a close resemblance to the Macquarie Island variety of *L. varium*. The Campbell Island variety of *L. varium* is larger, and there is an increased complexity in the vascular system. To quote HOLLOWAY, "Thus along with the luxuriant growth of this variety, there go both a change in the configuration of the stele and also a tendency towards a greater differentiation of the tissues composing it." The largest variety of *L. varium* from Otira Gorge has a still larger stele, and there is a much greater disintegration of the xylem with formation of phloem islands. Further, the anatomy of the epiphytic species *L. Billardieri* corresponds closely with that of the largest variety of *L. varium*, but the xylem is in the form of a complex sponge as a result of its greater size. This leads on to the condition seen in *L. Phlegmaria*. On the other hand, the small stele from the delicate plant of *L. Billardieri*, var. *gracile* (fig. 18 (6)), corresponds very closely with that of the smaller steles of *L. varium*. HOLLOWAY indicates the significance of these observations as follows: "From the study of the chain of forms which occur in New Zealand connecting *L. selago* through *L. varium* with *L. Billardieri*, it will be seen, first, that there is a definite type of stelar anatomy characteristic of the whole series, and, secondly, that a gradual change takes place in the vascular arrangement from a strictly radial form in the smaller growing species, to a form in larger species in which the radial or stellate arrangement is broken up by cross-connections, which result in the isolation of some of the xylem and phloem into islands."

Some measurements and observations were made on the ratio of stele to stem, and on the distribution of mechanical tissues, but no direct evidence was obtained indicating that these factors have any marked influence on the morphology of the stele.

CONCLUSION.

The detailed examination of the stelar structure, and its ontogenetic development in the Psilotales and in *Lycopodium*, reveals a general but not a detailed similarity of behaviour on increase of size. The changes in form of the xylem that appear on passing from a small to a large size of stele are, however, comparable in one respect. In neither of them is the larger stele merely a magnified image of the smaller, but the structure of the xylem becomes increasingly disintegrated on passing from smaller to larger size. In the sporeling, the proportion of surface to bulk in the minute tract of xylem is high. By the principle of similar structures, as size increases the surface will vary as the square of the linear dimensions and the bulk as the cube, provided the form be unchanged. It has been demonstrated in a number of instances, by actual measurement, that the changes on passing to a stele of larger size are such as to maintain a relatively high proportion of surface to bulk, and that, in point of fact, that proportion is considerably higher than it would have been supposing the larger tract of xylem had been of cylindrical or approximately cylindrical form. This result is obtained in both classes by progressive decentralisation and disintegration of the xylem. The structural evidence advanced thus indicates that Size is a factor in determining the internal morphology of the stele in the plants examined.

In conclusion I wish to express my thanks to Professor A. L. SEWARD and to Mr BURKILL, Botanic Gardens, Singapore, for some of the material used in this investigation, to Professor BOWER for much helpful advice in preparing this paper, and to the Carnegie Trust for their assistance in the production of the tables and illustrations in this memoir.

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Size in Relation to Internal Morphology.

No 2. The Vascular System of Selaginella.

C.W. Wardlaw

Botany Department

University of Glasgow

10/1/25.

I herewith present as a thesis for the degree of Ph.D., the following papers on

<u>Size in Relation to Internal Morphology</u>

(i) "The distribution of the Xylem in Psilotum, Tmesipteris, and Lycopodium", published in the Transactions of the Royal Society of Edinburgh,

and

(ii) "The Vascular system of Selaginella," in typescript.

I declare that both are the result of my own researches.

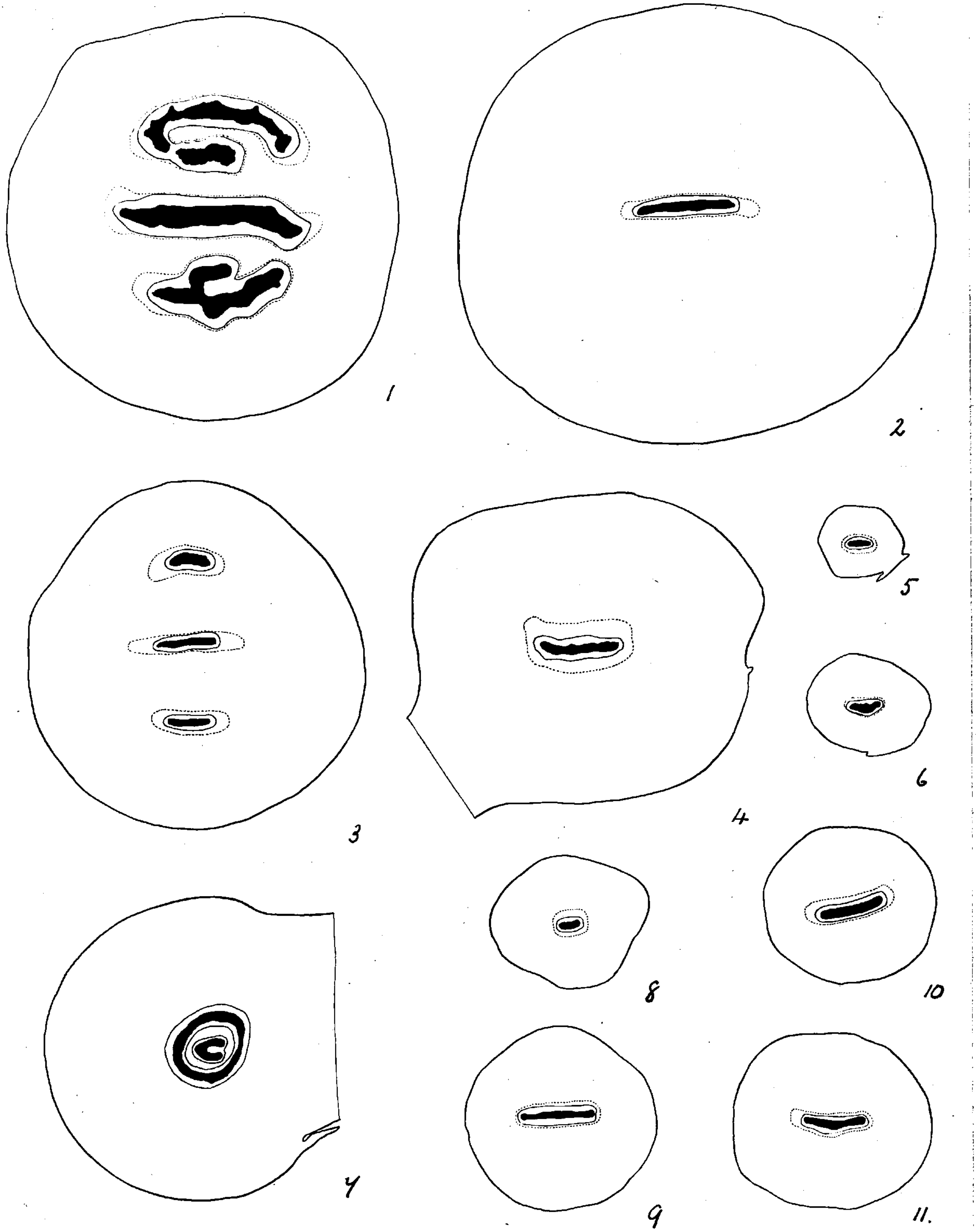
Claude W. Wardlaw.

SIZE IN RELATION TO INTERNAL MORPHOLOGY.

No.2. The Vascular System of SELAGINELLA.

by

Claude W. Wardlaw, B.Sc.



The vascular system in various species of Selaginella.

1. S.Willdenowii:2. S. grandis: 3. S.Wallichii: 4 S. Rassellata: 5.S.pilifera: 6. S.involvens:7. S.Lyallii 8. S.Martensii: 9.S.Volgelii: 10. S.erythropus: 11. S.cuspidata. x 16

SIZE IN RELATION TO INTERNAL MORPHOLOGY.

No.2. The Vascular System of Selaginella.

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The influence of Size as a factor in the stelar morphology of the Filicales (2) and of some Primitive Plants (3) has already been discussed in the Proceedings of this Society. The aim of the present investigation is to determine by actual measurement, to what extent Size may have acted as a causal factor in determining the structure and arrangement of the vascular system of *Selaginella*.

A survey of previous work indicates that most of the investigations were carried out with a view to systematic classification or with respect to physiological anatomy. Little has been written of the causes which determine the banded structure of the stele in species such as *S. Martensii*, polystely in *S. Willdenowii*, or solenostely in *S. Lyallii*, or of the appearance of the pith in *S. spinosa*. Some general references to this aspect are to be found in the writings of Bower, Lang and Tansley, which will be discussed in the course of this paper. It is proposed here to study the form of the vascular tract in relation to the causes which have influenced it. In dealing with plants whose ancestors reach back to the Palaeozoic, the stele may properly be regarded as having acquired a characteristic structure in the course of descent. We may rightly use such characters for comparison and classification wherever there is evidence of a settled structure having been evolved. Since we are primarily concerned with living organisms we may also regard the stele as an active organ or agent for doing work (Von Goebel (14) p. 5) and we shall expect to find a certain "interdependence of form and function." The genus is represented by a large number of species many of which are polymorphic. They have a wide geographical distribution, and in some floras they dominate the ground vegetation. Further they show adaptation to all degrees of xerophily and hygrophily. It would appear from these facts that the genus is successfully retaining its position in the midst of the more highly differentiated Phanerogams. This would justify the investigator in regarding the stele and other organs in these plants, not as labouring under a phyletic handicap, but as capable of reacting to the influence of physiological and causal factors. In absence of accurate knowledge as to the function of the various tissues of the stele it is a matter of the greatest difficulty to determine what these factors are, how they are applied and to what extent. Causal morphology as Prof. Lang (19) points out, can only be studied in favourable cases. With regard to stelar morphology, such cases are to be found where the family as a whole is homogeneous, with a wide range of species, varying degrees of xerophily, diversity of habit (erect, creeping, climbing and pendulous), and lastly a considerable range in actual size. By critical examination of data from such a source it may be possible to determine by inductive methods the factors involved and the extent of their influence. It will be of further interest to contrast the resulting conclusions with phyletic and comparative views.

GENERAL REMARKS ON STELAR STRUCTURE IN SELAGINELLA.

A considerable diversity of stelar structure is characteristic of the genus. "The "gross anatomy" of the vascular system of the "shoot axes of Selaginella is strikingly variable within the genus, "which indeed presents a range of vascular structure not only un-"qualled among other Pteridophytic genera, but almost comparable "with the range exhibited by the whole phylum of Leptosporangiate "Ferns." (Tansley[23], Lectures, p.134.) Harvey Gibson[13] has grouped the species which he studied round certain type forms:-

(A). Martensii type with dorsiventral axis and banded stele;

(B). Oregana type with homophyllous leaves but banded stele;

(C). Anomalous monostelic species including S.Braunii and S.spinosa:

(D). Galeottei type, regularly bi-stelic:

(E). Inaequalifolia type with three or more parallel stelar bands:

(F). Lyallii type with solenostelic rhizome.

Such diversity of structure within a genus like Selaginella leads the morphologist to seek those factors which determine the nature of the vascular system. For this purpose , those complex species such as S.Willdenowii from which development can be traced from the simple sporeling to the complex stelar structure of the adult will be of the greatest use. With the exception of S.spinosa which is unique among living species in its stelar arrangements, all the members of the genus have certain features in common. (1). They have all homogeneous xylem surrounded by parenchyma, phloem and pericycle. (2). Except in those cases where the stele is very small, i.e., in sporelings or small species, the stele is in the form of a thin band, the xylem consisting of a thin ribbon of tracheides surrounded by the ~~other~~ other vascular tissues. This is the case not only for the greater number of species which are definitely dorsiventral but also for radial homophyllous species such as S. oregana, S. rupestris and S. arenicola. In the stems of the larger species such as S. WILLdenowii, S. Wallichii and S. inaequalifolia, there is a multiplicity of these bands, and in the solenostelic species S. Lyallii and S. uliginosa the vascular system is a cylinder whose centre is occupied by pith.

From a consideration of the simpler species alone, e.g. S. Martensii, it might appear that the banded structure is simply an adaptation to the general habit of the shoot, since the stelar band always lies parallel to the plane of dorsiventrality. This can hardly be regarded as the whole explanation when we consider solenostely in S. Lyallii, polystely in S. Willdenowii and the T-shaped stele in the erect shoots of S. Braunii. An interesting analogy may be taken from the stele in Lycopodium. In the radial species Holloway (6) has shown that the xylem is arranged radially in the stele*. When branching of the shoot is about to take place the xylem is rearranged into bands which lie parallel to the plane of branching. Segments from these bands pass off into the branch and there is then a return to the radial arrangement. In plagiotropic species on the other hand, where the branches always pass off on the same plane, the xylem always remains disposed as a series of parallel bands of tracheides.

In *Selaginella* likewise, while we may regard the particular orientation of the stelar band as correlated with the general dorsiventrality of the shoot, the actual disposal of the tracheides in the form of a thin ribbon is referable to other factors. As in *Lycopodium* the leaf-traces are small and have little influence on the morphology of the stele. Mechanical support is provided for by the presence of a thick sclerotic outer cortex.. It is to the physiology of the conducting tracts, therefore, that we must look in order to explain the distribution of the vascular tissues.

ANALYSIS OF THE VASCULAR SYSTEM IN DIFFERENT SPECIES.

Selaginella Martensii.

In monostelic species such as *S. Martensii*, *S. cuspidata*, *S. grandis*, *S. atroviridis*, etc., the stele in the sporeling or at the thin base of the stem is approximately radial with small marginal protoxylem groups. The tracheides are small and form a solid core, surrounded by parenchyma, phloem and pericycle. In the course of ontogenetic development the diameter of the stem increases to its maximum size, and there is an accompanying increase in the amount of vascular tissue. The stele, however, does not expand equally in all directions but develops strongly in one plane, thus forming a thin ribbon which as a rule lies in the plane of dorsiventrality of the shoot. The thickening of the ribbon is mainly due to the increase in size of the individual units of the stele. The development of the stele in some monostelic species is illustrated in FIG. 1, for *S. Martensii*, *S. grandis* and *S. cuspidata*.

Fig.1. 1, 2, S. Martensii. 3-7, S. grandis. 8-11, S. cuspidata, var. elongata. These figures show the development of the vascular system in monostelic species with increase in size. The stelar ribbon increases in length but remains of uniform thickness. The small sections are from the base of the shoot, the large ones from the thick part of the shoot.
Xylem in black × 55.

In each case the sections were taken midway between the departure of two branches. Harvey Gibson (15) and others have dealt with the chief histological and anatomical characters of a large number of these monostelic species.

Selaginella Willdenowii.

A number of the larger polystelic species such as S.Willdenowii, S.Wallichii, S.Lobbii, etc., have been described by Harvey Gibson (15) under the title Inaequalifolia type. These species are characterised by the presenee of three or more parallel stelar ribbons in the adult stem. In the primary creeping axis, however, there is only one stele, which in the course of ontogenetic development increases in size and gives rise to dorsal and ventral steles, thus arriving at the condition found in the adult plant. Harvey Gibson finds that this holds good for a number of species which he examined. An extract from his description of S.Lobbii will serve to indicate the nature of these changes:- "In the primary creeping stem a condition "of things similar to that seen in S.Inaequalifolia appears. In the " earliest conditions that I have been able to examine there is a four " rayed xylem mass, with four points of insertion of leaf-traces. The "protoxylem elements are partially sunk in the metaxylem .... " .... The two ventrally placed bands soon separate from the main " xylem mass, though they are still united by a common pericycle. The " dorsal cord then becomes isolated, and the tristelic condition of " the erect stems is reached." p.185.

A similar transition from the monostelic to the tristelic condition is found on passing from the thin basal region into the thick ~~erect stem of a climbing~~

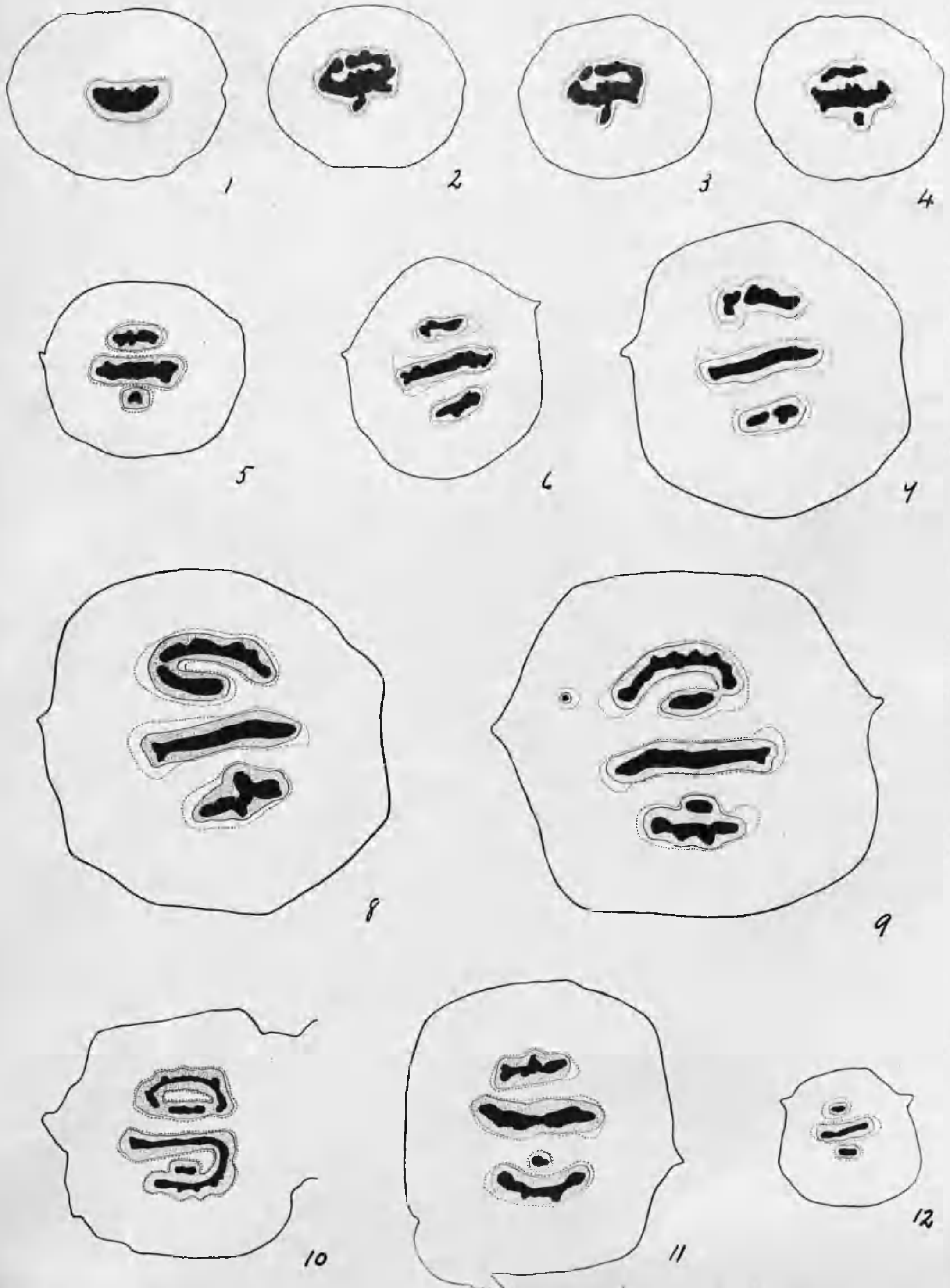


Fig. 2. Selaginella Willdenowii. 1, from base of shoot near junction with the creeping stem. 2-5, transition to the tristelic state, showing the method of formation of the dorsal and ventral steles. 6-9, sections taken successively higher up in same shoot, showing the origin of additional stelar ribbons. 10, section through the apical bud, showing the vascular system in meristematic form. 11, from creeping stem. 12, from a distal branch. The increase in complexity accompanies increase in size.

(× 22)

upper region of the large climbing branches of S.Willdenowii and S.Wallichii, The illustration brought forward in this paper was obtained from plants of this kind.

S.Willdenowii - The habit of the plant is climbing and the shoot may attain to a height of twelve to twenty feet. The plant examined here consisted of a short length of creeping stem from which arose , as a branch, a long climbing stem ,regularly branched and altogether some four feet in length.

The arrangement of the vascular system in the creeping stem and in the erect shoot was essentially similar, but sufficient material of the former was not available for tracing development over any great length. At the point of junction with the horizontal stem the erect shoot was thin, but on passing upwards there was a gradual increase in girth, with a slight decrease again as the apex was approached. This erect shoot was sectioned serially from the base upwards. The changes in stelar structure from base to apex are shown in Fig.2. At the base of the shoot there is a single ribbon-shaped stele, slightly crescentic,consisting of a central band of xylem surrounded by parenchyma,phloem and pericycle,just as in the typical monostelic species. Midway between the horizontal stem and the first branch the vascular system of the erect shoot was found to consist of three stelar bands. The changes leading to this from the monostelic condition are shown in Fig.2,I-V. The xylem ribbon increases in width and curls round at both ends so as to form a dorsal cord, Fig.2,II,III,) which is separated from the parent band by parenchyma and phloem. At first all is contained within the same pericycle, but later the mass separates into two bands. These at first occupy the same lacuna,but afterwards they part and lie in separate cavities.

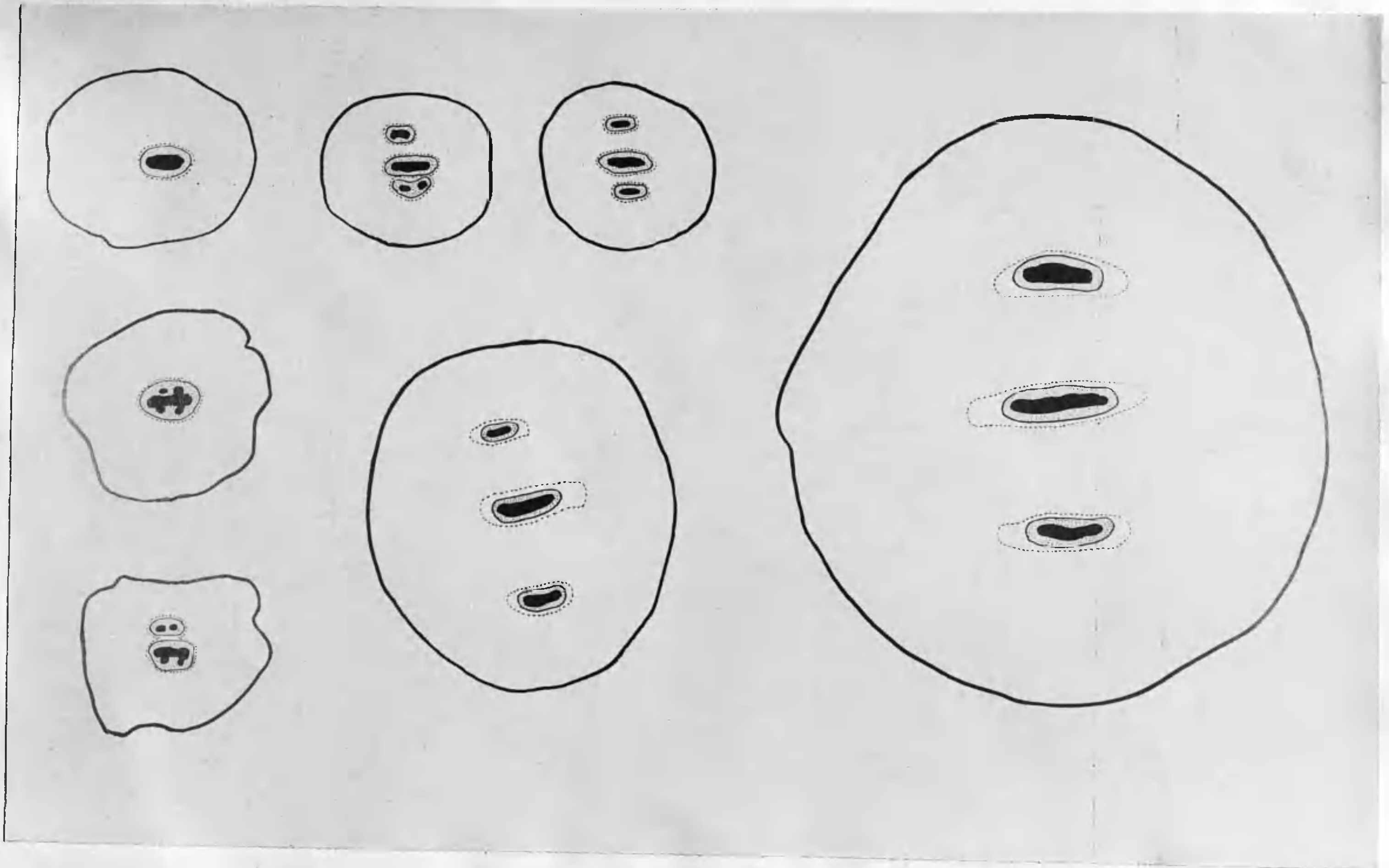


Fig. 3. S. Wallichii. Series of sections from the base to the thickest part of the same plant. 1, monostelic condition at base of stem. 2 - 5, transition to tristelic condition. 6, higher up in the shoot. 7, thickest part of the shoot. (x 22)

At the same time a ray of xylem passes off from the ventral side, of the main ribbon and becomes isolated as a ventral stele. Thus the tristelic condition is brought about. With further increases in the amount of vascular tissue the dorsal and ventral ribbons increase in width, their thickness remaining more or less constant. Higher up in the thick part of the shoot, where the amount of conducting tissue was considerable, additional stelar bands were formed from the dorsal and ventral steles, (Fig. 2, VIII, IX), and transverse sections through the bulky apical bud showed five parallel bands laid down in meristematic form, (Fig. 2, X). Sections through branches showed that they possessed the same general characters as the stem, the tristelic condition being common.

The thick stems of S. Lobbii, S. inaequalifolia, and S. viridangula are very similar and may have as many as five separate stelar ribbons.

S. Wallichii. A similar analysis of an erect stem of S. Wallichii was made from the base upwards. The successive changes are shown in Fig. 3. Here the tristelic state is usual in stems and branches, and in this sp species the number of bands is increased beyond three only in very thick stems. S. Mettenii and S. gracilis are like S. Wallichii with a single stele at the base of the shoot, and three stelar ribbons in thick shoots and branches.

Selaginella Braunii

Intermediate between monostelic and polystelic types in complexity is S. Braunii, Baker., in which the adult creeping stem is bi-stelic and the erect axis monostelic. In the basal region of the rhizome near the spore there is a small protostele with solid xylem. With increase in size a ventral ridge appears which afterwards passes off as a ventral stele. With further increase in size the two steles

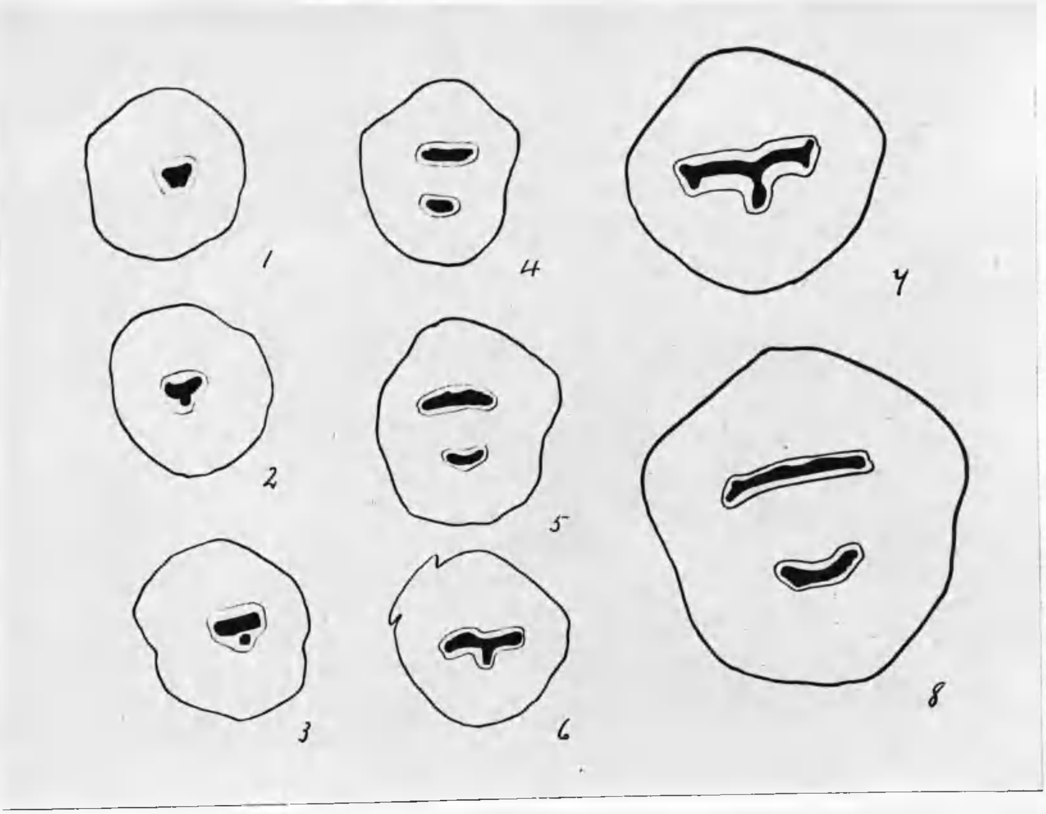


Fig. 4. S. Braunii, 1 - 5, series of sections from rhizome of one plant showing the transition from the monostelic to the bi-stelic condition. 6, section of an erect stem of the same plant showing the single stelar ribbon with a ventral ridge. 7, section of a thick erect stem showing the prominent ventral ridge of xylem. 8, from the rhizome of the same plant showing the two stelar ribbons. (x 22)

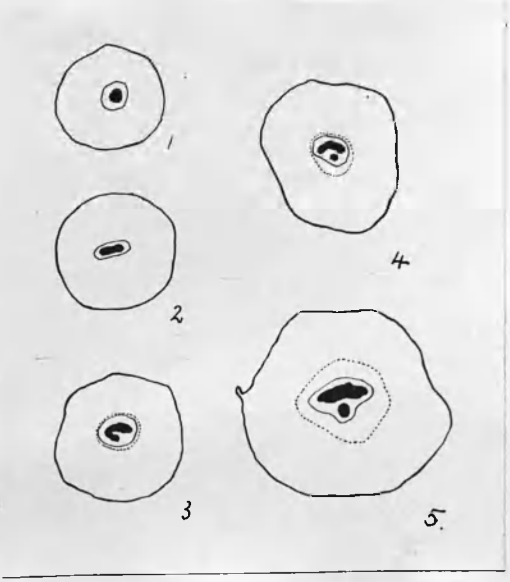


Fig. 5. S. uncinata; 1, 2, near base of shoot, with single xylem strand. 3, 4, formation of ventral cord of xylem. 5, from a thick stem, showing the ventral cord. (x 22)

widen out and form two broad ribbons which lie parallel to one another The stele of the erect shoot is formed from branches of both steles of the rhizome. It is essentially a ribbon with marginal protoxylems, and on the ventral side there is a well developed ridge of metaxylem. See Fig. 4, Y.

Harvey Gibson has placed this species along with S. spinosa as an anomalous monostelic species which may be associated with the Martensii type.

Selaginella uncinata.

The last of the species to be described at this point is S. uncinata, the advances in whose stelar complexity are shown in Fig. 5. According to Harvey Gibson (15) "In this species a slightly higher stage is reached in the evolution of the vascular ~~system~~ system" and he has placed it at the end of those species belonging to the Martensii type. At the base of the shoot there is a small cylindrical stele which flattens out to form a ribbon. The latter has marginal protoxylem groups at the point where the leaf-traces are inserted. On passing upwards in the shoot the marginal protoxylem bends round towards the ventral side. The number of tracheides in this ridge is augmented and it finally separates off as a ventral cord. The latter does not form a separate stele but remains inside the same pericycle and is separated from the main band of xylem by parenchyma and phloem. This condition in the fully developed stele of S. uncinata is like some of the transition stages on the way to polystely in S. Wallichii or S. Braunii.

In all the polystelic species there is a temporary union of the different steles at the point of origin of a branch, but only on the side at which the branch arises. As a rule the leaf-traces are inserted on the median or main stele.

These data have been surveyed in part by morphologists such as De Bary (11), Dangeard (10), and Harvey Gibson (15), and have been used for classification and phylesis. It is proposed here to examine them from the physiological and causal point of view. The complexity of the vascular system of the Filicales and the elaboration of form in ontogenetic development in large species have been shown by Prof. Bower (2) to be closely correlated with actual size. A study of the vascular system, particularly where the latter is present in relatively large proportion, suggests that size is also one of the factors in the stelar morphology of Selaginella.

FACTORS IN THE STELAR MORPHOLOGY OF SELAGINELLA.

The outstanding characteristics of the vascular system of Selaginella are :-

1. The distribution of the tracheides in a thin ribbon in relation to physiological needs.
2. The width of the stelar band in relation to the diameter of the stem.

1. The banded structure is most probably related to the physiological activities of the stele. Recent researches by Dixon (12) reveal the importance of surface relation between the xylem and associated thin-walled tissues, an example of which has recently been worked out by for Psilotum and Lycopodium. (27). A general summary of the physiology

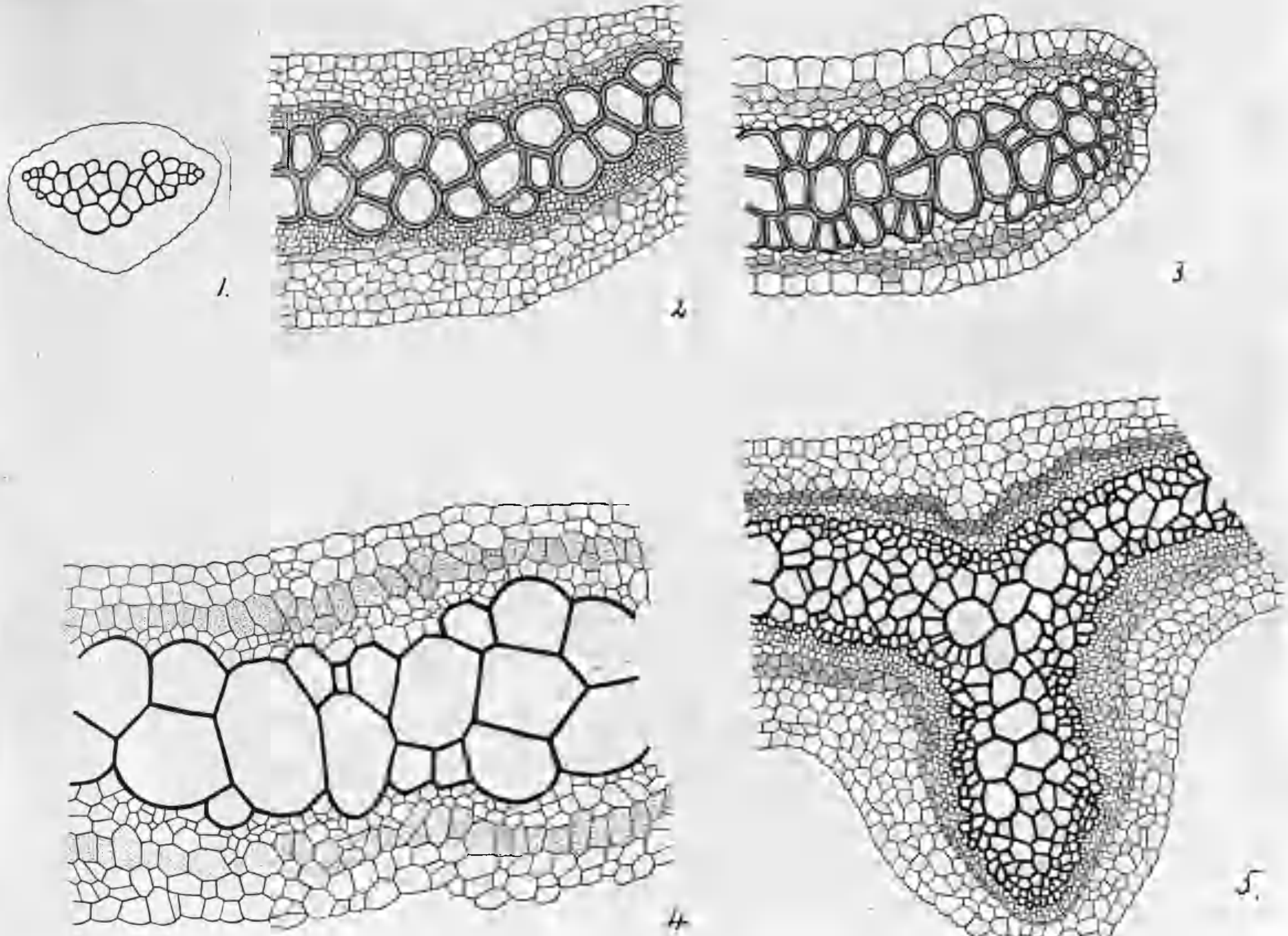
Fig.6. Detailed structure of steles.

1, 2, S.cuspidata, var. elongata, 1, small stele from the thin basal region of the shoot. 2, portion of stele from a thick stem.

3, S.Martensii, 4, S.Willdenowii, 5, S.Braunii, from a stout erect stem. The xylem has a prominent ventral ridge.

(phloem stippled) (X 235)

In all cases the arrangement of the xylem is such as to provide a large surface of contact with the adjoining thin-walled tissues.


1.
2.
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of the vascular system is definitely related to the surroundings, and in a recent paper Uphof (25) notes that the elements of the xylem in <u>Selaginella</u> are much wider in mesophytes than in xerophytes, because of the greater transpiration in the former. Extreme xerophytes such as <u>S. sanguinolenta</u> have extremely small tracheides indeed. He also notes that xerophytic species grown in a moist atmosphere show an increase in the amount of protoxylem and metaxylem, and larger tracheidal cavities.

It has been suggested in certain of the Ferns where the xylem is present in bulky homogeneous masses that there is a tendency for the liquids in the more central tracheides to stagnate, a condition which has probably led to the formation of "mixed pith". In passing it may be noted that the distribution of the xylem in <u>Selaginella</u> is such as to avoid physiological difficulties of this kind.

In <u>Selaginella</u> the thickness of the xylem band varies in different parts of the same plant. The thickness at any one point is very largely determined by the size of the individual tracheides present, and this is closely correlated with the associated physiological conditions and requirements. In all cases, however, a large proportion of surface to bulk is an advantage, and this is generally achieved by the arrangement of the xylem in the form of a thin ribbon. This is illustrated by the detailed drawings in Fig. 6.

2. It has been shown that in the course of ontogenetic development the stele in <u>Selaginella</u>, at first approximately cylindrical, develops strongly in one plane only, so forming a thin ribbon whose width increases, but whose thickness remains more or less constant.

The disposal of a large amount of vascular tissue in this way would result in the formation of a wide stelar band, and if the form and distribution of the latter were not modified in any way its width would approximate to the diameter of the stem itself, and in some cases would increase considerably beyond this. But as a matter of fact in the actual plant this does not happen. It will be shown that a fairly constant relation exists between the position and width of the stelar ribbon and the outline of the stem. In those cases where the amount of conducting tissue is large, if the xylem continue to be disposed in the form of a thin band, some modification in the form and disposal of this band will be necessary in order to meet the difficulties resulting from increase in size. In Selaginella the modifications in form due to the incidence of the size factor may differ in degree and in kind. The result is seen in various types of polystelic and solenostelic structures.

MEASUREMENTS.

In Table I the ratios of stele to stem in several species of Selaginella are set forth. Most of these are based on personal observation, and were obtained in the following way. In each case sections were cut from rhizomes, shoots and branches at various intervals, the sections in all cases being taken midway between the departure of two branches. In this way the stelar complications in relation to branching were avoided.

In each section the diameter of the stem and the width of the stelar ribbon were measured under a magnification of 44 diameters. The diameter here refers to that axis of the stem which lies in the same plane as the stelar ribbon. As a rule this the major axis in both. These /

Table I. Relation between length of Stelar ribbon and diameter of Stem.

I Species.	II Part of Plant.	III Diameter of Stem. mm.	IV Width of Median Stele in mm.	V. Total Width of Stelar ribbons in mm.	VI Ratio:- Median stele : Stem (Stem=1)	VII Ratio:- Total stele : Stem (Stem=1)	VIII Nature of Vascular System.
S. cuspidata, var elongata	Base of Shoot, near spore	·41	·16	—	·39	—	Single stelar ribbon
do	From Shoot.	1·36	·52	—	·38	—	do.
do	Thickest part of Shoot.	2·14	·84	—	·39	—	do.
do.	Thin distal branch.	·66	·25	—	·38	—	do.
S. grandis.	Base of Shoot.	1·27	·36	—	·28	—	Single stelar ribbon.
do	Thickest part of shoot.	4·80	1·02	—	·21	—	do.
S. Martensii.	Base of Shoot.	·93	·25	—	·24	—	Single stelar ribbon.
do.	Thickest part of Shoot.	1·45	·34	—	·19	—	do.
do.	Distal branch.	1·00	·19	—	·19	—	do.
S. Rassellata.	Base of Shoot.	·93	·25	—	·24	—	Single stelar ribbon
do	Thickest part of Shoot.	3·41	·93	—	·27	—	do.
S. Caulescens	From stout Shoot	1·30	·57	—	·44	—	Single stelar ribbon.
S. uncinata.	do.	1·09	·36	—	·33	—	Stelar ribbon with ventral xylem cord.
S. atroviridis.	do.	—	—	—	·30	—	Single stelar ribbon
S. plumosa.	do.	—	—	—	·24	—	do.
S. pilifera.	do.	—	—	—	·33	—	do.
S. involvens	do.	—	—	—	·30	—	do.
S. Volgelii.	do.	—	—	—	·44	—	do.
S. erythropus.	do.	—	—	—	·44	—	do.
S. Oregana. after Harvey Gibson	do.	·53	·15	—	·28	—	do.
S. Willdenowii.	Base of Shoot.	1·98	·45	·45	·38	·38	Single stelar ribbon.
do	Near base of Shoot.	1·80	·84	1·40	·47	·48	Three stelar ribbons
do	Successively higher up in same Shoot.	2·43	1·14	2·32	·47	·95	Three stelar ribbons
do		3·20	1·52	4·18	·47	1·31	Four stelar ribbons, the dorsal with 2 xylem bands
do	Through apical bud.	2·09	·95	3·43	·45	1·64	Two xylem bands.
do	Thin distal branch.	1·11	·50	·44	·45	0·69	Three stelar ribbons
do	Thick Shoot.	4·00	2·00.	6·41	·50	1·60	Two stelar ribbons
S. Lobbii.	Base of Shoot.	1·25	·27	·27	·22	·22	Single stelar ribbon.
do.	Thickest part of Shoot.	1·90	·43	1·40	·38	·90	Two stelar ribbons.
S. inaequalifolia. (from Harvey Gibson)	From Shoot.	1·00	·44	1·61	·44	1·61	Two stelar ribbons
do. from Sachs.	From Shoot.	·50	·19	·39	·38	·48	Three stelar ribbons.
S. Wallichii.	Base of Shoot.	1·36	·34	·34	·25	·25	Single stelar ribbon
do.	Near base of Shoot	1·20	·34	·61	·28	·51	Three stelar ribbons
do.	Thickest part of Shoot.	3·64	·80	1·40	·22	·47	Three stelar ribbons
S. Braunii.	Basal region of rhizome	1·00	·36	·36	·36	·36	Single stelar ribbon with ventral cord.
do.	From thin rhizome	·95	·39	·55	·41	·58	Two stelar ribbons.
do.	From thick rhizome	1·93	·91	1·50	·47	·44	Two stelar ribbons
do.	From erect stem	1·60	·90	1·04	·56	·64	Single stelar ribbon, with prominent ventral ridge.

These measurements are stated in Columns III and IV By dividing the figures in Col. IV by those in Col. III the ratio of the width of the stelar ribbon to the diameter of the stem is obtained for each section. These ratios are stated in Col. VI, the diameter of the stem being stated as unity in each case. In the polystelic species the width of the median stele is stated in Col. IV, and the ratio stele:stem in Col. VI. The combined width of all the steles in the polystelic species is given in Col. V, and the ratio of this width to the diameter of the stem is shown in Col. VII. As the figures in Col. V are intended to show what the width of the stelar ribbon would be if ~~they~~ all the steles were formed into one broad band, this measurement was obtained by taking the width of the median stele and adding to it the width of the xylem bands in the other steles.

DISCUSSION OF MEASUREMENTS.

In the monostelic species examined the ratio of stele to stem varies from .2:1 to .45:1. In some of these species by analysing the stelar system of a whole plant, it was found that the ratio stele:stem was remarkably constant throughout the plant. An abstract of some of these ratios is stated in Table I. The ratios given for other species are averages of many measurements. The important deduction from these observations is that among all the monostelic species examined, where the vascular tissue is disposed in the form of a thin band, the ratio of stele to stem does not in any case exceed .45:1.

But in the case of the polystelic species an entirely different state of affairs is found. The corresponding measurements are stated in the lower part of Table I. In the case of S. Willdenowii the figures show that the width of the main stelar band bears a definite relation to the diameter of the stem. This ratio stele :stem is not exceeded, the extra vascular tissue being disposed in the form of additional stelar ribbons. The combined width of the ribbons placed margin to margin would approximate to the diameter of the shoot in the thin basal region, and would increase beyond this very considerably in the thickest part of the shoot. Six measurements for S. Willdenowii show that the ratio of the median stele to the stem is constant at .46:1 (approx.). As the amount of vascular tissue is augmented the median stele does not exceed this limit, the additional conducting tissue being disposed as dorsal and ventral bands. The behaviour of the latter is significant. They are at first narrow ribbons, but with increase in size they ~~broaden out~~ widen out, but only to a certain width, after which they in turn give rise to other parallel stelar ribbons. These changes are illustrated for a single plant in Fig. 2. In the largest section it was found that the combined widths of the five cords was 1.64 times the diameter of the stem. This striking example would suggest that the multiplicity of xylem bands in polystelic species is very closely correlated with the actual size of the stelar ribbon to be accommodated within a definite ~~area~~ space. In the monostelic species on the other hand, where the amount of vascular tissue is relatively small, it has been shown that the ratio of stele to stem is usually less than .45:1 (except at the time of branching), and in these cases there is only a single stelar ribbon.

Similar measurements for other polystelic species point to the same general conclusion. S. Lobbii has five stelar ribbons in the thickest part of the shoot whose combined width approximates to the diameter of the stem. Similarly Harvey Gibson's figure of a thick stem of S.inaequalifolia shows five stelar ribbons whose combined width placed margin to margin would be 1.61 times the diameter of the stem. It is clear in this case that a ribbon of this breadth could not possibly be accommodated across the diameter of the stem, and the fact that the stelar cords show a tendency to widen out and not to thicken gives point to the physiological argument already advanced.

The occurrence of two stelar ribbons in the creeping rhizome of S.Braunii is in keeping with the ratio which their combined widths bear to the diameter of the stem, i.e., .77:1, the ratio of the median stele to the stem being .47:1. In the erect stem, however, there is only one stelar band which bears to the diameter of the stem the ratio .56:1. This ratio is already considerably higher than what is found in most monostelic species, and it is significant that in the stout erect stems of S.Braunii there is a strongly developed ridge of xylem on the ventral side which prevents the ratio from becoming still higher, i.e., .67:1. At the same time the characteristic thickness of the xylem is maintained. In most species such ventral ridges appear at the time of branching, but examination of S.Braunii showed that the ventral ridge was not in relation to the departure of a branch stele, since other ventral ridges were found to occur at the time of branching.

S.uncinata may be taken as a case in which the stele has only gone through the first stages in the transition to polystely under the influence of the size factor.

The progressive disintegration of the stele with increase in size has been demonstrated for a number of species. If these changes are due to the incidence of causal factors it might be

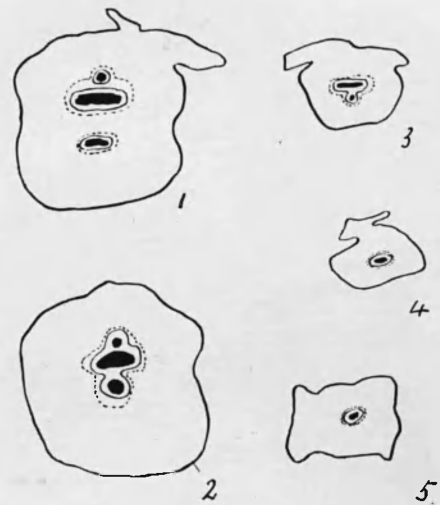


Fig.7. S. Wallichii, 1 -5, series of sections showing the fusion of steles as the cone is approached. 1, tristelic condition in stem below the cone. 2, 3, fusion together of steles. 4, at base of cone. 5, section through the cone showing the small stele.
This series illustrates the decrease in size accompanied by a decrease in complexity. (x 22)

expected that the converse would hold good. As a matter of fact this is found to be the case. When the strobilus is approached there is a decrease in the diameter of the shoot, and in polystelic species such as S.Willdenowii, S.Wallichii and S.inaequalifolia the steles decrease in size and fuse together, so that in the cone there is a single stele with a small core of xylem and marginal protoxylem. Miss Mitchell (18) has described the anatomy of the cone in a number of the polystelic species and has demonstrated the progressive fusion of the steles which accompanies the decrease in size as the cone is approached. Fig.7 illustrates this point for S.Wallichii, the details for other species being very similar.

SELAGINELLA LAEVIGATA.var.LYALLII

(a). The rhizome.

In the species of Selaginella dealt with up to this point the vascular system has been in the form of a thin ribbon, or a number of thin ribbons. In the very interesting species S.laevigata, Baker, var.Lyallii, Spr. (Baker's Handbook, No.251 (1)), and S.uliginosa, however, the vascular system of the horizontally growing rhizome is a solenostele. The anatomy of the former has been dealt with by Harvey Gibson (15) and Bruchmann (4), and of the latter by Dangeard (10) Osborn (19) and Miss Steel (21). In transverse section the xylem is disposed in the form of a thin ring, one two or three tracheides in thickness, surrounded by parenchyma and phloem on both sides. There is an internal and external endodermis, a small pith, and an insignificant lacuna. As the stele enlarges the xylem ring retains its characteristic thickness and a ridge of xylem

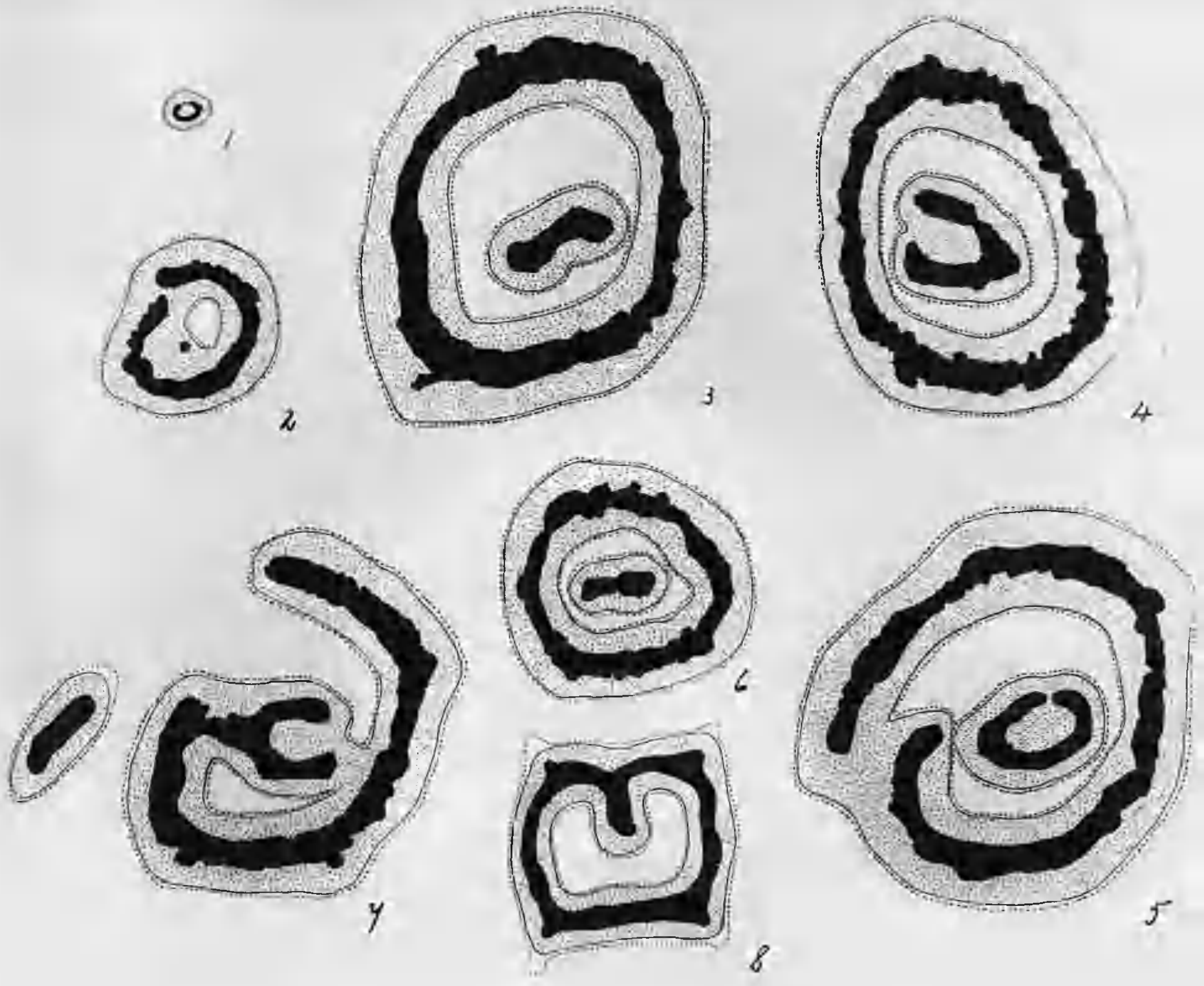


Fig.8. Steles from the rhizome of S.Lyallii.

1, monostele from very young rhizome, consisting of a ring of tracheides with internal and external phloem.
2 -7, series of sections from the proximal to the distal end of one rhizome showing the changes in complexity which accompany changes in size.
8, section from another rhizome, showing the way in which the inner stele is formed. x 55.

(xylem black; phloem, parenchyma, and pericycle stippled; unbroken line represents the limit of the stele, and the broken line the position of the endodermis.)

appears on the inner side. This enlarges and passes off from the main stele and a central cord is thus formed. The behaviour of this inner strand with increase in size is characteristic. It widens out forming a thin ribbon, and with further increase in size the latter bends round and becomes U-shaped. Finally in large steles this inner ring is completed, so that the vascular system is polycyclic and reminds one of the very similar developmental sequence in the stele of Matonia pectinata; Tansley and Lulham (22).

7? See below!

The sections in Fig. 8, 2-8, are from a single rhizome of S. Lyallii, No. 2 from the basal or proximal end, No. 8 from the distal end, and the others from intermediate points. No. 2 shows the typical solenostelic structure, the xylem being represented in black, phloem and parenchyma stippled, and the endodermis by a broken lime. In section No. 3 the amount of vascular tissue has increased considerably, and an inner cord surrounded by an endodermis has been formed. In No. 4, with further increases in size, the inner stele has become U-shaped, and in No. 5 the xylem ring of the inner stele is almost complete. After this there was a diminution in the size of the stele and a return to the simpler construction in No. 6, followed by a widening out again in section No. 7, where the inner stele again becomes prominent. No. 8, from another plant shows the way in which the inner stele arises, and No. 1 shows the small monostele found in young plants. The rhizome of S. Lyallii thus provides another case where changes in structure are closely related to actual size.

Measurements show that a fairly constant relation exists between the diameter of the stele and that of the stem. The average ratio of stele to stem is .28:1, the ratio being slightly higher in larger steles and lower in smaller ones.. This tendency on the part of the vascular system to occupy a central position in the stem has been remarked in the case of other polystelic species. In *S. Lyallii* when the stele is of large size the ratio of stem to stele is kept within limits by the formation of an inner vascular cylinder. In the rhizome of *Matonia pectinata* two or more concentric inner cylinders may be formed when the stele is of large size. In a large stem of *Matonia pectinata* with three vascular rings measurements showed that if all the vascular tissue had been disposed in one single ring of the characteristic thickness, the diameter of this ring would have been equal to the diameter of the stem itself. Data of this kind indicate the significance of the size factor. The occurrence of solenostely in *Selaginella* has led to a considerable amount of discussion particularly from the comparative and phyletic point of view, but it still remains an open question how far one can examine such material from the standpoint of causal morphology. This will be discussed at a later point.

Despite the very considerable differences between the solenostele of *S. Lyallii* and the ribbon-shaped steles of other species, from the viewpoint of the present discussion they have several features in common, viz., (1) the xylem is in the form of a thin band (2) the vascular system occupies a central position surrounded by a large cortex, and (3) with increase in size accessory steles are formed.

The rhizome of *S. uliginosa* is also solenostelic, (Fig. 9 and 10) and shows the same general characters as the stele of *S. Lyallii*, but here the vascular system is small in relation to the xerophytic mode of life, and there is only a single vascular cylinder.

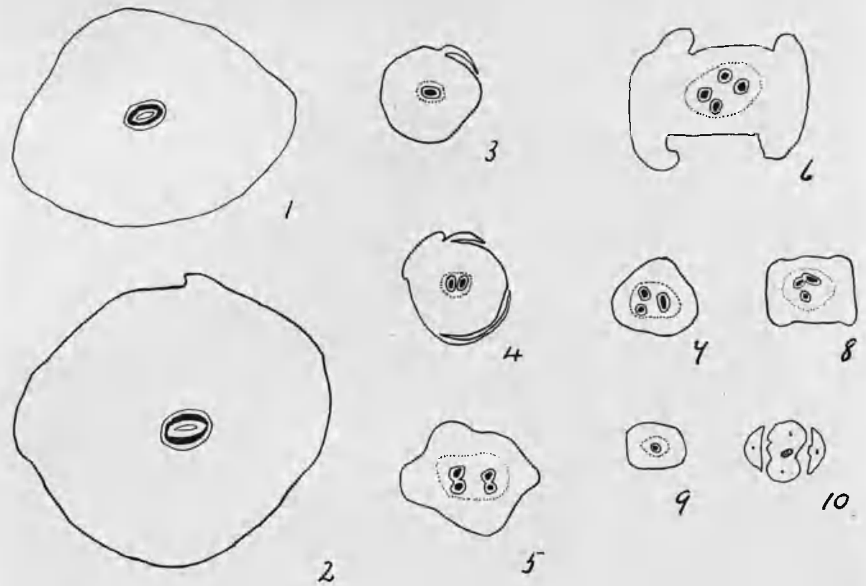


Fig. 9. S. uliginosa, 1, 2, thin and thick rhizomes showing the small solenostele. 3, base of the erect stem with a single stele. 4, 5, 6, sections successively higher up in the erect stem showing the formation of four separate steles. 7 - 10, fusion together of steles as the apex of the shoot is approached. Changes in the nature of the vascular system take place both with increase and decrease in size. X 22

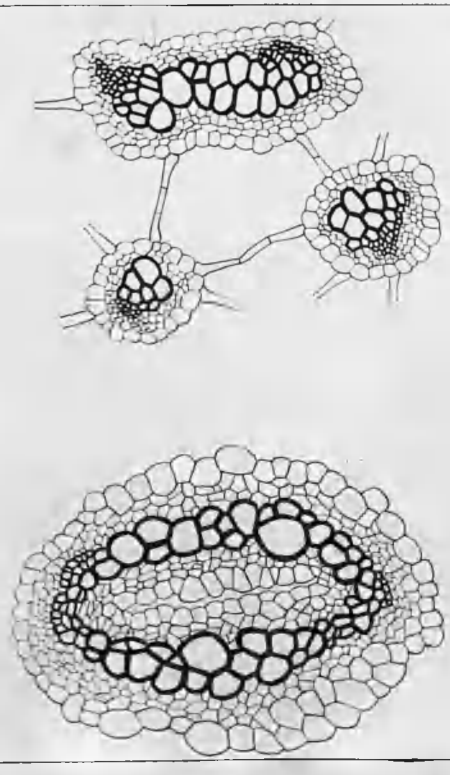


Fig. 10. S. uliginosa, distribution of the tissues in the steles of the erect stem and of the rhizome. (X 235)

(b). The erect stem.

In the erect stems of S. Lyallii, which arise from the creeping rhizome, an entirely different arrangement of the vascular system is found. The branch stele passes off from the solenostele as a U-shaped strand and this very quickly breaks up into a number of small separate steles. As we pass upwards in the shoot these increase in size and give rise to additional steles of characteristic size and structure. Their number is variable, sometimes six, ten, twelve and even up to sixteen. The number is not associated with the ultimate branching of the erect shoot since a decrease in size and consequent fusion together of the steles may take place ~~before any~~ before any branches pass off. As the distal region of the shoot is approached the separate steles decrease in size and fuse together till finally in the thin distal branch a cross section shows only two steles.

A series of sections from the base to the apex of a single stem is shown in Fig. 11; these show the departure of the U-shaped strand, its disintegration into several small steles, the increase in the number of the latter up to 14, and finally the decrease in size and number as the apex of the shoot is approached. The relation between the number of strands and their collective cross-sectional area is set forth in Table II. The measurements show that a very close relation exists between the number of steles and their actual bulk as measured by cross-sectional area, section 7 with 14 separate steles having the greatest total area of conducting tissue in transverse section. Only four of the steles receive leaftraces. These are placed in the stem so as to occupy the four corners of a square, and as a rule all the accessory

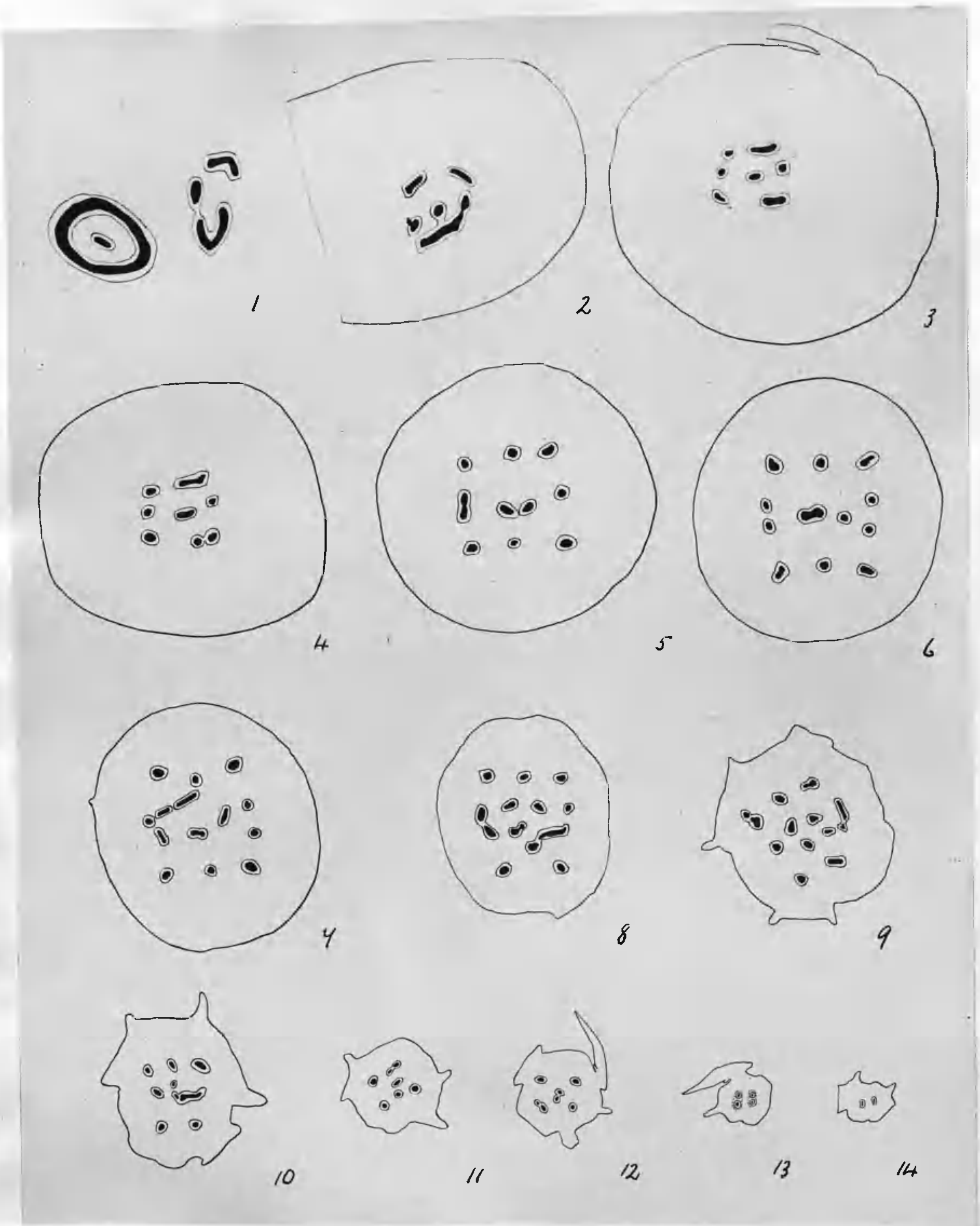


Fig. 11. S.Lyallii. 1 -14, series of sections from the base to the distal region of an erect stem, showing an increase in the number of steles up to section7, and thereafter a decrease down to two , No.14, in the distal branch. 1, shows the departure of the branch stele from the solenostele. X 22

Table II.

Selaginella Lyallii, Erect Stem.

Number of Section	Diameter of Stem in mm.	Collective Cross-sectional area of Steles in sq. cm. (x 44).	Number of Steles.
1	—	—	2
2	—	—	4
3	2.5	2.31	6
4	2.4	2.38	8
5	2.4	3.59	10
6	2.4	3.62	12
7	2.1	4.17	14
8	1.7	3.41	12
9	1.5	2.50	11
10	1.3	1.80	8
11	.8	.77	6
12	.7	.61	5
13	.5	.24	4
14	.4	.12	2

* The actual cross-sectional areas will be obtained by dividing the figures in the third column by 44^2.

strands lie within the region between these steles, so that the whole vascular system thus occupies a fairly central position. De Bary(11) refers to the shoots of <u>S. Lyallii</u> as having " ten or twelve bundles distributed in three equidistant rows in an almost quadratic surface", and Harvey Gibson(15) has described the unbranched portion of the ~~root~~ erect shoot as having four primary steles and several accessory steles. With respect to the latter he says :- " after examining several shoots I found so much variation in the branching of the accessory steles, that I felt that the number and order of these could not be of fundamental importance." It is reasonable to suggest that this variability in the number of accessory steles is related to some variable factor. What other factors are present leading to the formation of a large number of small steles is not at present clear. We do observe, however, that they are of characteristic size, which may be related to the physiology of these particular conduits. A similar and parallel increase in the number of accessory conducting conducting strands has been observed by Salisbury(20) in the petioles of <u>Polygonum</u>. In both cases with the formation of additional conducting tissue the existing bundles do not increase indefinitely in size, but show a tendency to disintegrate into bundles of more or less average size. The fact that the number of steles is not definite, but is very closely correlated with the total bulk of the conducting tissue, and further that this applies both to increase and decrease in size, all point to the probability that one of the determining factors is actual size.. In the cone where the vascular system is very minute ~~threr~~ there are two very small strands joined together by their pericycles (see Miss Mitchell), and in some very small shoots which I examined ~~threr~~ there were only two steles.

In the erect shoots of S. uliginosa the vascular system is somewhat similar. At the base of the shoot there is a single strand, which divides into two and then into three or four in the thickest part of the shoot, and these fuse together again into one single strand as the apex of the shoot is approached. In this case it is rather curious that all the steles should lie within the same lacuna. The more xerophytic nature of S. uliginosa compared with S. Lyallii is reflected in the reduced nature of its vascular system both in the rhizome and erect stem. Fig. 9, 10.

THE STELAR LACUNA.

The measurements for S. Wallichii, (Table I), show that the ratio of the total stelar ribbon to the diameter of the stem in a large tristelic stem, is small, only .47:1. This would seem at first sight to invalidate the explanation of polystely with reference to size, since some of the monostelic species such as S. caulescens, S. erythropus, etc., have a single stelar ribbon which bears to the diameter of the stem the ratio .45:1. This led to an investigation of the development of the large stelar lacunae which are found in some species. In S. Wallichii it was observed that while the stelar ribbons were relatively narrow, the lacunae in which they were suspended were much broader, so that their combined breadth was almost equal to the diameter of the stem. The combined breadth of the three stelar ribbons, on the other hand, was only about half the diameter of the stem. In order to trace this divergence between the width of the stelar ribbons and of their respective lacunae a bulky apical bud was selected, through which a series of transverse sections was cut from the apex backwards into the older part of the stem. The illustrations in Fig.12 , I- IV, were drawn to scale from such a series and they show the respective developments of the stem, the steles, and of the lacunae, as differentiation and expansion of tissues take place. Near the apex., (Fig.12, I,) the three steles are seen in meristematic form. All the cells are exceedingly small, and there are no lacunae , the stelar tissue being continuous with the cortex. A little lower down, as further differentiation proceeds, the pericyclic layer divides tangentially, the outer layer as described by Treub (24) Vladescu(26) and Harvey Gibson (15) being that which will develop into the endodermis, and the inner that which will form the pericycle or limiting layer of the stele. Shortly after this the stelar lacunae become visible, Fig.12, II, where the periphery of the lacunae is shown by a broken line. At this point the cortical cells ~~and those~~ next the endodermis are of the same average size as the cells of the pericycle, but as the tissues continue to develop and expand, the cortical cells enlarge more rapidly and to a greater extent than do the cells of the stele. The general result of these changes is an increase in the diameter and bulk of the stem. A particular result is the development of the stelar lacunae, since the expansion of all the cells round a lacuna leads to a proportional distension of the latter. The expansion of the stelar tissue, however, proceeds much more slowly, and to a lesser extent, so that in the adult condition we find small stelar ribbons suspended by means of drawn out trabecular endodermal cells, in relatively large lacunae. In dorsiventral species there is a greater proportional increase in the width than in the thickness of the stelar

Fig.12, S.Wallichii, series of sections through the apex, to sh the development of the cortex, the steles and the lacunae.

1, section through extreme apex: tissues just differentiated.

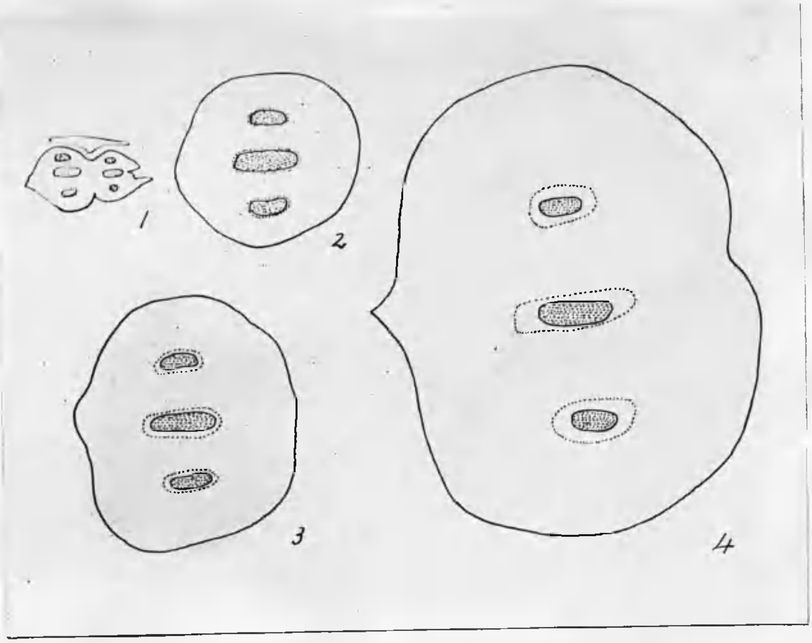
2, lower down than No.1, showing the first appearance of the lacunae.

3, 4, successively lower down, showing the distension of the lacunae. The steles remain practically unaltered in size. X22

Fig.13. S.spinosa, These figures illustrate the development of the lacuna in a radial species.

1, through the extreme apex showing the first appearance of the lacuna.

2 -5, sections successively lower down, showing that the stele does not increase much in size, whereas the cortex, and consequently the lacuna, become considerably distended. X55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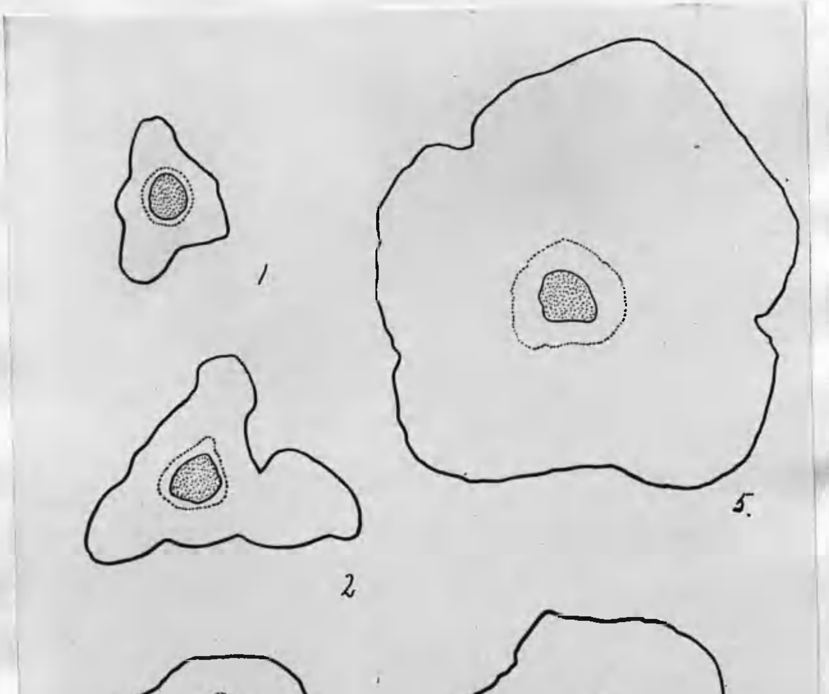
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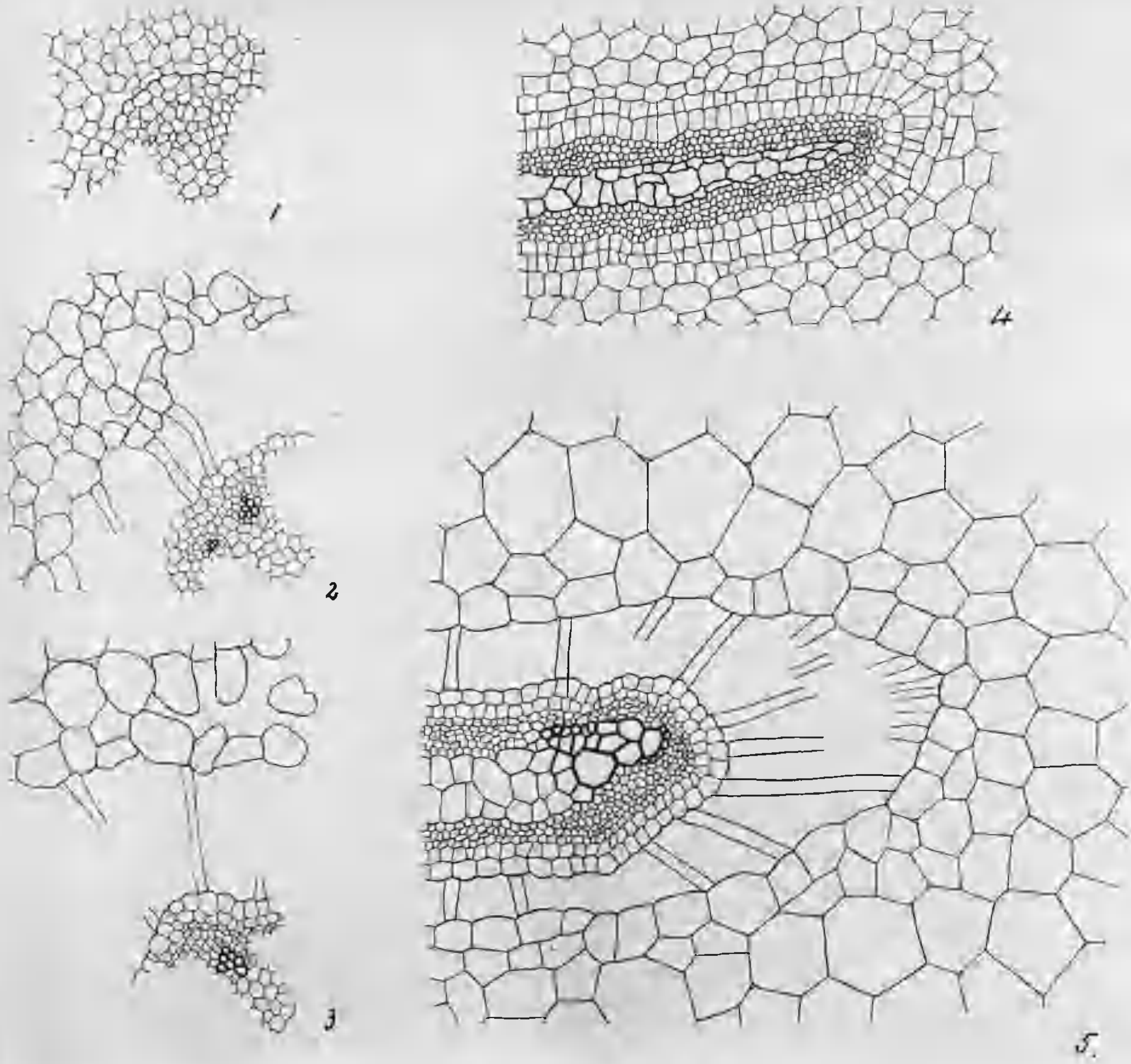


Fig.14. 1, 2, 3, S.spinosa: 4, 5, S.Wallichii.

S.spinosa, 1- section through apex, showing the first appearance of the lacuna. The cortical and stelar cells are of the same average size. 2, section taken lower down, showing the well developed lacuna. The cells of the cortex abutting on the ~~stele~~ lacuna are now much larger than the cells of the stele. 3, lacuna still larger, and disparity between size of cortical cells and stelar cells still greater. This section taken lower down than No. 2. (x 315)

S.Wallichii. 4- section through apex; lacuna just showing. 5, section a little lower down showing the well developed lacuna. Here the difference between the size of the cortical and stelar cells is well marked. (x 235)

Table III

Selagmella Wallichii. Relation between the Stele, lacuna & Stem.

No.	I Diameter of Stem in cm.	II Width of Median Stele in cm.	III Width of Median Lacuna in cm.	IV Ratio:– Stele : Stem. (Stem=1)	V Ratio:– Lacuna : Stem (Stem=1)	VI Total width of three Stelar ribbons in cm.	VII Ratio:– Total stelar ribbon : Stem (Stem=1)	VIII Part of Stem, and nature of the lacuna.
1.	1·4	·6	None	·43	—	—	—	Section through apex: Stelar tissue just differentiated: no lacuna.
2.	4·1	1·5	1·5	·34	·34	3·3	·80	Through apex, lower down than No. 1. First appearance of lacuna.
3.	5·0	1·5	1·9	·30	·38	3·4	·68	Through apex, lower down than No. 2. Lacuna more conspicuous.
4.	8·0	1·8	2·9	·23	·36	3·9	·49	One cm. below apex. Lacuna well developed.
5.	15·4	3·5	5·5	·22	·35	8·8	·56	Thick stem with large lacuna.
6.	9·1	2·1	3·3	·23	·36	4·5	·50	Stem of medium thickness: lacuna conspicuous.
7.	5·2	1·6	1·8	·31	·35	3·5	·64	Near base of stem: lacuna not conspicuous.

These measurements were obtained under a magnification of ~~44~~ diameters. The actual dimensions will be obtained by dividing the figures in Cols. I, II, III, VI by 44.

lacuna, because of the relative numbers of bordering cortical cells which take part in the expansion. In a radial species such as S.spinosa on the other hand, the circular stele is suspended in a large circular lacuna, Fig.13, as seen in transverse section.

The drawings in Fig.14, I – V, show the detailed structure in two instances, S.spinosa and S.Wallichii, and indicate the relative sizes of the stelar and cortical tissues before and after expansion. The measurements in Table III show the nature of the relationships between the stele and lacuna and the diameter of the stem, as development proceeds from the apical meristem where the tissues are first differentiated, to the final condition seen in the adult stem. The observations refer to the median stele of S.Wallichii. Three ratios are shown, (1) the ratio of the width ~~of the width~~ of the median stele to the diameter of the stem, (Col.IV, (2) the ratio of the width of the median lacuna to the diameter of the stem, Col.V, and (3) the ratio of the combined widths of the three stelar ribbons to the diameter of the stem, Col.VII. The measurements were taken under a magnification of 44 diameters, and are stated in cms.

Sections 1-4 refer to the four diagrams in Fig.12. As we proceed from the apex backwards the stem increases in diameter from 1.4 cms. to 8.0 cms. In section 2 the lacuna is just visible, and the figures for sections 2-3 and 4 show that while the stelar ~~ri~~ ribbon increases only slightly in breadth, the breadth of the stelar lacuna is almost doubled, i.e., from 1.5cms. to 2.9 cms. Before secondary expansions take place the ratio of the median stele to the stem is about .40:1. As the tissues expand, however, this ratio decreases, but the ratio of lacuna to stem on the other hand remains approximately constant. In thick stems, section 5, the ratio stele:stem /

stele:stem is low, while the ratio lacuna:stem remains approximately the same. The ratio of the total stelar ribbon to the stem likewise falls off in thick stems, .56:1 in section 5, but in the apical meristem where the tissues were differentiated this ratio is high, .80:1, and conforms to what was found in similar stems of *S. Willdenowii*. Similarly in section 5 the ratio of the combined widths of the three stelar lacunae to the diameter of the stem is .86:1, this being an approximation of the proportions of stele to stem as laid down at the time of formation. Thus in the adult stems of *S. Wallichii* and similar species, although the ratio of stele to stem does not bear out the thesis advanced, when we consider what the ratios were at the time when the tissues were differentiated in the apical meristem, we find that the results fall into line with the generalisation advanced for other polystelic species.

CHANGES IN THE APICAL MERISTEM.

The vascular tissues are continuous up into the apical meristem, so that a section through the apical bud shows the cortical and stelar tissues in meristematic form. In these Cryptogams the relative dimensions, and the structure and distribution of the vascular system are determined in the apex, the only secondary changes being the distension of tissues and the thickening of cell walls. Apart from these the arrangements laid down in the apex are those which will be found in the adult con-

~~dition of any partic~~

dition of any particular part. The development of the lacuna provides an example of change between the meristematic and adult condition.

In the individual development of a complex polystelic species such as S. Willdenowii all the changes in structure on passing from the monostelic to the polystelic state, and the converse as the cone is approached, take place in the soft tissue of the apical meristem. The question arises as to the nature of the causes or stimuli leading to these changes. " Possible influences" says Prof. Lang (14) " that have at various times been suggested are functional stimuli, the inductive influence of older preformed parts on the developing region, and formative stimuli of unknown nature proceeding from the developing region."

In the apex of Selaginella changes in the size of the vascular system are accompanied by structural changes, the latter being of such a nature as to make for the same general physiological conditions that obtain lower down in the older parts of the shoot. The significance of a large proportion of surface to bulk in the xylem has already been noted. In the stele of the sporeling this is provided automatically by the small bulk of the xylem. This proportion would decrease however, with increase in size, if the form of the xylem remained unaltered, but as a matter of fact with increase in size the changes in the structure of the xylem as initiated in the meristem are such as to maintain the large surface of interchange. Thus while the functional influence does not come into play at the time when the structure is being determined, it is possible that the inductive influence of the older parts may play a part in relation to these changes.

Whatever the factors are, the fact is that quantitative changes do take place in the apex and these are accompanied by modifications in form which tend to maintain the same general conditions.

Selaginella Lyallii.

S. LYALLII provides an interesting example of changes in the apex under the influence of other factors. Tansley (23) regards the polystelic state " as an elaboration of the simple stele to meet increasing complexity of the assimilating branch system, just as in the Ferns we find elaboration to meet increasing complexity of the frond, but carried out on totally different lines." p.135. He further remarks," In one species S. Lyallii, this rhizome actually possesses a typical Filicinean solenostele, the gaps in which are formed by the departure of aerial branch traces instead of leaf-traces:" On the other hand it has been suggested that the solenostely is in relation to the horizontal position of the rhizome (6).
A considerable amount of evidence is now to hand in support of the latter view.

Bruchmann (7) has shown that if twigs from an erect stem are placed on moist soil in a horizontal position the apex of the twig continues to grow and develops into a rhizome like shoot, and as this takes place the separate steles of the erect stem fuse together and form a monostele. With increase in size the latter becomes a typical solenostele.

Some very thin distal branches from material obtained from the Royal Botanic Gardens, Edinburgh, were placed on moist soil under a bell-jar. Some time after apical growth was continued, but the resulting stem was rhizomatous in character. From this small rhiz-

~~ome roots~~

Fig.15. Young plants of *S.Lyallii*, resulting from the continued growth of distal branches of the erect stem laid in a horizontal position.The larger leaves indicate the distal branches.

1, young plant showing a root and two erect branches.

2, another plant slightly older.

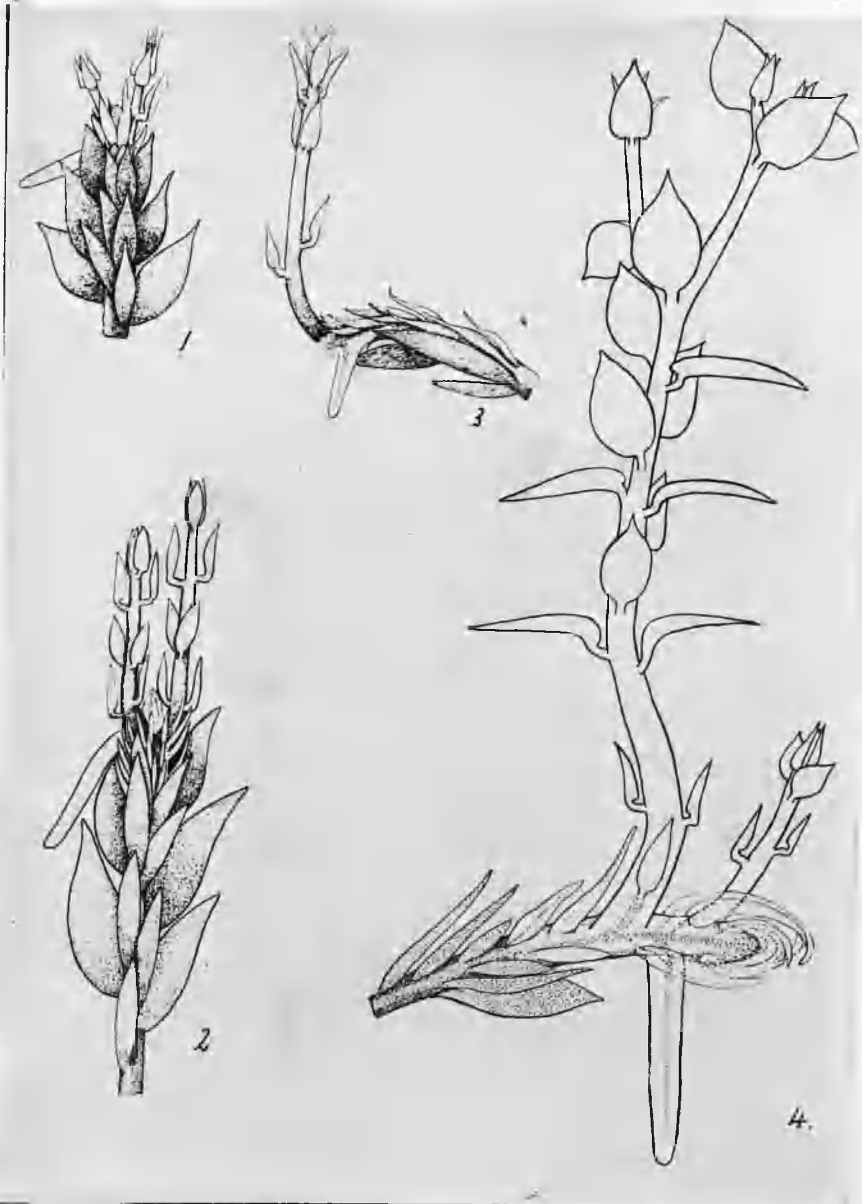
3, young plant.This specimen shows that the apex of the twig has continued growth and developed as a rhizome, from which roots and erect shoots arise.

4, an older plant.The rhizome is now quite definitely formed. (x 6).

Fig.16. *S.Lyallii*, series of sections froma young plant like those in Fig.15, showing the change in the nature of the vascular system from that of an erect stem to that of a rhizome.

1, 2, fusion of the two steles of the twig.

3, 4, rearrangement of the xylem to form a ring, with central and peripheral phloem and parenchyma. (x 315)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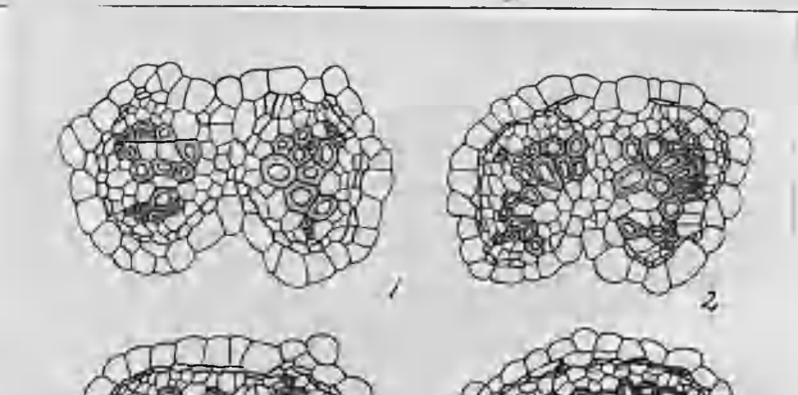
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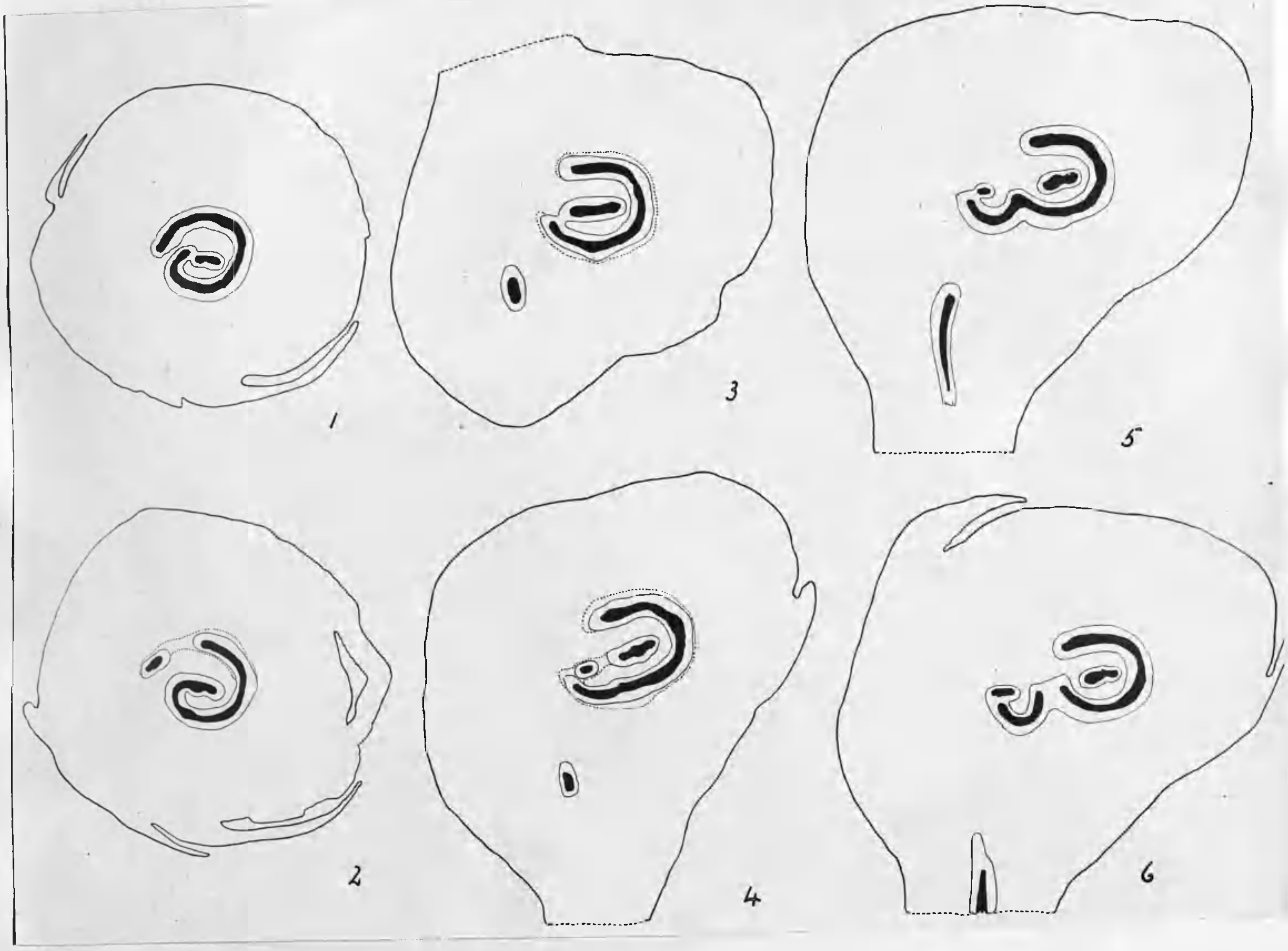
ome roots and erect aerial shoots were formed. Some of the young plant obtained in this way are shown in Fig.15. Changes in internal struc= ture accompanied these changes in external form. The distal branches in S.Lyallii have usually two small steles, and it was observed that as the change towards the rhizomatous condition took place the two strands coalesced, so that all the vascular tissue was encased within one pericycle. Each of the separate steles consisted of a central mass of xylem surrounded by parenchyma and phloem. As the fusion of the steles took place the two xylem strands joined up, and then became rearranged into a ring whose centre was occupied by parenchyma and a little phloem. On the outside the xylem ~~the xylem~~ was surrounded by parenchyma, phloem and pericycle, Fig.16. This monostele expands and develops into a typical solenostele. This may be regarded as a case in which the behaviour of the apex has been modified under the influence of change in position.

As a rule the branches of the rhizome grow upwards and assume an erect position, and the vascular system becomes polystelic with ten to fifteen separate steles. In some material of S.Lyallii from the Royal Botanic Gardens, Edinburgh, however, it was observed that some of the branches did not develop in the usual way. They had commenced development as erect shoots but had remained in a horizontal position and had become typical rhizomes, from which roots and erect shoots grew out. By means of a series of transverse sections the vascular system of such a branch was traced from the point of ~~origin~~ departure from the main rhizome to the point where the branch had become definitely rhizomatous. This series is shown in Fig.17. The branch stele arises from the solenostele as a U-shaped

Fig. 17. Selaginella Lyallii. Series of sections showing the changes in the vascular system of a rhizomatous branch. 1, solenostele of the main rhizome with a central stele. 2, 3, interruption of the xylem ring by the departure of a root stele. 4, 5, 6, root trace passing out through the cortex, and origin of the branch trace from the solenostele with the formation of a ramular gap. 7, separation of branch trace completed. 8, 9, 10, 11, 12, breaking up of the branch trace into many small steles. 13 - 18, fusion together of steles with the formation of a solenostele as the rhizomatous region of the branch is approached.

(x 16)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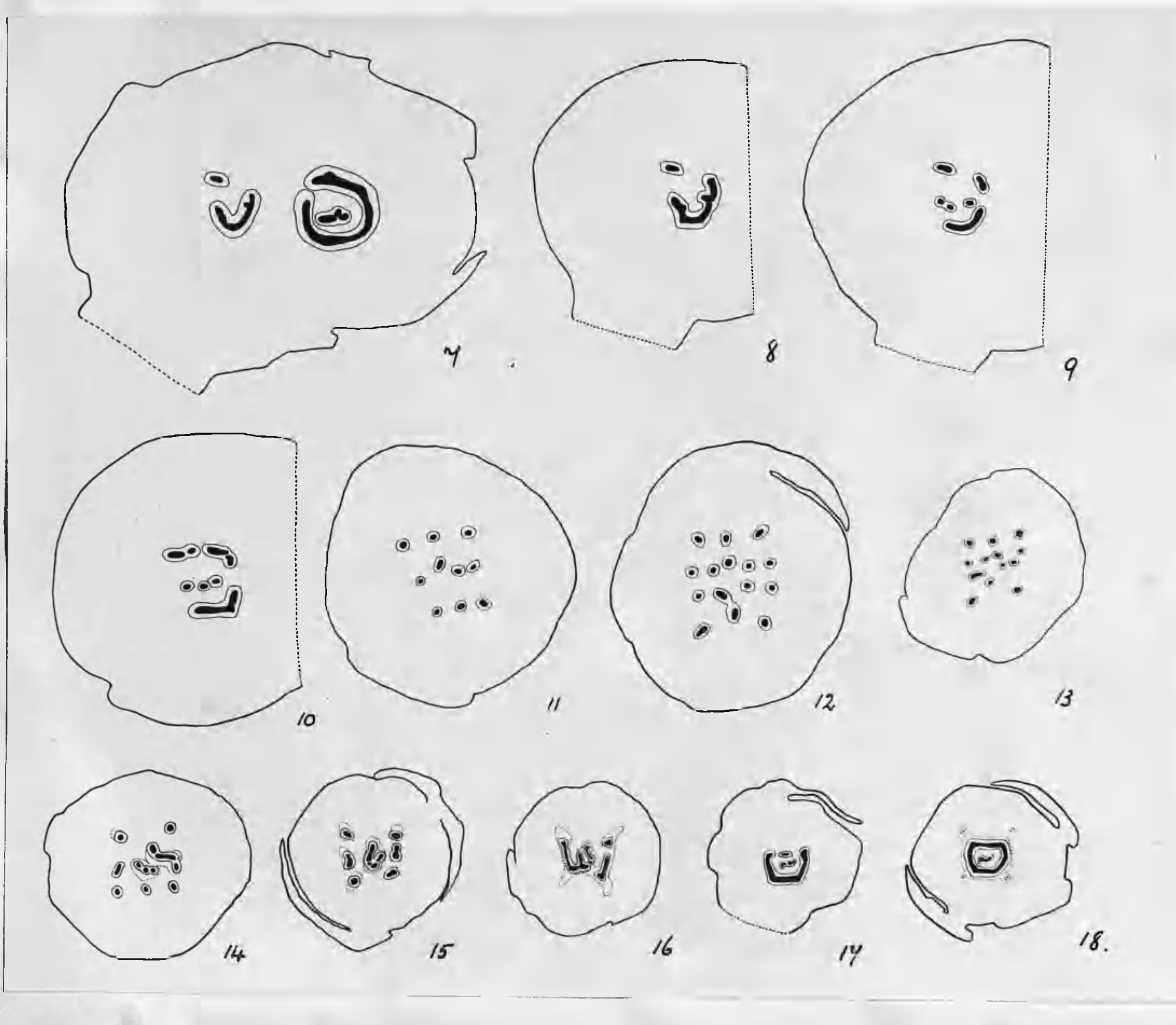
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strand ,and leaves a ramular gap in the solenostele. This U-shaped strand quickly divides up into a number of separate steles, thereby following the characteristic procedure observed in typical erect stems. Fifteen separate steles were observed at the point where the vascular system reached its maximum size. Further along the diameter of the stem decreased and was accompanied by a coalescence of the steles. As the rhizomatous distal region of the branch was approached the steles fused together in such a way as to form a solenostele with a central cord. This structure once formed was retained . Here again we have a definite structural change in the apex due to the influence of change in position. Several similar branches were examined and all showed the same general sequence. A short reference to this has been made by Prof.Lang, (14).

The outstanding fact from these two series of observations is that the solenostelic structure in this species may be arrived at in two entirely different ways, i.e., by the expansion of a monostele, and by a gamostely. In view of the plastic nature of the vascular arrangements in this species as shown by these observations, it would appear that the solenostele in this instance is referable to factors other than the insertion of the aerial branch system. Prof.Lang (17) has summarised the position as follows :-"This is so fundamentally different from the relation of the solenostelic and dictyostelic condition in ferns as to suggest that the homoplastic resemblance is here probably not a homology of organisation, but due to different factors." p.11.

The existance of such plasticity strengthens the argument for approaching these species from the standpoint of causal morphology.

SIZE A FACTOR IN STELAR MORPHOLOGY.

The detailed measurements and illustration set forth indicate that Size is a factor in the stelar morphology of Selaginella. It does not, however, act as an isolated cause, but interacts with other factors, so that the nature of the stele may be regarded as " the resultant of a number of factors." (7).

(1). The xylem is disposed in the form of a thin ribbon an arrangement which makes for a large surface of interchange with the adjacent living thin-walled tissues. When the stele increases in size the xylem band does not thicken but widens out so that the large surface of interchange is maintained.

(2). This widening of the stelar ribbon introduces another interacting factor, namely that which relates to the distribution and accommodation of the vascular system in the stem, so as to make for the greatest constructional stability. In those species where the width of the stelar ribbon is small compared with the diameter of the stem the difficulty of accommodating the vascular system does not arise, and in actual practice we find that these species are all monostelic. On the other hand, in those species where the stele is of relatively large size , and where the total width of the stele in relation to the diameter of the stem is ~~greatx~~ large , the problem of adequately disposing the stelar ribbon arises. It has been shown in these cases that if the monostelic condition were maintained the ribbon would extend right across the diameter of the stem, and considerably beyond this in thick stems. In actual practice, however, when the stelar ribbon is of such width it divides up into a median stele, and dorsal and

Ventral steles, and the latter behave in a similar manner with further increases in size. The constancy of the ratio width of median stele : diameter of stem in *S. Willdenowii* suggests that there is some other factor present which tends towards a central as against a peripheral disposal of the vascular system. A similar encroachment of the stele on the stem is avoided in the erect stems of *S. Braunii* by the formation of a ventral ridge. The size-factor is also seen at work in the solenostele of *S. Lyallii*. Here with increase in size an inner stelar ribbon appears, and in stout rhizomes the vascular system is polycyclic. In the erect stems of the same species changes in the nature of the vascular system are also found to accompany increase in size. These data suggest that actual size has been a factor in the initiation of polystely in *Selaginella*. Finally the converse is seen where a decrease in size takes place. In polystelic species as the cone is approached a fusion of steles takes place, so that in the axis of the cone there is only a single stele.

These considerations indicate that Size is one of the factors in determining the morphology of the vascular system of *Selaginella*.

DISCUSSION OF CAUSAL AND SYSTEMATIC VIEWS.

In this paper the structure of the vascular system has been discussed from the physiological and causal point of view. Explanations of this kind are open to objection on the ground that the influence of the ancestry of the plants has not received due consideration. In view of the present outlook on descent (5) it is a matter of considerable interest to compare the phyletic and causal outlook.

"If size acts as a limiting factor determining the confor-
" mation of the conducting tracts in an enlarging plant, how far
" can characters thus imposed by mere physical laws upon plants of
" distinct affinity be held as valid material for comparison as
" to descent, and ultimately for systematic arrangement? How far
" can polycycly in Ferns be used as a sign of affinity? Are changes
" in form to be held as anything else than a developmental re-
" sponse to the incidence of the limiting factor of Size? Is
" solenostely in Ferns or <u>S.Lyallii</u> anything more than a method
" similarly carried out of evading its ~~influence~~ incidence? Such
" questions as these impose increased caution in comparison, but
" they need not negative the use of such characters altogether." *

In <u>Selaginella</u> the radial type has been regarded as relatively primitive, while those species with dorsiventral shoots are more specialised and derivative (4). Harvey Gibson (15) has remarked on the disparity between the systematic classifications based mainly on external characters, and classification according to internal structure. In <u>TableIV</u> a brief précis of Baker's classification (1) has been made and a description of the vascular system in each case. We find the two known solenostelic species widely separated, the articulated bi-stelic species of the <u>Galeottei</u> type are not confined to one division, and <u>S.Willdenowii</u> and <u>S.Mettenii</u> are separated in different groups from the other polystelic species. Thus the stelar morphology does not always conform to the classification based on external form.

*. I am indebted to Prof. Bower for the use of this paragraph. It is an extract from an unpublished paper.

Table IV --- Systematic classification and the nature of the vascular system.

DIVISION after Baker	SPECIES	NATURE OF ~~STELE~~ Vascular System
I. Selaginella proper.	S. spinosa	Solid xylem with central protoxylem at base of shoot: peripheral protoxylem with central pith in upper part of shoot.
	S. Preissiana	Small stele almost radial, solid xylem core.
	S. uliginosa	Solenostele in rhizome: four steles in erect shoot.
	S. rupestris	Typical bandedstele.
	S. oregana	Banded stele.
	S. sanguinolenta	Banded stele.
II. Stachygynandrum.	S. delica~~t~~tissima	Two steles.
	S. Douglasii	Typical bandedstele.
1. Decumbentes.	S. uncinata	Banded stele with ventral cord.
	S. Bakeriana	Banded stele.
	S. Mettenii	Three stelar ribbons.
	S. atroviridis	Banded stele.
2. Ascendentes.	S. Martensii	Banded stele.
	S. rubella	Two steles.
	S. Galeott~~e~~i	Two steles.
3. Rosulatae	S. cuspidata.	Banded stele.
4. Sarmentosae.	S. Wallichii	Three stelar ribbons.
	S. gracilis	Three stelar ribbons.
	S. Lobbii	Three to five stelar ribbons.
	S. Victoriae	Three stelar ribbons.
	S. inaequalifolia	Three to five stelar ribbons.
	do. var. perelegans	Three stelar ribbons.
	S. canaliculata	Three stelar ribbons.
	S. viridangula	Three stelar ribbons.
5. Scandentes.	S. Willdenowii.	Three to five stelar ribbons.
6. Caulescentes	S. caulescens	Banded stele.
	S. Braunii	Two stelar ribbons in rhizone. banded stele with ventral cord in erect shoot.
	S. grandis	Banded stele.
	S. Volgelii	Banded stele.
	S. laevigata, v. Lyallii	Solenostele in rhizome; many small steles in the erect stem.
III. Homostachys.	....	....
IV. Heterostachys.	S. bisulcata	Banded stele.
	S. suberosa	Banded stele.
	S. stenophylla	Banded stele.

S.Lyallii has been regarded by some as probably a highly specialised and derivative type (4)(23), and by others as a primitive type showing features similar to those of some of the fossil members of the family(15). In the solenostelic species S.uliginosa whose vascular arrangements are very like those of S.Lyallii, Miss Steel (21) has collected a body of evidence which points to the primitive nature of this species, viz. radial symmetry, bulky apex, Selago condition in the strobilus, large number of microspores and four megaspores, indiscriminate arrangement of the mega- and micro- sporangia, and the nature of the leaves. From the comparative point of view on the other hand, the similarity of stelar development to that of the solenostele of the Fern might be held to favour the probability of its being an advanced type. But the evidence which has been advanced here in S.Lyallii would point to the conclusion that the solenostele in this case is probably the resultant of several factors, since it has been shown that the structure is in relation to the horizontal position, and further that it may be formed in two ways, namely, (1) by the expansion of a medullated monostele and (2) by the fusion of a number of separate steles, that is by gamostely.

With respect to the forms with banded steles we find that the majority conform to the Martensii type. These occur in all of Baker's subdivisions. The polystelic types such as S.inaequalifolia have been regarded as derivative types and have been placed by Harvey Gibson (15) as "representing the highest and most specialised development of the stem in the genus". But from the argument which has been advanced here, the main difference between the Martensii type and the Inaequalifolia type with respect to stelar structure is a a quantitative difference. The distribution of the stelar tissues is the same in both , they both provide the same physiological conditions, but in species such as S.Willdenowii and S.inaequalifolia etc., the vascular tissue is present in relatively large proportion, while in the Martensii type the proportion is small. If this large amount of vascular tissue has to be disposed in the form of a thin band, this will need to be broken up in order that it may be properly accommodated within the hard rind of the stem. If this is so, then it follows that polystely in these cases would not necessarily be a derivative condition in the phyletic sense, but would be a modification in form consequent on increase in size. Hence the isolated position of species which show solenostely or polystely in Baker's systematic arrangement of the genus need not be held as destructive of the validity of that classification.

In conclusion I wish to express my thanks to Dr.A.W.Hill, Royal Botanic Gardens, Kew, to Prof.Wright Smith, Royal Botanic Gardens, Edinburgh, and Mr.Banks, Glasgow Botanic Gardens, for material used in this investigation, and to Prof.Bower for material and for much helpful advice in preparing this paper.

The

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