II. *The Morphology and Anatomy of the Stem of the Genus Lycopodium.**By* CHARLES EDWARD JONES, *B.Sc., F.L.S.*

(Plates 3–5.)

Read 7th April, 1904.

THERE have been in the past very few original communications restricted to an investigation of the genus *Lycopodium*, although between the years 1846 and 1874 several papers were published which dealt with special features, mainly for the purpose of comparison with allied genera, and, as a result, a general but fragmentary conception of the structure of Lycopods has been evolved, the substance of which has been incorporated into text-books, and occasionally additions have been made when the writers have preferred to get the facts first-hand. An explanation of the development of the peculiar root-like structure and a comparative description including the anatomical features of exotic species have never been published, and it is with the intention of providing a fuller comparative account of the stem and its anatomy and with the object of elucidating the formation of what may become a very complex vascular arrangement that this investigation was undertaken.

Turning to the early literature concerned with *Lycopodium*, the paper written by Hegelmaier (5) in 1872 stands out pre-eminently as a carefully prepared and reliable comparative survey of the characters of the commonest species (*Lycopodium clavatum*, *annotinum*, *alpinum*, *inundatum*, and *Selago*). Before Hegelmaier, one or two well-known botanists had published results. In 1846 Nägeli (1) was already endeavouring to decipher the structure of the growing apices in plants, and for this purpose examined the apex of the stem of *Lycopodium clavatum*. In this paper he refuted the impression which then prevailed that the vascular portion consists of one bundle, and pointed out that the vascular cylinder consists of a number of vascular strands in accordance with the number of protoxylems. He observed that the leaf-traces and the protoxylems differentiate simultaneously, and therefore concluded, not without considering other possibilities, that each vascular strand passes off into a leaf-trace. Nägeli's paper (3) gives an account of the root-development, more especially of the branching of the root-system, for *L. clavatum*. There is a figure of a very definite apical cell and a detailed account of the formation of root-hairs, but no definite information about the connection of the vascular cylinder in the root with that of the stem. Cramer (2) examined the apex of *L. Selago* and studied more particularly the leaf-arrangement. He showed that there is considerable variation, that sometimes the leaves fall on a spiral—of which the commonest is 2/9—and sometimes they are arranged in whorls; also he found that there is no relation between the number of leaves and the number of protoxylems. Before

publishing an account of the structure of *Lycopodium* in his text-book, Sachs (4) made observations for himself, and even if he was not the first to recognise the phloem-nature of the elements lying between the xylem-bands, he cleared away the idea of cambium-layers which is found in previous writings, and further he called attention to the sieve-tubes which lie in the centre of the phloem-bands. Two important papers appeared in 1872, that by Hegelmaier (5), which has already been mentioned, and the account by Russow (6) in the 'Vergleichende Untersuchungen.' The former paper is the most complete original account of the morphology which has been written, but is confined almost entirely to five species; the latter is a brief but pithy summary of the chief facts which the author observed in what was presumably a limited examination undertaken in the course of extensive comparative investigations. Russow's account of the structure is not altogether accurate; the statement appears (p. 129) that "the phloem (Phloem-körper) surrounds the whole of the xylem and penetrates it by radiating extensions which fill up the spaces between the xylem-bands"; as he mentions later that the protophloems alternate with the protoxylems, and that the differentiation of both phloem and xylem proceeds centripetally, it is evident that the "Phloem-körper" includes the phloem-sheath, which at that time might have been regarded as part of the phloem. At the same time he does not distinguish between them, although he could not fail to have seen the well-known iodine reaction; again, the numbers which he states for the protoxylems of the species must have been based upon cursory examination. Otherwise he presents a remarkably correct account of the structure of the different cells, including protoxylems, phloem-elements, and cortex. Hegelmaier's contribution is not so vigorous as that of Russow, but his conclusions have for the most part stood the test of later investigations undertaken with improved apparatus. It will be sufficient here to mention the chief items which he discusses:—(1) The bilateral character of most of the stems and branches which he examined, as shown externally and internally: although the arrangement of parallel bands was found to lie approximately in a horizontal position, he rejected the idea that this is caused by a force acting vertically; (2) descriptions and figures of the general configurations of the vascular structure and the want of proportion between leaf-traces and protoxylems; (3) the structure of the apex, which he finds to be devoid of an apical cell, and the methods of differentiation of tissues proceeding from the apex; (4) the numbers, arrangement, and development of the leaves; (5) the methods of branching; (6) the formation of the sporangia, and, finally, an account of the bulbils of *L. Selago* and the mucilage-cavities of *L. inundatum*. In 'Die Coniferen und Gnetaceen' (7), which was also published in 1872, Strasburger gave an account of his examination of the apex of *L. Selago*, and concluded that in *Lycopodium* there is not a single apical cell as in Ferns, but that a single cell gives rise to periblem and dermatogen and one or two cells form the origin of the plerome, so that the apex of the stem in *Lycopodium* would be intermediate between the single apical cell on the one hand and the three more or less definite meristems on the other. In this paper the author also published a description of the bulbils of *L. Selago*, which did not agree with that given by Hegelmaier, but in the following year, having repeated his observations (8), he was able to confirm Hegelmaier's results. In the 'Histologische Beiträge' (10),

Strasburger has treated of one or two features in the structure of *Lycopodium*. He begins (p. 458) by noting the similarity between the structure of the vascular cylinder in *Lycopodium* and *Selaginella*, and says that the "central cylinder of a *Lycopodium* may be regarded phylogenetically as a union of steles (similar to that found in *Selaginella*) and as gamostelic." This was written at a time when Van Tieghem's stelar conceptions received general acceptance, but a similar view is put forward in the morphological portion of the 'Text-book of Botany.' From this view of the structure of the vascular cylinder in *Lycopodium* I entirely dissent, and an explanation is offered in the course of the paper of the development of the complex structure from a simple form found in the seedling, with which the union of schizosteles is quite incompatible.

It cannot be said that the account of *Lycopodium* (13) which appeared in Engler and Prantl's 'Pflanzenfamilien' has added much to our knowledge of the genus; the figures (p. 579) showing four very different configurations are instructive, but require some interpretation which is not given in the text. The paper on *L. clavatum* by David and Weber (11) did not add any new facts. Linsbauer's paper (12) is concerned mainly with details of histology. He separates the orthotropic forms from the plagiotropic, and suggests that in orthotropic species the vascular cylinder is comparatively small and the xylems are broken up; the last point is quite in agreement with the writer's conclusions. In the 'Annals of Botany' Mr. L. A. Boodle (14) described two species of *Lycopodium*: *L. volubile*, Frost, which belongs to the dimorphic group and is characterised by a very definite series of parallel bands of xylem and phloem; and *L. salakense*, Treub, in which the xylems and phloems are intermingled, presenting an appearance similar to that described for *L. cernuum* below.

It is convenient to begin the discussion of the morphological structure of the Lycopods by considering first the essential characters of a well-known species, and to proceed from this to a comparative description of other species. Since *Lycopodium clavatum* is generally taken as a type for the genus, the salient features of that species are briefly indicated.

LYCOPODIUM CLAVATUM, Linn.

A feature that characterises most of the temperate species of *Lycopodium* is the plagiotropic habit, and this tendency is well marked in the case of *L. clavatum*. The plant is found creeping along the ground, either on bare slopes or in grass, although its original habitat would probably be in woods or on the outskirts of woods, where by uprooting of the trees the plant would find the necessary condition for the burial of its spores. It is found growing with xerophytic plants, and shows a structure which is well adapted to unfavourable environment. The stem attains a considerable length, often a metre or more; it sends out branches every few centimetres and these show the same plagiotropic tendency. The end of the shoot or branch is often nearly erect, but radial symmetry is not found after the very early so-called seedling stages of the plant, except in the strobilus and in the stalk below the strobilus. In accordance with its dorsiventral structure, the roots, which are produced irregularly at intervals, arise from the lower surface, the branches arise laterally, and the leaves, more particularly those

inserted on the lower side, are curved upwards. The branches form either *short shoots* which produce secondary and sometimes tertiary branches, seldom grow beyond a few centimetres, and develop no roots, or *long shoots* which reproduce the structure of the main axis. The short shoots persist as long as the main axis on which they arise; the long shoots not only help to spread out the original plant, but also serve as a means of propagation when the main stem dies away behind, and each long shoot then becomes an independent plant. The arrangement of the leaves in the adult condition conforms to no recognised system: the leaves do not fall on a spiral, but it is possible to group the leaves into pseudo-whorls, and alternate pseudo-whorls are similar. This arrangement is not always obvious, but due regard must be paid to changes occurring at the insertion of branches. A very constant feature, practically for all Lycopods, is the prolongation of the leaf-base. As an external feature, and one likely to be preserved in casts and impressions, it might prove to be of some importance in the identification of fossil remains, even though many of the Coniferæ are similarly distinguished.

Passing from external features to the internal structure of the stem, the arrangement of the vascular tissues is similar to that which occurs in roots (Pl. 3. fig. 2 and Pl. 4. fig. 8); round the periphery there are situated a varying number of protoxylem-groups, and arranged alternately between these a similar number of protophloems. The vascular tissue fills up the centre—whether, as in young stages or in ultimate branches, this consists of solid xylem, or, as in the main stem and larger branches, opposite xylems are joined up—and the general appearance is presented of alternating xylem- and phloem-bands. Around the vascular tissue is situated a pericycle varying generally from two to six layers, narrower opposite the protoxylems and broader opposite the phloems, and this is again surrounded by a 2–3-layered endodermis. The cortex consists of three zones (Pl. 3. fig. 1), a broad zone, c_1 , made up of cells with thick lignified walls, which abut upon the endodermis, a region of thin-walled cells, c_2 , encircled by a narrow outer zone, c_3 , in which the cells have their walls slightly thickened. The stem is to a very great extent covered by leaf-bases, and in these a loose mesophyll separates the outer zone of cortical cells from the epidermis, but in the stem proper these layers are in contact. The vascular cylinder (Pl. 3. fig. 2) is somewhat oval and dorsiventrality is obvious in the arrangement of the vascular tissues. The parallel bands of the xylem and phloem lie approximately in a horizontal plane. The xylem-patches situated dorsally and ventrally are either heart-shaped, crescentic, or in the form of an Σ . The number of protoxylems is fairly constant throughout the axis, and changes in the number are often associated with the development of a branch. The main axis of well-grown plants contains twelve to sixteen or more protoxylems, the long shoots show about as many as the original axis from which they develop, the short shoots have fewer (six to four). The protoxylems are very obvious, not so the protophloems; it is easy to trace the protophloems near the apex, more especially since they are differentiated early, but in the mature condition they are not so definite; the best differentiation between phloem and pericycle was obtained in sections stained with hæmatoxylin and subsequently washed with water. As stated before, the protophloems and protoxylems alternate, so that the arrangement of these is radial. The disposition of the sieve-tubes is definite, as they form a single row in the centre of the

phloem-strips. Outside the vascular tissue the endodermis is sharply differentiated from the pericycle and stains very similarly to the xylem; the inner cortex, and to a less degree the outer cortex, forms the mechanical tissue, while the median zone serves for water-storage. The cells of the median zone run obliquely, at about an angle of 20° with the vertical as seen in longitudinal section.

The leaf-traces pass down into the stem, entering near the upper insertion of the leaf, bend inwards at a slight angle with the vertical, and shortly connect on to a protoxylem. As there is a single leaf-trace it might be expected that the number of leaves on the stem or branch would furnish an indication of the number of protoxylems, and the leaf-traces would in turn join up to the various protoxylems. This is not found to be the case. Where the number of leaves on the smaller branches is reduced to four or six, then it is usual to find a corresponding number of protoxylems; but where the number of protoxylems increases beyond six, then there is no apparent proportion between the two. Pl. 4. fig. 9 gives the general appearance of a stem with thirteen protoxylems, and in the figure the points at which the successive leaf-traces connect up to the central cylinder are represented, the insertion of the traces having been followed through six nodes. The positions of the protoxylems vary slightly, and their number may change, especially towards the ventral side; but taking the protoxylems, either lateral or dorsal, which remain nearly constant in position, it will be observed that in the six whorls of leaves some protoxylems connect with as many as six leaf-traces, others only with four.

LYCOPODIUM ANNOTINUM, Linn.

This species in its structure approaches *L. clavatum* very nearly. The main axis creeps along the ground, producing roots ventrally and branches laterally. The leaves on the main shoots can be resolved into alternating pseudo-whorls, and a common arrangement consists of alternations of six and seven leaves. The roots and branches are fewer in number than in *L. clavatum*, there is not the same marked difference between short and long shoots, and the number of short shoots is smaller. On branches of the second and higher orders the leaves are arranged in alternate whorls of four, and this applies also to branches of the first order which do not form runner-shoots. All parts of the plant, except the strobilar branches, are plagiotropic. The internal structure of the stem, so far as the vascular cylinder (Pl. 4. fig. 10) is concerned, is essentially similar to that of *L. clavatum*. The number of protoxylems in the specimens examined did not exceed twelve and the branches showed six to eight. The cortex is not, however, differentiated into three zones, but practically the whole consists of thick-walled tissue; the leaf-bases are decurrent, so that the stem is almost entirely invested, and, concomitantly with the absence of the aqueous tissue, the epidermis is more heavily cuticularised. The transverse section shows a cavity between the cortical tissue and the mesophyll of the decurrent leaf-base. This cavity extends from the point where the leaf joins the stem and continues through the swollen leaf-base, but does not continue into the free portion of the leaf. The position of the cavity c_1 is indicated in Pl. 4. fig. 11, and between the epidermis and the cavity there are three or four layers of parenchymatous cells (fig. 12). The probable function of the space is for aeration, since it contains no

mucilage and the mesophyll-cells are not well provided with intercellular spaces. A fungus was found permeating the tissues very generally, but there was no reason to suppose that this was regularly present.

L. annotinum shows very distinctly a feature which occurs in many of the Lycopods, *i. e.* the peculiar thickenings and pittings in the walls of the mesophyll-cells, and, generally speaking, striations and pittings are particularly noticeable upon the walls of all cells of Lycopods. The appearance presented in the loose cells of the leaf-base, as seen in the surface view (figs. 12 and 13), is that of oval plates marked with very definite pits. Some of the pits are very large, others much smaller. The whole appearance is that of a magnified sieve-area. In section (fig. 12) it is found that these plates represent thicker portions of the wall, and whereas there are ordinary pits which correspond on the two sides, there are also depressions which occur on one side only, and the larger pits in surface view correspond to these.

LYCOPodium COMPLANATUM, Linn. ; *L. CHAMÆCYPARISSUS*, A. Br. ; *L. ALPINUM*, Linn.

It is convenient to take these three forms together. In the first place, Mr. J. G. Baker, in his 'Fern Allies,' unites *L. Chamæcyparissus* as a variety with *L. complanatum*, and these two are included in the small category of Lycopods which have dimorphic leaves, an interesting group suggestive of *Selaginella*. It would not be expected, therefore, that it would be difficult to distinguish *L. alpinum*, which is placed in the *clavatum* section, from the others, as there should be a difference both in the leaves and also in the presence or absence of a stalk to the strobilus. As a matter of fact, while it is an easy matter to distinguish a typical specimen of *alpinum* from a typical specimen of *complanatum*, there has been considerable diversity of opinion between British botanists whether *L. complanatum* has ever been found in this country, and whether these plants are not really specimens of *L. alpinum*. Even those favourably inclined to the inclusion of *L. complanatum* among British plants recognise only one or two localities for it. Mr. Baker was kind enough to supply me with a dried specimen of *L. complanatum* from Germany, and I am also indebted to him for confirming the names of some other specimens of Lycopods which I received unnamed. Interest attaches to *L. Chamæcyparissus* because Sachs's historic figure is referred to that species. A herbarium specimen was obtained which was not suitable for detailed examination.

In several respects the three forms are similar in their external characters. The main stems are distinctly dorsiventral, the leaves on the stem are few in number, but the leaf-bases are well marked. First-order branches are produced only at considerable distances, but branches of a higher order are numerous and follow upon one another quickly, with the result that a tassel of branches may be found arising on branches of the first or second order.

The sections of the stems of *L. complanatum* and *L. Chamæcyparissus* are practically identical (Pl. 4. fig. 14), and differ very little from sections of *L. clavatum*. Probably the most constant difference lies in the cortex, which shows three zones, but the innermost zone is very broad, the median zone is less sharply defined and does not assume the appearance of water-tissue, and the outer zone is reduced to one or two layers. A considerable

amount of variation has been observed in the stems of *L. complanatum*; in some sections the phloem- and xylem-bands are quite parallel and horizontally situated, in others the bands bend outwards towards the ventral side in a V-shape, and at times one or two phloem-patches are isolated by xylem. The vascular structure of *L. alpinum* (Pl. 3. fig. 3 and Pl. 4. fig. 15) is also very variable, and while on the one hand it differs very slightly, if at all, from the irregular arrangement observed in *L. complanatum*, on the other hand there is a great tendency to form isolated phloem-patches or phloem-islands; and in other respects, notably the irregular differentiation of the xylem near the apex, it forms a connecting-link with the second group of Lycopods which is described later and which is characterised by the separation of distinct phloem-islands. In certain longitudinal sections of *L. complanatum* some of the inner cortical cells showed definite but not very obvious spiral thickenings. These are shown in Pl. 4. fig. 16, which indicates the spiral markings and the pits which occur in the cortical cells, also the general appearance of the endodermis, pericycle, and vascular tissues. In view of the difficulty of deciding by means of external morphological features the distinction between *L. complanatum* and *L. alpinum*, an attempt was made to get an anatomical distinction based upon the occurrence of these cells with spiral markings; but they were not distinguishable in some specimens that were definitely assigned to *L. complanatum*, and a better criterion would seem to be the greater tendency to irregularity in the stem of *L. alpinum*. In this connection Mr. G. C. Druce was kind enough to supply me with specimen portions of English plants referred to *L. complanatum*. A very great similarity is apparent, in the case of all three species, in the smaller branches, which generally show a tetrarch structure. The cortical cells have their long diameter approximately horizontal, and the anisophyllous arrangement would seem to justify placing them in the same group.

LYCOPODIUM OBSCURUM, Linn.

This species is placed by Mr. J. G. Baker in the *cernuum* group, which contains erect species with a tree-like habit, and will be known to all botanists who are familiar with the rock-garden at Kew. The anatomical characters of this species are very similar to those of *L. clavatum*, and differ considerably from those of *L. cernuum*, which, as will be seen later, are highly specialised. The erect stem bears a number of roots at the base, and alternating pseudo-whorls of five or six leaves; on the ultimate branches there are alternating whorls of three leaves. The arrangement of the bundles in the smaller branches is tetrarch, so that externally and internally the symmetry is radial; but in the stem the number of protoxylems varies from nine to eleven, and the dorsiventral structure is similar to that noted for *L. clavatum*.

LYCOPODIUM INUNDATUM, Linn.

The habitat of this plant is well known; it occurs in swampy ground close to ponds and lakes. It is the only British form which is not subalpine, and may be found in several districts in the south of England. An important character is the presence of mucilage-cavities, which are described by Hegelmaier. Mr. J. G. Baker makes a small

group of three plants with *L. inundatum*, *Drummondii*, and *alopecuroides*, all of which grow in swampy ground; it would be interesting to know whether they all have mucilage-cavities. In the course of the present investigation no other species was found which contained mucilage-cavities normally. This species furnishes an instance of a plant provided with xerophytic modification which nevertheless grows in water-logged soil. This may be ascribed to the fact that it grows in soil which is rich in humus, and that these modifications are necessary for the plant to obtain and keep the necessary water. Generally the stem keeps close to the ground, produces a considerable number of roots, branches freely when it is growing quickly, and the apices are markedly orthotropic. The strobilus is produced in drier situations, and the structure of this part of the stem is radial.

The best-grown specimens show eight to ten protoxylems (Pl. 4. fig. 19), but frequently they are fewer and in the branches a striking tetrarch structure is obtained (fig. 20). Hegelmaier gives a small figure of the same type as that shown (fig. 27), but his figure does not indicate the protoxylems, which are clearly distinguishable from the metaxylem. The amount of xylem is very considerable compared with the phloem, as there is a central plate of xylem; and, further, the xylem is very broad at the periphery, where it is in juxtaposition to the pericycle, whereas the phloem is particularly narrow. This tetrarch structure is regarded as a reduced condition.

The cells of the cortex are nearly all thin-walled, but there is an appreciable amount of variation in the centrally situated cells in plants taken from different localities. In some, air-spaces are well marked, but in others, where the cells are more compact, the mucilage-cavities are better developed. The mucilage-cavities lie outside the leaf-trace bundle, and run some distance upwards into the leaf and pass down into the stem, but stop at the base of the leaf in the strobilus.

LYCOPodium SELAGO, Linn.; LYCOPodium SERRATUM, Thunb.

Both of these species are included in Mr. Baker's first group, of which *L. Selago* is taken as the type. The erect growth of *L. Selago* is well known, but *L. serratum* is sub-erect and may grow much longer than the former; otherwise there are several noticeable points of similarity—*e. g.*, in the indefinite arrangement of the sporangia, the unequal development of sporophylls, the formation of bulbils, and the manner in which the roots grow downwards through the cortex of the stem. The vascular cylinder in *L. Selago* is small (Pl. 4. fig. 21), the number of protoxylems is at the most six or seven, the xylem is flattened out, and, as is generally the case where the protoxylems are few, there is a central xylem-portion, so that opposite phloems are not joined. The middle portion of the cortex consists of large loosely arranged cells, surrounded by a zone of cells with thicker walls. The leaf-bases contain large cavities, as in *L. annotinum*. A striking feature in sections is the presence of roots, of which as many as seven may be found near the base, and these are found to arise quite high up in the plant, even above the point where the stem has branched.

If the stem is growing quite erect the roots do not pass out, but gradually die out, and it is only when the stem is growing obliquely that the roots emerge, and thus at the base

of the plants where the stem is plagiotropic a cluster of roots may be observed, and then above this no further trace of them is evident outside. Besides growing to a greater length than *L. Selago*, *L. serratum* is marked by, comparatively speaking, large leaves, which vary, however, in breadth from 1 to 5 mm. The vascular cylinder may attain considerably greater proportions in *L. serratum* (Pl. 4. fig. 22), and the general configuration of xylem and phloem is more broken; this, as in the case of *L. alpinum*, leads to the formation of isolated phloem-regions and three phloem-islands are shown, but, in these, sieve-tubes are not well developed. Cavities do not occur at the base of the leaves as in *L. Selago*. In the smaller plants, which had been formed from bulbils, two or three roots were found in the cortex, and in old plants as many as nine were observed in some sections. These roots do not grow very far, but from the central cylinder new roots are continually being produced every few centimetres, and the old ones gradually die out. The triarch stage (fig. 23) is taken from the stem of a young plant derived from a bilbil.

Of other species which were very cursorily examined, *L. volubile*, Frost, shows, as Mr. Boodle has already indicated, a definite banded structure. A specimen named *L. uliginosum* is very similar to *L. annotinum*, and shows the same development of cortex, but the cavities in the leaf-base are wanting. *L. tetragonum*, Hook, is similar to *L. Selago*; internal roots are found, and the xylem is cruciate and shows the same broad periphery. *L. reflexum*, Lam., resembles *L. serratum* both in the star-like arrangement of xylem and the isolation of portions of phloems and also in the presence of internal roots.

LYCOPODIUM SQUARROSUM, Frost.

In the abstract of a paper communicated to the British Association by the writer in 1897, which was subsequently published as a note in the 'Annals of Botany' (vol. xii. 1898, p. 558), it was pointed out that there are a number of Lycopods, mostly tropical epiphytes, which differ in several anatomical points from species found in this country and in Europe generally. Of these *L. squarrosus* was taken as a type, and included with it were *L. Dalhousieanum*, *Phlegmaria*, and *nummularifolium*. Externally these plants are characterised by radial symmetry and orthotropic growth. Several features in their internal structure are distinctive: the xylem is not arranged in separate narrow strips, but owing to cross-connections the general configuration is more irregular, and by these cross-connections the phloem in the centre is cut off into isolated portions or islands; the differentiation of the protoxylem does not proceed uniformly from the outer elements to those of the centre as is the case in the *clavatum* type, and the outer portions of some of the xylems, consisting of protoxylems only or together with a few metaxylem-elements, are isolated from the main mass; the sieve-tubes are grouped together in a cluster; also there is little or no mechanical tissue formed in the cortex. Most of these plants have leaves which are large for Lycopods; they show well-marked leaf-bases, but the leaves are whorled in several cases, or very nearly so.

In *L. squarrosus* the leaves are not regular, and alternating pseudo-whorls of six or seven leaves occur; the branches very gradually decrease in size, and dichotomy is the

rule. The stem (Pl. 3. fig. 4 and Pl. 4. fig. 24) shows very distinctly the characters mentioned above; in the centre one or two groups of sieve-tubes with the surrounding parenchyma are isolated as islands, and a similar arrangement of phloem is quite as distinct towards the outside. It will be noticed, too (fig. 24), that there is a break in the connection between the protoxylem and the central tissues of metaxylem at five points, and this break occurs in the metaxylem and not where the protoxylem passes into metaxylem. At the position *r.* (Pl. 3. fig. 4), a root is coming off, and it will be seen that the vascular tissue of the root joins on to two protoxylems and one phloem of the stem. In the case of all these epiphytic forms roots may be expected at the base of the stem; during the present investigation they were found only in this species, but that is accounted for by the fact that the material obtained of the other plants of this group did not come from the base. A figure is given in Engler and Prantl's 'Pflanzenfamilien' (i. Teil, 4 Abt. fig. 365, p. 579), in which a root is shown traversing the cortex in the stem of *L. Phlegmaria*.

LYCOPODIUM DALHOUSIEANUM, Spring.

On the oldest part of the stem of *Lycopodium Dalhousieanum* obtainable, which probably represented a branch of the first order, there were seven leaf-bases, which corresponded with an alternating arrangement of three or four leaves, but on a smaller branch there were regularly alternating whorls of three leaves. The vascular cylinder (Pl. 3. fig. 5) is not so definite as in *L. squarrosum*, but in the larger branches phloem-islands are quite distinguishable. A peculiar configuration is one exactly similar to that figured for *L. Phlegmaria* by Pritzel in the 'Pflanzenfamilien' (fig. 365 A, p. 579), in which there are two parallel strands of metaxylem separated by a phloem-band having the sieve-tubes in one line; but outside this the xylem-portions are feebly developed and isolated, and, as the structure of the branch was followed up, cross-connecting portions of the xylem were found, and a very definite phloem-island was formed in the centre in which the sieve-tubes were characteristically grouped. The leaf-bases showed no well-defined mesophyll-cells, and intercellular spaces were not very apparent—both of which facts may be correlated with the well-marked development of the leaves.

LYCOPODIUM PHLEGMARIA, Linn. ; LYCOPODIUM NUMMULARIFOLIUM, Blume.

These epiphytic species—the former with a wide distribution through the tropics of the Old World, the latter confined to the Malay Region and the islands to the east—both correspond with the *squarrosum* type.

The material available in the case of each of these species consisted only of branches, and in consequence, as may be seen from the diagram, the sections of *L. Phlegmaria* do not show the phloem-islands clearly delimited throughout, although the isolated portions of the xylem are well marked; but the section of *L. nummularifolium* represented in the diagram (Pl. 4. fig. 25) is distinctly radial and the phloem-islands with the grouped sieve-tubes are quite definite. The radial construction of *L. nummularifolium* is especially noticeable as contrasted with the dorsiventral arrangement of the leaves.

LYCOPODIUM CERNUUM, Linn.

A more complex arrangement of the tissues was found in two specimens, both of which were assigned to *L. cernuum*, and this assumption was confirmed by Mr. J. G. Baker. The one specimen was brought to me from Singapore, and, although the material appeared to include two possible varieties, the general character and internal anatomy were similar throughout. A striking feature was the plagiotropic growth of the stem, which was similar to that of *L. clavatum*; while the strobili furnished the clue to identification as *cernuum*, and the vascular structure was most decidedly radial.

The second specimen was part of the typically erect-growing plant, and agreed with the plant from Singapore in presenting an internal structure which at first sight recalls a *Gleichenia* (Pl. 3. fig. 6 and Pl. 4. fig. 27). The configuration is nearly, if not quite, as peculiar as that of *L. salakense*, Treub, which was described by Mr. Boodle (14). There is a figure of the general structure in Engler and Prantl's 'Pflanzenfamilien' and a general plan is given (Pl. 4. fig. 27), as well as a photographic reproduction of the transverse section of the stem (Pl. 3. fig. 6). It will be seen that the xylems and phloems are entirely intermingled, and the phloem-islands often consist of only a few phloem-elements, or several phloem-groups may be connected together. The protoxylems are very broad. The branches show the same interspersions of the phloem-elements among the xylem, but the proportion of them is considerably less; it was also interesting to find that the root presents a similar appearance to that of the branches. Another feature observed in the stem is the thickened area towards the outside of the cortex; this is very well marked both in the erect and plagiotropic shoots.

In addition to the five species enumerated, *L. dichotomum*, Jacq., *L. linifolium*, Linn., and *L. strictum*, Baker, would appear to conform to the type of *L. squarrosum*. In *L. dichotomum* the configuration of the vascular cylinder is not so definite as might be expected; in the larger stems the cross-connections of the xylem-bands are sufficiently well developed to give rise to isolated patches of phloem, but in the branches the arrangement of parallel bands seems more obvious. Externally, *L. dichotomum* may be distinguished by the very definite areas which are marked by the leaf-bases. The stems of *L. linifolium* and *L. strictum* present a striking similarity to one another in their structure, which corresponds with that of *L. nummularifolium*.

LYCOPODIUM CLAVATUM, L. Seedling Plants.

Having outlined the general extent of variation which occurs in the structure of the vascular cylinder of various species of *Lycopodium*, it becomes a matter of considerable interest to endeavour to ascertain how this structure has been developed. It is entirely owing to the kindness of Dr. Lang that I can bring forward the following evidence, which is based upon the structure of the stem of young plants of *L. clavatum*, as he handed over to me several of the young plants which he obtained during his successful search for the prothalli of that species. Two of the youngest of these are shown in Pl. 4. fig. 28. The youngest plant (A), shown on the left, seems to have retained its radial symmetry. The stem-portion is connected up with the remains of the prothallus, but the first root is wanting, the roots which are shown being adventitious. The lower

portion of the stem bears reduced leaves; these become larger and more numerous till the ordinary condition of the young plant is reached about 3 inches above the prothallus. A plant as young as this seems to show a truly radial facies and is orthotropous. The other plant (B) is probably a good deal older, but not much longer. This differs from the previous plant, since at a certain point the growth has been modified and the structure is suddenly altered. It is possible that this break represents the interruption of growth at the end of the season. This obvious interruption was evident in all but the youngest plants, and in certain cases is clearly shown to occur where a branch arises. It is a possibility that the interruption is due to the transfer of activity from the stem to a branch, when the young plant would present a sympodium and not a monopodium; but this would not be in keeping with the ordinary process of branching which obtains in the species. It will be observed that the principal root in B springs from the stem at a much higher point. The more dorsiventral the shoots the more widely separated are the roots, and in the case of erect stems they are clustered towards the base. The principal feature observed in sections of the young stem is that the vascular bundles present a triarch or tetrarch arrangement (Pl. 5. fig. 29), exactly similar to the structure which may be found in the roots of Gymnosperms or Dicotyledons: the xylem forms a central xylem-plate, so that the four phloem-portions are separated; the pericycle is one- to three-layered and the endodermis shows one or two rows of cells. The thick-walled cortex extends through four rows, and lies against thin-walled tissue which is easily broken down; beyond this a zone, about three cells deep, adjoins the epidermis, which is provided with a well-marked stratified cuticle. The young stem presents, therefore, exactly a similar arrangement of cortex to that which is found in the adult stem. So far as the stem was followed downwards a triarch or tetrarch structure was maintained, but it is not impossible that this might be modified into a diarch structure. A section which was shown to me, labelled "first root," showed what might be regarded as a diarch or tetrarch structure, in which the phloem occupied the central position and separated the two xylem-patches. Such a structure is not uncommon in the adventitious roots, where it is easily explained; but if this obtains in the first root there would be very good reason to look upon it as a late development from the stem, and not as primary. Passing upwards it will be found that, owing to changes which should be considered in reference to the apical meristem, the protoxylem extends along the periphery (Pl. 5. fig. 31), so that it overlaps the phloem, and eventually the far end connects up the central xylem-plate and the phloem becomes isolated (fig. 32). The same process occurs again in the case of the same or another protoxylem, and thus the structure changes from tetrarch to pentarch and then to hexarch (figs. 33 & 34). Similarly, seven, eight, or more protoxylems are differentiated. This process is not only to be observed in the young stem, but, if successive transverse sections of the adult stem are traced up, there is found to be a continual variation in the numbers of the protoxylems of the stem, in many cases associated with the formation of branches. In this way, if a long shoot is being formed, say, upon a stem showing twelve protoxylems, this may drop to ten, or fewer, in the branch which arises, and then by the splitting of a protoxylem eleven are formed, and this repeated leads to the same number as the original stem possessed. It generally

happens that as soon as six or seven protoxylems are formed, either because more phloem is required than can lie in the bays or because sufficient xylem is not formed to keep the central portion intact, two phloems become connected across (fig. 34), and thus the banded structure originates which characterises the *clavatum* group. After the stem has attained a complicated structure, then in the branches, more especially those arising on the short shoots or branches of the second or higher orders generally, owing to the small number of protoxylems which pass off, the structure is reduced, until, in branches which have only six or fewer protoxylems, these are again connected up in the centre by metaxylem and the original triarch or tetrarch structure is attained; this must be regarded as a reduced structure, as in the case of *L. inundatum* (Pl. 4. fig. 20). It is doubtful whether in any seedling the protoxylems have such a broad periphery as shown in this figure. This explanation, it will be observed, does not lend any support to the gamostelic nature of the structure of the vascular cylinder which has been postulated, but is of the nature of a gamodesmy in which the strands which pursue a sinuous course are constantly dividing and reuniting.

Young plants of *LYCOPODIUM SELAGO*, Linn., and *LYCOPODIUM SERRATUM*, Thunb.

Failing any other young plants derived from the prothallus which would furnish comparative evidence, the young plants derived from bulbils were examined. The external morphology of these bulbils has been described by Hegelmaier (5) and Strasburger (8); but these authors do not discuss the vascular structure, except to note that a small bundle, the equivalent of a leaf-trace, passes upwards, and the traces pass off from it. Starting from the base of a young plant, to which the bulbil was attached, the original simple bundle was found. This contains a single xylem-mass, which spreads out and separates into two portions, leaving a phloem-band in the middle (Pl. 5. fig. 35); this diarch stage is the commonest one to be found at the base of the stems of the young plants both of *L. Selago* and *serratum*. It is a structure which occurs fairly commonly also in roots, both where these run through the stem and also in small external roots or rootlets. The protoxylems can generally be distinguished on the outside of the periphery of the xylem in a median position. The phloem-tissue is so homogeneous that it is not possible to say whether it should be regarded as made up of two portions or one. By the extension and subsequent division of one of the two xylems a triarch structure is developed. In this case, generally the xylems are still separated, and this may persist after a tetrarch condition is reached.

In these young plants growing from bulbils the origin of the vascular cylinder is different, in so far that it arises from a leaf-trace, and also since the phloem forms the central portion; but the method of increasing the protoxylems is exactly similar to that described for the seedling of *L. clavatum*.

There seems, then, to be no doubt that the vascular cylinder in the stem of Lycopods has started from a structure which is exactly similar to that found in roots at the present day, and also there is the same formation of thick-walled cortex immediately surrounding it. It may be presumed, as it has always been suggested, that it represents

a very primitive type. Without going so far as to assert that the root-structure has remained unaltered throughout the range of vascular Cryptogams and Phanerogams, it appears that the arrangement which served for Lycopods, both in stem and root, has proved to be suited to roots generally. But as soon as the structure of the vascular cylinder in Lycopods begins to get complex, even in young plants, there is a notable difference, because the disposition of the different elements is constantly changing; even if the protoxylems remain constant in number, the positions are constantly shifting, and the phloem-inlets spread out into bands, or *vice versa*, and cross-connections between different xylem-bands are formed. It is presumed that the complex structure found in *L. cernuum* and *L. salakense* is the outcome of more irregular development and consequent interspersal of numerous small patches of phloem through the xylem. Examinations of serial sections have been made in order to get exact measurements of the changes which take place. In the stem of *L. clavatum* a U-shaped patch of xylem on the dorsal side was found to remain unchanged throughout a distance of 1.5 cm.; a definite phloem-inlet could be noted for a length of 1.8 cm., but for about 6 mm. it joined into a V curve with another inlet; a small patch, consisting mainly of protoxylems, remained separate for a distance of 1 cm.; other laterally situated portions of the xylem were observed to run for distances of 7 and 8 mm. before they joined up with the central mass of xylem. The stem of *L. squarrosum* lends itself to a determination of this kind. Eight figures (Pl. 5, figs. 37-44) are shown, of which the distance between the first and last was 2.5 cm. The number of protoxylems remains fairly constant, being for the most part sixteen, except in one section, where it has increased to seventeen, but they are constantly changing their positions. A phloem-island (p_1), which is evident in four sections, remains isolated for more than 1 cm. and then joins up to phloem nearer the periphery, and later becomes isolated again; the portion of phloem (p_2), though not isolated, remains tolerably fixed in position and definite through a length of 6 mm. The horseshoe-shaped mass of xylem (x_1), isolated in figs. 39 and 40, can be distinguished in four sections for a distance of 1 cm. The portion of xylem (x_2) remains separated for a similar distance. It is also instructive to observe how the directions of the phloem-areas change. In fig. 37 the phloem is continuous on a line which makes a slight angle with the horizontal, but it is not again renewed in this direction. A peculiar phase of continuity is that shown in fig. 44, where it assumes the shape of a 7. The conclusions to be drawn from these measurements are that the most definite phases may persist from 1-1.5 cm., and others for shorter distances; but it is more apparent that gradual changes are constantly occurring, since the strands seldom run vertically and the different parts are alternately joining up and separating.

Roots.—The structure of the roots has not been critically examined, except in so far as they were found running through the stems of such species as *L. Selago*, *serratum*, and *squarrosum*. It is noticeable, in contrast with the vascular cylinder of the stem, that the bundles of these roots and their orientation remain nearly constant. A very large percentage of the roots are alike, and show the structure which is represented in fig. 36. The vascular system of the root connects up with two xylems and the intervening

phloem of the vascular cylinder of the stem. In most cases the extensions of xylem passing off join up behind as the root-trace separates, with the result that a crescent-shaped mass of xylem is formed with protoxylems at the horns of the crescent, and the bay is occupied with phloem. In fewer cases the xylems do not join up, and then, as in branches, four protoxylems often may be detected. The roots all have a similar orientation, even where several are found, and relatively they change their position but little; the horns of the crescent are always turned outwards. With regard to the length of these roots, which do not emerge from the stem, they have been found to run down for distances varying from 1 cm. to 2.3 cm.

APEX.—Except in the early paper by Nägeli (1), describing the structure in the root-apex of *L. clavatum*, the evidence has been entirely opposed to the existence of a single apical cell in Lycopods, and this decision may be accepted; but Strasburger (7) and, less definitely, Hegelmaier (5) have pointed out that in longitudinal sections of the stem a deeper cell is generally found at the apex, and Strasburger traced out the development of dermatogen and periblem from one outer cell and the development of the phloem from one or two inner cells. The writer has obtained results on the whole very similar to those of Strasburger, but it is not proposed to enter into the discussion of the apex and the differentiation of tissues. The photograph of a narrow apex of the stem of *L. inundatum* shows the divisions very clearly, and has therefore been reproduced (Pl. 3, fig. 7). The deeper cell at the apex has divided into two by a longitudinal division, and the cell below has undergone transverse division; the plerome and periblem can also be demarcated.

BRANCHING.—It is generally stated that in Lycopods the branching of the stem is always monopodial, although it sometimes simulates a dichotomy. The opposite view has also been put forward that the branching is normally a dichotomy, and that monopodial branching is due to the retardation or cessation of growth of one axis. There is, again, the question whether dichotomy is to be limited to those cases where a true apical cell is found and where the two branches arise from the two halves of the apical cell. In Pritzel's account of *Lycopodium* (13) the statement appears that the growing-point ceases to form new tissue and two new lateral growing-points are developed; but the evidence upon which this opinion is based is not given. I am inclined to regard these definitions as too extreme, and in the case where no definite cell exists, then the formation of two similar apices, either traceable in the young condition or based upon the evidence of subsequent similar development of the tissues, may be termed a dichotomy. In *L. complanatum* it is possible to recognise, shortly before the strobili are formed, not only on that part of the plant which will form the strobilus but also on adjacent sterile shoots, branchings which would in this sense be termed dichotomies. Sometimes it is possible to recognise them externally, as is generally the case with *L. complanatum*. In the allied form, *L. alpinum*, they are not so well defined, and it is necessary to cut sections through the tassels of branches, when the forking is generally monopodial, but occasionally a dichotomy is met with. In the creeping Lycopods monopodial branching is found, except in the strobilar region or below it. In epiphytic forms dichotomies are probably the rule.

As a type of monopodial branching, figures of *L. clavatum* are given (Pl. 5. figs. 44-49). In this case the branches arise laterally and the vascular elements broaden out in the vertical plane. Eventually, in several of the xylem-bands towards the side where the branch will come off, the xylem-elements become smaller, and at this point the separation will occur between the stem and branch portions of the vascular elements. It will be observed (fig. 45) that four or five bands of xylem, together with the included phloems, give off connections to the branch: the number varies with the size of the branch. The protoxylems together with metaxylem then separate off, the result being that on the adjacent sides of stem and branch protoxylems are wanting. Very shortly, however (fig. 50), protoxylems become evident at these points. It was found by examining a branch-origin near the apex that after the branch is cut off, about the stage represented in fig. 48, the meristem begins to form protoxylem in addition to the metaxylem, at the point where protoxylems normally occur. There is, therefore, a break in the continuity of the protoxylem.

The connection of the root is practically similar to the connection of a branch, but the roots run off horizontally, while the vascular cylinders of the branches pass off at a small angle.

The connection of the vascular cylinder between the two branches of a dichotomy is formed in a similar way (Pl. 5. figs. 51-54). Before the dichotomy occurs the tissues broaden out in the plane of separation (figs. 51 & 52). Smaller xylem-elements are produced at the centre of the xylem-strands, and at these points separation takes place. In some sections there appeared to be evidence that before the xylems separate pericycle-elements are developed along the centre line, as if the pericycle were pushing into the centre of the cylinder (fig. 35). But in other cases if the first elements formed between the xylem are considered to be pericyclic, then they have for a time no connection with the normal pericyclic ring of cells. Certainly these central elements resemble pericycle rather than phloem, but it is not possible to get a criterion which will distinguish them. Then with regard to the formation of protoxylems at the proximal ends of the separating cylinders, these may begin to be formed without any apparent cause or connection with pre-existing protoxylem-elements, or in some cases a patch of xylem consisting mainly of protoxylem-elements (figs. 51 & 52) is found on the line of division at the periphery on either side; when the xylems have separated, these divide into two and pass inwards, connecting on to the proximal ends of the bands where protoxylems are wanting. Since dichotomies do not occur in most cases, except in the smaller branches, the connection between the branches generally consists of not more than two xylem-bands. The figures represent a dichotomy in *L. complanatum*, a species in which this form of branching is very frequent below the strobili. It will be noticeable that with neither of these forms of branching do gaps occur, except with regard to protoxylems.

The structure of the leaf-trace, as it passes off from the vascular cylinder through the cortex, is indicated in fig. 58. The xylem-elements in the centre are well marked; around them are thin-walled cells having the appearance of pericycle, and outside may be traced a ring of endodermal cells.

Turning to some histological details which have not been satisfactorily established,

it may be stated that, with regard to sieve-tubes, they were found to be very similar to the sieve-tubes of other Pteridophyta. It is almost impossible to detect them in sections mounted in balsam, and for this reason microtome-sections could not generally be used for their examination. Stained with chlor-zinc-iodine, or better with Russow's solution, they showed up very clearly, and resemble perhaps most nearly the sieve-tubes of *Pinus*, having sieve-areas and sieve-plates (figs. 56, 57). With the magnifications used, and without undertaking a long series of investigations with special stains, it does not seem to be possible to determine whether callus is present, although it may be expected. The sieve-tubes are very long and end-walls very rare, but they appear to be transverse or slightly oblique and are quite thin. It will be noted that the structure of the sieve-plates is not correctly represented in the figure given in Janczewski's paper (9).

The endodermal layers of several species, and taken at different points, were examined to see whether the development of the cuticular bands could be followed out. In the species for which a single layer of endodermis has been previously recorded, *L. Selago* and *inundatum*, the early formation of a cuticular thickening on the radial walls, or on radial and external walls simultaneously, was observed, but it does not appear all round the stem at the same time. This unequal development is a distinct feature of *Lycopodium*, both as regards the endodermis and the thickening of the cortex. In other cases, even although the stems were in an early stage of differentiation, cuticularisation appeared to be produced simultaneously on the walls of two layers of cells.

The formation of spiral thickenings in the inner cortical cells of a specimen of *L. complanatum* has been already mentioned, and beyond that no spiral tracheids were found outside the true xylem. The appearance of spiral markings seen in cortical cells in transverse sections was always found to be due to pits.

The proportion of phloem to xylem has been variously estimated: in the stems of such species as *L. clavatum* and *complanatum*, where the phloem-bands are narrow, the proportion of phloem does not appear to be less than in the stem of most Ferns, while the area of the phloem in the section of the stem of *L. alpinum* shown (Pl. 4. fig. 15) is proportionately greater; the stem of *L. squarrosum* shows a maximum amount of phloem, while in the other epiphytic Lycopods examined there is proportionally less with a minimum in the case of *L. cernuum*. In the branches the proportion of phloem decreases. The most obvious explanation is to correlate the amount of phloem with the needs of the plant for storage-accommodation, since the phloem contains so much proteid material, and this would be in keeping with the large amount of phloem found in the stem of the epiphytic species.

ANATOMY AND CLASSIFICATION.

It is interesting to see how far the results of anatomical investigation are in accord with the classification adopted by systematists. It will be evident that the twenty species mentioned in this paper have been separated into two groups, the second containing a number of epiphytic forms and the first plants with horizontally growing stems, while species with erect stems may be included in either group.

Although this distinction appears to be a physiological one, the basis upon which the groups are delimited is strictly morphological; in the one case, the vascular elements have separated into parallel bands, while in the other differentiation at the meristem leads to the formation of more or less isolated areas. In the subgenus *Selago*, Mr. J. G. Baker identifies two groups under the type species *Selago* and *taxifolium*. The species in each group conform to the same type; but the group of *L. Selago* follows the *clavatum* type, while the group of *taxifolium*, of which most are epiphytic, shows the *squarrosus* type. Practically similar arguments apply to the group of *L. inundatum* and *L. Phlegmaria* which are included in the subgenus *Lepidotis*. The species of *L. squarrosus* and *L. Dalhousieanum* are included with *L. strictum* in the subgenus *Subselago*, which contains species both with erect and pendulous stems. The anatomical characters, as I have indicated, would bring *L. strictum* close to *L. nummularifolium*, and these and *L. Phlegmaria* would be closely allied to *L. squarrosus* and *L. Dalhousieanum*. Finally, I should separate *L. obscurum* very widely from *L. cernuum*, and the affinities of *L. alpinum* seem to me to lie rather with *L. complanatum* than with *L. clavatum*. In making these comparisons, it is not intended to suggest that anatomical structure is to be adopted as a basis of classification, except as an accessory to the more important morphological features which are usually employed by systematists.

It may be mentioned here that, in any hypothesis which endeavours to explain the dorsiventral structure in the creeping stems, the fact must not be overlooked that the banded structure is well marked in the stem of the erect-growing species of *L. obscurum* and the radial structure is maintained in plagiotropic stems of *L. cernuum*.

Before adding a summary of the more important results obtained, I desire to state that this work was originally begun in the Botanical Laboratory at University College, Liverpool, and was continued at the Royal College of Science, London. In addition to the help which I have acknowledged in the body of the paper, I wish to express my thanks to Dr. D. H. Scott, F.R.S., who supplied me with some of the material used in the investigation, and who has always given me most cordially the benefit of his assistance and advice.

SUMMARY.

1. The development of anatomical structure in the vascular system of Lycopods has proceeded along two lines: on the one hand, as the protoxylems increase in number, a series of alternating bands of xylem and phloem is developed; on the other, the phloem is scattered through the mass of xylem in more or less isolated patches, until a structure is produced which simulates that found in a *Gleichenia*. The first form is developed in creeping stems, the second is characteristic of tropical epiphytes, and an extreme development is found in *L. cernuum* and in *L. salakense*.

2. The young stem in the seedling shows a triarch or tetrarch structure, in all essentials similar to the structure generally associated with roots.

3. The complex arrangement found in larger stems is developed from this triarch or tetrarch condition by the division of one of the protoxylems into two strands, and by the separation of a phloem into two portions; subsequently another protoxylem

divides, and this process, together with the splitting of the phloem, is repeated until the number of protoxylems and protophloems reaches the number shown in the large stem. In the early stages there is generally a central xylem-plate, but when the number of protoxylems increases to five or six (*a*) the phloem differentiates in bands reaching from one side to the other, or (*b*) the phloems differentiate as isolated groups which break up the continuity of the xylem in the centre.

4. Subsequently in the branches the number of strands diminishes, and in the ultimate branches the reduced structure is similar to that found shortly after the seedling stage.

5. The disposition of xylem and phloem is constantly altering, not only at the periphery, but also throughout the section generally. The length through which a definite portion of tissue, such as a phloem-island or phloem-inlet, may be traced, varies from about 8 mm. to 1.5 mm.

6. Branching is monopodial or dichotomous. The former is commonly found in creeping species and some erect specimens. The latter occurs frequently in the vegetative shoots of epiphytes and just below the strobilar regions of various species.

7. The sieve-tubes are similar to those found generally in Pteridophyta.

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EXPLANATION OF THE PLATES.

PLATE 3.

- Fig. 1. *Lycopodium clavatum*. Transverse section of the stem : c_1 , innermost region of cortex ; c_2 , median zone of cortex ; c_3 , outer zone of cortex ; l , leaf-base. $\times 20$.
2. *Lycopodium clavatum*. Diagrammatic drawing of the vascular cylinder of the stem : $s.t.$, sieve-tubes ; $pp.$, protophloem ; $px.$, protoxylem ; $per.$, pericycle ; $e.$, endodermal cells ; $c.$, cortex ; $l.t.$, leaf-trace. $\times 100$.
3. *Lycopodium alpinum*. Photograph of transverse section of stem. $\times 20$.
4. „ *squarrosum*. Photograph of transverse section of the stem, showing phloem-islands : $px.$, protoxylem ; $s.$, sieve-tubes ; $p.i.$, phloem-island ; $r.$, root. $\times 50$.
5. *Lycopodium Dalhousieanum*. Photograph of transverse section of the stem : $p.i.$, phloem-island ; $px.$, protoxylem. $\times 50$.
6. *Lycopodium cernuum*. Photograph of transverse section of stem : $p.$, peripheral phloem-area ; $p.i.$, phloem-island ; $px.$, protoxylem. $\times 50$.
7. *Lycopodium inundatum*. Apex of stem. $\times 300$.

PLATE 4.

- Fig. 8. *Lycopodium clavatum*. Diagram showing general arrangement of xylem and phloem in transverse section of the stem, xylem shaded. $\times 30$.
9. *Lycopodium clavatum*. Diagram showing how leaf-traces join on to vascular cylinder through 6 nodes.
10. *Lycopodium annotinum*. Diagram of the stem. $\times 30$.
11. „ „ Longitudinal section of the stem, showing the cavities which occur at the base of the leaves. $\times 5$.
12. *Lycopodium annotinum*. Longitudinal section of leaf-base : $e.$, epidermis ; $m.$, loose cells at the base of the leaf ; $c.$, cavity. $\times 200$.
13. *Lycopodium annotinum*. Appearance of pits in surface view. $\times 240$.
14. „ *complanatum*. Diagram of stem. $\times 30$.
15. „ *alpinum*. „ „ $\times 30$.
16. „ *complanatum*. Longitudinal section of stem, showing general character of cells : $p.$, phloem-parenchyma ; $s.$, sieve-tubes ; $x.$, xylem ; $per.$, pericycle ; $e.$, endodermis ; $c.$, cortex. Some of the cortical cells have spiral thickenings. $\times 150$.
17. (Deleted.)
18. *Lycopodium obscurum*. Longitudinal section of stem, showing outer cortical cells. $\times 240$.
19. „ *inundatum*. Diagram of stem. $\times 40$.
20. „ „ Transverse section of branch. $\times 250$.
21. „ *Selago*. Diagram of stem. $\times 40$.
- 22, 23. „ *serratum*. Diagram of old and young stems. $\times 40$.
24. „ *squarrosum*. Diagram of stem. $\times 40$.
25. „ *nummularifolium*. Diagram of stem. $\times 40$.
26. „ *Phlegmaria*. „ „ $\times 40$.
27. „ *cernuum*. „ „ $\times 40$.
28. „ *clavatum*. Two seedlings. A, shows remains of prothallus. $\times 1$.

PLATE 5.

- Fig. 29** *Lycopodium clavatum*. Seedling. Transverse section of stem: *px.*, protoxylem; *p.*, phloem; *per.*, pericycle; *e.*, endodermis; *c*₁, *c*₂, *c*₃, inner, median, and outer zones of cortex; *e.p.*, epidermis. × 100.
- 30-34.** *Lycopodium clavatum*. Seedling. Diagrams showing how protoxylems increase in number.
- 35.** „ *serratum*. Transverse section of young plant derived from bulbil: *p.*, phloem; *x.*, xylem; *per.*, pericycle; *e.*, endodermis; *c.*, cortex; *t.c.*, thick-walled cortex which surrounds a root running through the stem. × 250.
- 36.** *Lycopodium Selago*. Transverse section of root running through the stem: *p.*, phloem; *px.*, protoxylem; *per.*, pericycle; *e.*, endodermis; *c.*, thick-walled cortex of stem. × 250.
- 37-44.** *Lycopodium squarrosum*. Diagrams of stem to show changes occurring in the vascular cylinder.
- 45-50.** *Lycopodium clavatum*. Diagrams of stem to show monopodial branching.
- 51-54.** „ *complanatum*. Diagrams of stem to show dichotomous branching. Phloem-areas indicated by dotted lines.
- 55.** *Lycopodium complanatum*. Transverse section of stem at a dichotomy: *x.*, smaller xylem-elements; *px.*, protoxylem; *p.*, phloem. × 80.
- 56.** *Lycopodium cernuum*. Sieve-tube in longitudinal section. × 65.
- 57.** „ „ „ „ „ „ × 800.
- 58.** „ *alpinum*. Transverse section of leaf-trace in cortex: *x.*, xylem; *per.*, pericycle; *c.*, cortex. × 300.

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