A Study of the Anatomy of Trichopus zeylanicus Gaertn.

BY

ERIC VERNON WATSON.

WITH PLATES CCXLVIII–CCLII.

(A) Introductory.

Trichopus zeylanicus Gaertn. is a small, erect perennial herb, a native of damp, low-lying, sandy situations in the shelter of trees in Ceylon and the East Indies, presenting many remarkable features which have given rise to a great deal of discussion as to its true affinities.

In Edwards's Botanical Register (1832) this plant was placed in the Aristolochiaceae; in Endlicher's Genera Plantarum (1836–40) *Trichopus* appears as one of a number of "Genera non satis nota," to which Aristolochian affinities were ascribed. For some time the balance of opinion remained in favour of its inclusion in the Aristolochiaceae, but in 1869 Beccari carried out the first reasonably detailed investigation of the plant; and, after paying some attention to the broader features of its anatomy, in addition to reviewing the external characters, Beccari concluded that *Trichopus* belongs more properly to the Dioscoreaceae.

Subsequent to this period *Trichopus* has been regarded as an anomalous monotypic genus of the Dioscoreaceae, and in 1894 Queva showed that the main features of its anatomy fell into line with this family, and summarised the chief points in which it diverged from the normal Dioscoreaceous plan of construction.

(B) Source of Material and Objects of the Present Investigation.

The work was carried out in the laboratories of the Royal Botanic Garden, Edinburgh, and the material used consisted of a number of plants collected by Petch in Ceylon and procured by I. H. Burkill. It should be noted that the form occurring in the hills of Travancore (Singampatty), and figured in the "Icones Plantarum Indiae Orientalis" (1874) under the name *Trichopodium zeylanicum* Thw., differs markedly in the shape and venation of the leaves from the Ceylon form, and

[Notes, R.B.G., Edin., No. XCIII, July 1936.]

accordingly it may be expected that there would be corresponding differences between the more minute details of the anatomy of the two forms.

The object of the present investigation was to confirm, and, as far as possible, to extend the work of Queva on the anatomy of *Trichopus zeylanicus* (1894), with a view to establishing how far the details of anatomical construction go to confirm the conclusion that the affinities of this species lie with the Dioscoreaceae. At the same time an attempt has been made to present in as complete a form as possible a detailed description of the anatomy of the vegetative organs, since no full account of the anatomy has hitherto been published.

The condition of the material available prevented a satisfactory elucidation of many points, and some sections of the work must thus appear somewhat incomplete. It was especially difficult to obtain an adequate series of sections of the reproductive shoot, so that an investigation of the vascular supply to the peduncles could scarcely be attempted. Similar difficulties were encountered in the treatment of the greatly hardened tissues of the rhizome.

The reproductive organs of the plant were not studied ; and in the absence of suitable material, the meristematic tissues could not be included in the investigation.

(C) General Description of the Plant, presenting the Details of its Anatomy.

Specific External Features and General Plan of Work.

Trichopus zeylanicus is seen to differ in its external morphology from the normal type of the Dioscoreaceae in the following main points :—

(1) The absence of any externally conspicuous tubers or swellings, either of root system or of stem structure.

(2) The fact that each aerial stem consists of but a single internode and bears only one foliage leaf.

(3) The complete absence of any trace of the climbing habit.

(4) The fact that the reproductive shoot is telescoped into a short axis of a few millimetres in length, on which the bracts and peduncles arise in close succession.

The anatomy of the different organs is described in the following order : (1) Root ; (2) Rhizome ; (3) Aerial stem ; (4) Leaf ; (5) Reproductive shoot. The most significant points in the anatomy of each are summarised shortly at the conclusion of the description of that organ ; and there follows an account of the principal features of interest in the various tissue systems as compared with the other members of the Dioscoreaceae.

Details of the Anatomy of the Individual Organs.

(1) *The Root.*

There is a well-developed root system in *Trichopus zeylanicus*, but it differs markedly from that of other members of the Dioscoreaceae. It is usual in the family for the roots to possess either annual or perennial swellings, or to be distinguished by numerous spiny protuberances. Thus in *Trichopus* there is a distinct departure from the normal, for its numerous slender roots at their thickest point scarcely exceed 2 mm. in diameter, and are without any form of spiny outgrowth.

The roots arise at irregular intervals from the basal portion of the rhizome, the vascular tissue being developed in direct continuity with the peripheral bundles of that organ. Each root extends for about 15 cm., remaining uniformly thick, and sending out a number of much finer ramifications. This uniformity in thickness is, however, not quite complete, there being a slight constriction at the crown of the root. This is associated with the greater width of the cortex as compared with the stele in the mid part of the organ, a feature which is found to be of interest in connection with the storage system of *Trichopus*.

The outermost layer of the root is composed of cells which appear in transverse section rounded, lenticular, or more often loosely irregular in shape, with strongly convex and slightly thickened external walls. This layer of cells constitutes a loose epidermal sheath, and the tissues of the root proper are limited by the strongly suberised inner walls of these cells.

The outer cortex consists of from two to three layers of small, more or less regularly arranged, and closely packed parenchymatous cells. These cells have fairly thick cellulosic walls, but show no trace of lignification. They take no part in the function of storage, which is confined to the cells of the inner cortex.

Proceeding inwards, a broad inner cortical zone occupies nearly two-thirds of the cross-sectional diameter of the root in the region of greatest thickness. The cells in this region are larger and appear more or less isodiametric in transverse section, but in longitudinal section are seen to be greatly elongated, and must be regarded as broadly cylindrical parenchymatous elements. The cellulosic walls are thin, and the tissue is well provided with intercellular spaces.

As already indicated, this inner cortical tissue serves very largely for storage, and as it would appear physiologically to be the equivalent of the extensive system of root tubers of other members of the family, considerable attention was paid to the nature of the storage system occurring here. The principal food reserve appears to consist of starch, and close aggregates of starch grains were found in the majority of the cells. Also occurring in this internal cortical zone are the raphide sacs.

These structures are numerous throughout the length of all the principal roots, and each consists of a wide, approximately cylindrical sac, containing a bundle of elongated, needle-shaped crystals of calcium oxalate embedded in a loose mucilaginous matrix. The cells which lie immediately external to the endodermis are much smaller in size, and the intercellular spaces are correspondingly less developed in this internal tissue.

There is nothing very abnormal in the structure of the single layer of cells comprising the endodermis. With the exception of certain thin-walled passage cells that occur at fairly regular points, opposite the protoxylem, each cell of the endodermis possesses the customary lignified internal and radial walls. The passage cells are developed in direct continuity with groups of thin-walled pericyclic cells, which are interesting, and appear to be rather characteristic of the Dioscoreaceae. In the crown of the root they are not well represented, and are often quite indistinguishable in their accustomed position between the protoxylem and the endodermis; while sections cut in the swollen mid part of the root show a very distinct group of thin-walled pericyclic cells, associated with one or two quite unthickened endodermal cells, opposite each of the xylem arches.

With the exception of the phloem patches, and the groups of thin-walled pericyclic cells described above, the stelar tissue is lignified throughout (Plate CCXLIX, Fig. 2). External to the phloem groups are found in most cases a few strongly thickened, sclerenchymatous elements, with lignified walls in direct connection with the endodermis. The number of xylem arches varies from twelve to fourteen at the crown of the root, with alternating phloem groups. At a point farther down the root, the number of separate phloem groups is reduced by anastomoses, so that in the thickest part only ten arches alternating with ten phloems can be seen. In the finer ramifications of the root system the number is still further reduced, so that, in sections of a lateral root about $\frac{1}{2}$ mm. in thickness, six arches only were found to be present. The lignified pith consists of cells which in transverse section present a very regular hexagonal outline, but are greatly elongated longitudinally, their lateral walls being perforated by minute pits.

It was observed that in the narrow, constricted crown region of the root, where passage areas and individual bundles are much more poorly developed, the pith is very extensive, while farther down, where the distinct passage areas can be very clearly seen, the pith is much more restricted, and the vascular bundles, though fewer, are individually better developed and extend farther in towards the centre of the root.

Neither phloem nor xylem was found to present features in any way different from what would be expected in a normal Monocotyledonous root. The phloem consists of uniformly small sieve tubes and

companion cells, and in the xylem variously pitted vessels are interspersed with lignified xylem parenchyma, which closely resembles the wider lignified parenchyma of the pith.

Summarising these observations on the root system, it will be seen that *Trichopus zeylanicus* differs from other members of the family in that the products of metabolism and food reserves are not stored in conspicuous tuberous swellings, but are distributed throughout the cortical tissue of the extensive root system. In other ways the root of this species is not to be regarded as presenting any strikingly peculiar features. The presence of only a single endodermal layer here is, however, of some interest, since a double endodermis is said by Knuth to be rather characteristic of the Dioscoreaceae.

(2) *The Rhizome.*

The rhizome in most of the plants examined consisted of a stout, short, vertical organ, either quite unbranched, or with one or two ramifications. However, in a few exceptional instances this organ was found to be greatly elongated horizontally, extending for a length of about 8 to 10 cm. without branching at all. It would seem, then, that in *Trichopus* the rhizome is subject to a considerable amount of variation in general form.

In the vertical type of rhizome the numerous roots and aerial stems are given off at extremely close intervals, and diametrically opposite each aerial stem there arises a scale-leaf. These short, acicular scale-leaves are very numerous, and form a complete protective covering over the upper parts of the rhizome. In the elongated terminal regions of the horizontal type of rhizome, however, stems and roots are given off at less frequent intervals, and there is accordingly a much scantier covering of scale-leaves.

A transverse section of the close, vertical type of rhizome is so complicated in outline by the large number of structures arising from it at such close intervals, that the following general description will be found to apply with strict accuracy only to those elongated parts of the organ which are not interrupted by the simultaneous passage outwards through the cortex of vascular tissue destined to supply several different roots and aerial stems.

The outline of a transverse section of the rhizome is approximately oval, and, extending rather less than half the way in towards the centre, there is a broad band of cortical tissue. The epidermis of the rhizome is made up of closely fitting tabular cells, the thickened outer walls of which are provided with a well-marked corrugated cuticle. The cortex is about ten cells thick, and the thin-walled, loosely packed, parenchymatous elements present a fairly uniform appearance. Certain enlarged sacs, similar to those found in the cortex of the root, contain the raphides. These raphide sacs are numerous, and as many as eight or ten may be included in a single transverse section. Starch is not

stored to any extent in the cortex, although small aggregations of grains sometimes occur in the innermost cells.

The endodermis consists of a single layer of cells with the usual thickening of the internal and radial walls. Gaps in this otherwise continuous sheath are furnished by occasional small, unthickened cells, corresponding in function to the passage cells found in the endodermis of the root. Internal to the endodermis a sheath of cells, oblong in transverse section, and without thickening or food reserve content, represents the pericycle.

The stele contains a great number of separate vascular bundles, embedded in a matrix composed of fairly large cells, irregular in outline and separated by only small intercellular spaces. The bundles are smaller and more numerous towards the periphery, while a few large bundles occupy the central pith region.

Each individual bundle is of the concentric type commonly found in the rhizomes of monocotyledons. Phloem, accompanied by thin-walled parenchyma, is surrounded by a sheath of reticulately pitted lignified elements. In addition, as Queva pointed out, a few small tracheides may be recognised in the anterior region. The sieve tubes of the phloem are of small cross-sectional diameter; this generalisation holds not only for the bundles of the rhizome, but also throughout the entire plant, wide sieve tubes such as are found in many Dioscoreaceae being quite absent from the vascular tissue of *Trichopus zeylanicus*. This description is applicable only to those bundles which are not destined to pass out into the stem at a point immediately above the position in which the cut is made: in these latter the xylem and phloem both take on the stem arrangement before that organ has become externally separated from the rhizome.

The principal significance of the pith cells of the rhizome would seem to be in connection with the storage of food reserves, as in all the examples examined the cells were found to be densely packed with starch grains.

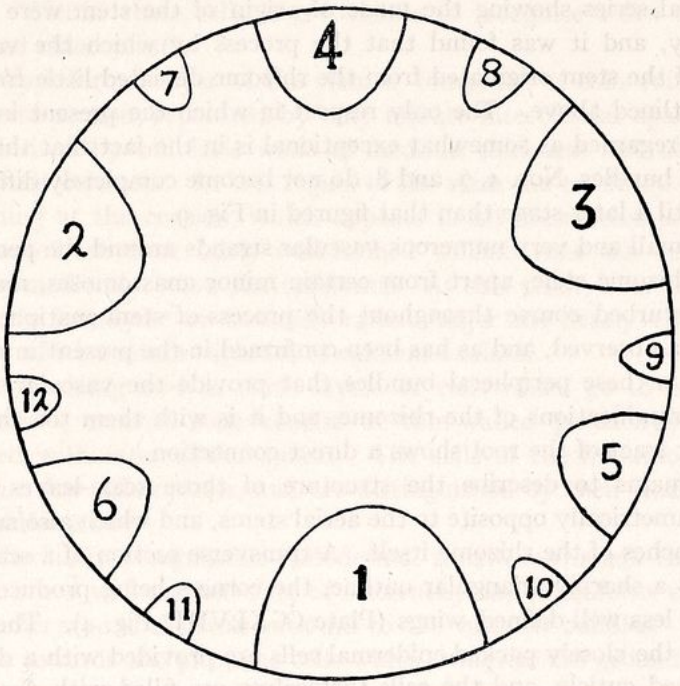
The chief feature of interest concerning the rhizome of *Trichopus zeylanicus*, as compared with other members of the family, would seem to lie in the existence within the pith of great quantities of reserve starch. The pith of the rhizome, with the cortex of the roots, may be looked upon as a greatly attenuated food storage system which is physiologically equivalent to the massive tubers of other Dioscoreaceae.

With reference to the course followed by individual bundles in the rhizome, Queva states that he had insufficient material at his disposal to investigate this point. Accordingly in the present enquiry a continuous series of sections was cut through a length of about 5 mm. from the elongated, horizontal type of rhizome, with the object of tracing so far as possible the mode of origin of the principal bundles of the aerial stem.

The twelve bundles which comprise the vascular tissue of the normal

stem may be numbered in the manner set out in the accompanying diagram. Nos. 1, 2, and 3 are the three main bundles, of which No. 1 is the largest. Diametrically opposite to No. 1 lies No. 4, opposite to No. 2, No. 5, and opposite to No. 3 is No. 6, these three being of the second order of magnitude; while in the normal condition, one on either side of each of these three, lie the remaining six small-sized bundles, which have been numbered from No. 7 to No. 12 in the diagram.

The outline drawings 1 to 9 (Plate CCL) illustrate how these bundles arise, and become grouped into the formation in which they pass out into the aerial stem; and how, simultaneously, a single narrow strand



1. Diagram to show method adopted in numbering bundles of stem.

passes out through the stele and across the cortex to furnish the vascular supply to the scale-leaf which grows out at a point diametrically opposite to the stem.

It will be seen that at an early stage the bundles that are to represent Nos. 1, 2, and 3 pass inwards towards the centre of the pith, and certain fusions between those bundles are associated with the increase in size which takes place in them at this point. These bundles are represented in the diagrams by the single lines of shading, as opposed to the cross-hatching employed for other stem bundles, and they will be seen (Fig. 4), at a point before the outline of the stele has been disturbed in any way, to be arranged in the form in which they remain unaltered during their passage out into, and up the course of, the aerial stem.

The bundles numbered 4 to 12, however, take up their position in

an even simpler manner. A single large strand, which will later divide into the group which become Nos. 4, 7, and 8, moves across from the anterior side. At the same time the lateral groups, comprising Nos. 5, 9, and 10, and Nos. 6, 11, and 12, fall naturally into position, being formed directly from the peripheral bundles which lie on either side of the point at which the stem is to emerge from the stele.

The dotted line in Figs. 6 to 9 is employed to indicate the line which appears at this point to separate the clear stem cells, devoid of food reserve, from the dark cells of the pith of the rhizome, which are densely packed with starch grains.

Several series showing the mode of origin of the stem were cut in this way, and it was found that the process by which the vascular tissue of the stem originated from the rhizome deviated little from the type outlined above. The only respect in which the present instance may be regarded as somewhat exceptional is in the fact that the three anterior bundles, Nos. 4, 7, and 8, do not become completely differentiated until a later stage than that figured in Fig. 9.

The small and very numerous vascular strands around the periphery of the rhizome stele, apart from certain minor anastomoses, maintain an undisturbed course throughout the process of stem enation. But, as Queva observed, and as has been confirmed in the present investigation, it is these peripheral bundles that provide the vascular supply for the ramifications of the rhizome, and it is with them too that the vascular tract of the root shows a direct connection.

It remains to describe the structure of those scale-leaves which arise diametrically opposite to the aerial stems, and which also subtend the branches of the rhizome itself. A transverse section of a scale-leaf presents a sharply triangular outline, the corners being produced into more or less well-defined wings (Plate CCXLVIII, Fig. 4). The outer walls of the closely packed epidermal cells are provided with a distinct corrugated cuticle, and the cells themselves are filled with dark contents. The mesophyll of the scale-leaf consists of a uniform loosely packed, thin-walled tissue, of rather large cells, irregular in shape. In this mesophyll there occur raphide sacs similar to those found in other parts of the plant.

The single central strand, which forms the vascular supply, is not clearly differentiated as regards its constituent elements. It is surrounded by a lignified sheath, which on either side is continued out into the lateral wings of the organ. In this way a rigid plate of tissue, expanded in the middle line to enclose the vascular bundle, serves as a scaffolding on which the looser tissues of the leaf are supported.

(3) *The Aerial Stem.*

(a) *General Anatomy of the Aerial Stem.*

The aerial stems, arising from the rhizome in the manner described, ascend to a height which varies from 1 to 10 cm. before the single leaf

is given off. Scattered irregularly over the surface of the stem are the glandular, capitate hairs which will be described in connection with the leaf, on which they occur in greater abundance.

The unevenly fluted transverse section is generally about 1 mm. in diameter, the wide stele being surrounded by a narrow cortical ring (Plate CCXLVIII, Fig. 2). The cells of the epidermis are small and uniform in shape, rectangular in transverse section, but elongated in the direction of the growing axis of the stem. The cellulosic walls are thick, the thickening being greatest on the external wall, which is also provided with a cuticle of the corrugated type found throughout the plant. Within these cells it is possible to recognise a few sparsely scattered chloroplasts.

The hypodermal layer of the stem is composed of cells rounded in transverse section, separated by only minute intercellular spaces, and characterised by cellulosic walls of medium thickness and abundant chloroplast contents. In this region of the stem the tendency towards thickening at the corners, which appears in all these cells, is greatly accentuated, so that fairly well-formed collenchyma can be recognised immediately below the epidermis. At this point, too, there are frequently found one or two cells rather larger and nearly circular in outline, which contain raphides of calcium oxalate.

The remaining two to three layers of cells which go to complete this narrow cortical zone consist of thin-walled parenchyma, well provided with intercellular spaces. The cells of the innermost layer contain a few chloroplasts, and are distinguished by their smaller and more uniform size.

No distinctly recognisable endodermal sheath surrounds the stelar region, but a well-marked ring of sclerenchyma, of uniform width, is continuous around the stele external to the vascular bundles. Passing inwards towards the pith, the cells which comprise the groundwork of the stele become increasingly large in size, while the lignification of the walls is progressively reduced in extent (Plate CCXLIX, Fig. 5). The individual vascular bundles are thus embedded in thick-walled tissue, but the degree of lignification in this tissue is much less than in the external sclerenchymatous sheath. The innermost, partially lignified cells of this tissue give place internally to a loose and much-disintegrated pith, with wide thin-walled elements filled with an abundance of starch grains. The degree to which this pith is developed varies in the different stems, and must depend largely on the condition of the individual stems at the time when the material was gathered. To whatever extent these thin-walled pith cells are developed, however, it is clear that their principal function is the storage of food reserves.

Reference has been made already to the disposition of the individual vascular bundles, in connection with the manner in which the aerial stems are given off from the rhizome. The posterior position is occupied by the largest bundle, No. 1, while antero-laterally lie Nos. 2 and

3, which are only slightly smaller in size. These three are the foliar strands, the remaining nine bundles found in the normal stem either passing out into the flowering shoot or being absorbed in a general anastomosis at the node. The details of the course of these bundles is discussed at a later point. At this stage it is necessary only to point out that Nos. 4, 5, and 6 form an inner ring of medium-sized bundles, while the strands numbered 7 to 12 comprise an outermost ring, each strand being of very small size (Plate CCXLVIII, Fig. 3).

Variations in this general plan do occur: thus in the stems of more robust growth an additional isolated strand may appear lateral to No. 1; similarly, in the most slender stems one or more of the outer ring, Nos. 7 to 12, may be aborted. Sections cut at various levels of the same stem show that anastomoses between the base and the node rarely or never occur, and that where thirteen bundles are recognisable in sections cut at a level just below the node these thirteen are also fully differentiated at the base of the stem.

The structure of the individual bundles appears at first sight to present considerable diversity in details, but four main types may be recognised: (1) The external ring of bundles, Nos. 7 to 12, all of small size. Here one can recognise two diverging arches of xylem tissue, each of which terminates posteriorly in one large vessel. In the "bay" thus formed lies a well-developed single mass of phloem (Plate CCXLIX, Fig. 3). (2) Bundles Nos. 4, 5, and 6; these are of larger size; and, while the phloem is retained in a single mass, it is found that four, or more rarely six, large vessels occur in the xylem (Plate CCXLIX, Fig. 4). In most cases two anterior and two posterior vessels of major importance can be seen. (3) Bundles 2 and 3; these bundles, which were seen to originate in the rhizome from the fusion of two average-sized rhizome strands, show in their plan of construction distinct evidence of anastomosis. One large vessel appears immediately anterior to the phloem; antero-laterally either one or two large vessels occur on each side, while two posterior vessels are usually situated external to the phloem. Further, the phloem here becomes subdivided into two, or more often into three, distinct groups, with narrow strips of xylem tissue passing out between them. (4) Finally, the greatest degree of elaboration is attained in the posterior bundle, No. 1, where, in addition to an extensive development of xylem tissue in the customary internal position, no fewer than four pairs of large vessels lie lateral to and external to the phloem. The phloem is here represented by four distinct patches, the two anterior phloem groups being separated by the vessels of the main anterior xylem mass, while between the anterior and posterior phloems, and between the two posterior groups, wedges of xylem tissue connect with the outlying vessels (Plate CCXLIX, Fig. 5).

It is seen, then, that a series of structural types of increasing complexity can be recognised in the vascular bundles which constitute the ring of conducting tissue in the stem.

(b) *The Course of the Bundles in the Stem.*

The bundles Nos. 1, 2, and 3 of the stem preserve their integrity at the node and continue into the petiole, No. 1 forming the strand of the midrib, and Nos. 2 and 3 the two principal lateral bundles of the leaf. The course followed by the remaining nine bundles of the normal stem depends on the rather remarkable relation existing between the stem, leaf, and flowering shoot in *Trichopus*.

In a small percentage of cases the stem passes up without any externally visible interruption into the petiole of the leaf, so that the swelling of tissue at the pulvinus of the leaf comes to surround entirely the growing point of the stem. A complete series of sections, cut at intervals of 10 μ, through this point of junction shows that the change from the stem arrangement to the petiole arrangement of vascular tissue takes place at the extreme base of the swelling. The rapid change takes place within a length of only 140 μ. The sclerenchymatous ring which surrounds the stele of the stem is disintegrated so as to form a separate lignified sheath around each of the separate petiole bundles; and the three strands, Nos. 1, 2, and 3, each receive vascular tissue from the groups lying on either side of them, while small strands pass inwards to end blindly in the pith region (Plate CCLI).

When a flowering shoot passes out at the junction of stem and petiole, however, the medium-sized bundles, Nos. 4, 5, and 6, pass into the pith and become split up into a number of strands which will ultimately pass out into the flowering shoot. The outer ring of small bundles, Nos. 7 to 12, however, as in the other type of construction, undergo anastomoses with the large foliar bundles, Nos. 1, 2, and 3, each of these latter receiving a small strand of vascular tissue from either side (Plate CCLII).

After the above arrangement has been completely established, a small strand is usually, but not invariably, broken off from each of the bundles Nos. 2 and 3, thus giving two small intermediate strands of vascular tissue which traverse the petiole between Nos. 1 and 2, and Nos. 1 and 3 respectively.

(c) *Comparative Discussion on the Anatomy of the Aerial Stem.*

Since the aerial stem of *Trichopus* comprises but a single internode, with a single leaf given off from the upper node, this monotypic genus presents necessarily in the general plan and course of its cauline and foliar vascular strands a strong contrast to other genera of the family. Accordingly, one finds that the bundles have become greatly reduced in number, and their course is so highly modified that it is impossible to bring the arrangement of the vascular tissue in this stem into line with the general plan recognised as typical of the Dioscoreaceae.

Nevertheless, there are many features in the anatomy of the stem of *Trichopus zeylanicus* which support most clearly its affinity with

others of the family. Thus, the corrugated cuticle, the occurrence of raphide cells just below the epidermis of the ridges of the stem, and the tendency towards the development of collenchyma in the outer layers of the cortex are features common to many species of *Dioscorea*.

Further, in the individual bundles the structure shows peculiarities which are specially characteristic of the Dioscoreaceae. The most prominent of these are (1) the tendency for the phloem to become subdivided into a number of separate patches in the larger bundles, and (2) the development of arches of xylem tissue through the phloem groups, with the result that certain of the large vessels come to be situated in a very unusual position external to the phloem.

Thus, while differences necessarily exist corresponding to the very different configuration of the stem in relation to other organs of the plant, the affinity of *Trichopus* with the Dioscoreaceae is clearly demonstrated by certain details of the structure of the stem.

(4) *The Leaf.*

(a) *External Morphology of the Leaf.*

The single leaf which arises at the apex of each aerial stem is borne on a petiole varying from 2 to 6 cm. in length, and this petiole is marked by a distinct basal swelling. The petiole passes gradually into the wide lamina, which varies in shape from broadly cordate to typically lanceolate, but is normally narrowly cordate and tapers to the rounded apex, in the notch of which lies a minute acumen.

The details given here of the external morphology of the leaf apply with strict accuracy only to the Ceylon form of *Trichopus*, material of which was used for the present investigation. This point may be emphasised here in connection with the leaf structure, since it is largely on the grounds of differences in the foliar organs that some authorities have recognised two distinct varieties of *Trichopus zeylanicus*.

The venation of the leaf in *Trichopus* is reticulate, but the finer ramifications are connected with three[1] main veins which follow a course from base to apex of the leaf. The centrally placed vein constitutes the midrib, while the two lateral veins pass outwards so as to reach the margin at a point about half-way along the length of the leaf. From this point to the apex these two veins are marginal in position. In addition to these three principal veins there are two others which occupy the marginal position in the proximal half of the leaf, and, originating in the branching of the two laterals, end at the point where these lateral veins reach the margin of the leaf.

Distributed over the surface of the petiole, and very numerous on both upper and lower epidermis of the lamina, are the capitate hairs which occur widely in the Dioscoreaceae, and are believed to be glandular in function. Each hair consists of a head of thin-walled

[1] Always three in material used, but may be five or even seven in number.

cells with dense protoplasmic contents, borne on a short stalk which fits into a slight depression of the epidermis.

A transverse section of the base of the petiole, in the region of the swelling, presents an outline which is marked by an anterior groove and a corresponding posterior prominence. Lateral to the anterior groove are two prominent crests, while two further bulges in the outline occur postero-laterally. Farther up the course of the petiole the V-shape of the transverse section becomes more distinctly marked and the anterior groove much deeper; and the two antero-lateral and one posterior prominence are much more sharply defined, in correlation with the greatly reduced extent of the ground tissue of the petiole (Plate CCXLVIII, Figs. 1 and 3).

(b) *Anatomical Structure of the Base of the Petiole.*

Within the epidermis, which consists of a single layer of small-sized, closely packed cells, the main mass of the tissue in this swollen basal region of the petiole is composed of parenchymatous elements separated by minute intercellular spaces. No clear differentiation into cortex and pith can be traced, but towards the centre one finds cells of a more uniformly large size with walls that are without any form of thickening; while immediately beneath the epidermis there are several layers of small-celled tissue, characterised by well-marked collenchymatous thickening.

Reserve food in the form of starch is almost completely absent from the petiole. Raphide sacs, however, are numerous, and a single section will normally pass through eight to ten of these sacs.

The vascular supply of the petiole consists of three principal bundles, in addition to which there may be two, or sometimes more, isolated intermediate strands.

As already indicated, the three main bundles represent Nos. 1, 2, and 3 of the vascular ring of the stem, with the addition in each case of a certain portion of the vascular tissue comprised by the remaining stem bundles 4 to 12. The posterior (midrib) bundle, derived from No. 1 of the stem, is the largest, the two antero-laterally placed bundles being approximately of equal size.

In each of these three bundles of the petiole it is possible to recognise certain points of difference from the type of structure seen in the vascular strands of the stem. Thus (1) there is a well-developed lignified sheath around each bundle, consisting posteriorly of two to three layers of true sclerenchymatous fibres, and thinning anteriorly to a uniform width of a single cell-layer; (2) the large vessels are of smaller diameter, and are in no instance external to the outermost phloem groups; and (3) the phloem is divided into a varying number of small, rather ill-defined patches, each phloem group being distinctly smaller than those found in the bundles of the stem.

The intermediate strands referred to above consist of a single ring

of lignified cells enclosing a few ill-defined tracheids and phloem cells. These intermediate bundles appear to represent the main trunks of a number of finer ramifications which end blindly in the tissues of the petiole.

(c) *Anatomical Structure of the Upper Part of the Petiole.*

Above the region of the basal swelling, the petiole undergoes certain alterations in the structural details of its several component tissue systems.

The epidermis consists no longer of cells of uniform dimensions, for in the region of the anterior groove the epidermal cells assume a very much larger size. In this small section of the epidermis the cells may attain to a size six times as great as that of the cells in the rest of the superficial layer.

The ground tissue, besides being greatly reduced in extent, shows an almost complete absence of raphide sacs. Further, the cells lying immediately below the epidermis in the anterior and antero-lateral regions of the petiole are abundantly filled with chloroplasts, a somewhat sparser chloroplast content distinguishing the hypodermal layer posteriorly.

With regard to the vascular tissue, the only change which is associated with the passage of the bundles up the petiole concerns the extent of the sclerenchymatous sheath. This sheath is increased in width until it comes to consist of four to five cell-layers anteriorly, and six to eight cell-layers in the posterior position around each bundle.

(d) *Anatomical Structure of the Lamina.*

The thin texture of the leaf-blade in *Trichopus* is well shown by the shape of a transverse section, which, swollen in the region of the midrib, becomes very sharply constricted on either side, the amount of tissue lying between the upper and the lower epidermis being remarkably small in the expanded portions of the leaf-blade (Plate CCXLVIII, Fig. 6).

In surface view the cells of the lower epidermis appear sinuous and irregular in outline, while those of the upper epidermis are more regular in shape. On both surfaces of the leaf the glandular, capitate hairs are borne abundantly, but stomata are confined to the under side. As is the rule in the family, the stomata are orientated irregularly over the surface. The cells of the upper epidermis are of a uniformly large size in transverse section, the distinctly thickened external walls being but slightly convex, so that the upper surface of the leaf, viewed in section, presents a remarkably flat appearance. In contrast, the cells of the lower epidermis are very uneven in size, those of the expanded portions of the lamina being much larger than those covering the under side of the midrib. Even the former, however, are small in comparison with the strikingly large dimensions of the upper epidermal cells (Plate CCXLVIII, Fig. 5).

The palisade tissue consists of a single layer of narrowly rectangular or rounded oblong cells, varying somewhat in size and fitting closely together with the intervention of few intercellular spaces. These cells occupy a narrow zone in the leaf section, in width equal only to about two-thirds of that occupied by the upper epidermis, but they are abundantly filled with chloroplasts, and constitute the most important photosynthetic tissue of the plant.

The rounded, orbicular, or broadly oblong cells of the spongy tissue are well supplied with chloroplasts, but do not comprise so compact a photosynthetic tissue as the palisade layer. In this region, too, raphide sacs of the usual broadly cylindrical shape are scattered sparsely but very regularly through the substance of the spongy chlorenchyma.

About the midrib, in addition to the fact of the lower epidermal cells being of much reduced size, the general configuration of the mesophyll becomes completely altered. Above the vascular bundle the chlorophyllous tissue is represented, not by true palisade cells, but by one to two rather irregular layers of cells containing chloroplasts, but in shape resembling the spongy rather than the palisade cells of the leaf. The remainder of the mesophyll in this region is composed of thin-walled, loosely packed, parenchymatous elements, which give place immediately beneath the epidermis to smaller cells with a varying amount of collenchymatous thickening, but with no trace of lignification (Plate CCXLIX, Fig. 1).

The structure of the vascular bundles in the lamina is little different from what is found in the petiole. In the lamina, however, the phloem becomes further split up, so that as many as seven distinct phloem groups may be formed. In addition, as the apex of the leaf is approached, the individual phloem patches become small and irregular, the vessels fewer and of decreased diameter, and the sclerenchymatous sheath becomes the most conspicuous feature of the strand.

(e) *Comparative Discussion on the Anatomy of the Leaf.*

In one very striking respect the leaf of *Trichopus* differs from the normal structural plan in the Dioscoreaceae. The difference lies in the complete absence of the anterior arch of vascular tissue (Queva's " arc antérieur ") from the petiole. This anterior strand, which takes origin at the base of the petiole, and assumes increasing importance higher up, is very characteristic of other genera of the family.

Secondly, there was found to be no trace of extra-floral nectaries on the leaves of *Trichopus*. This is not an important point, but it is significant that the leaves of many Dioscoreaceae are characterised by the presence of these groups of thin-walled glandular cells.

In other respects, however, the affinity of *Trichopus* with others of the Dioscoreaceae is clearly demonstrated. The shape and venation of the leaf, the pulvinar swelling at the base of the petiole, the disintegration of the phloem into several small groups, and the presence

of glandular capitate hairs on the leaf surface are all features in which the leaf conforms to the type of the family.

(5) *The Structure and Disposition of the Reproductive Axis and Peduncles.*

In the majority of the aerial stems of *Trichopus* there arises at the node, anteriorly and hence in a position diametrically opposite to the leaf, a short, conical reproductive shoot bearing a fascicle of flowers, and covered with minute protective bracts.

The outline of the main axis of this reproductive shoot, in transverse section, is irregularly oval, being continually interrupted by the passage outwards of the vascular supply to the peduncles and bracts. Within the close-fitting epidermal ring of cells is a narrow cortical zone, composed of parenchymatous cells. The individual bundles, derived from the stem in the manner described above, are small and scattered, and tend to resemble in structural plan the bundles of the rhizome. Within the pith region the separate strands become so greatly disorganised in connection with the enation of bracts and peduncles that their precise course is not readily made out.

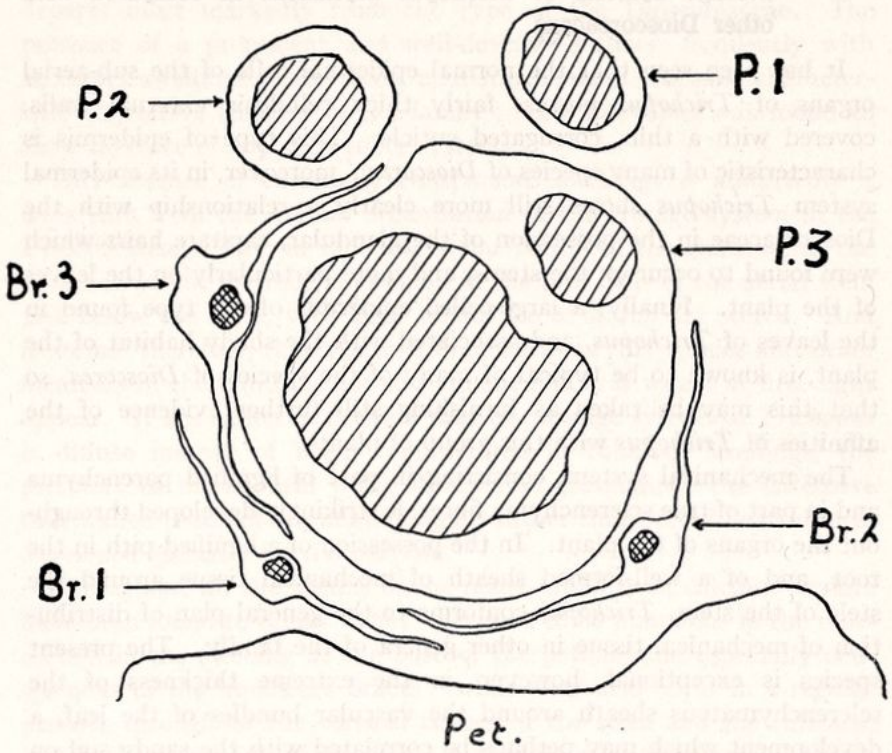
The peduncles are given off abaxially, so as to constitute two more or less distinct orthostichies, one on either side of the mid-anterior line. Diametrically opposite each peduncle arises a bract (Text Fig. 2). When branching takes place, the branch arises in the axil of a bract. It is evident, then, as far as one is able to make out, that the same constant relation is maintained between main axis and organs derived from it throughout the whole plant. The origin of the peduncles is directly comparable with the origin of the flowering shoot from the aerial stem, and again with the origin of the aerial stem from the rhizome. In each case the disturbance involves the innermost bundles, for it is the most centrally placed strands that constitute the vascular supply to the secondary structure ; and in each instance, too, a foliar structure is given off diametrically opposite to the branch. On the other hand, the branching of the main axis of the rhizome is to be compared with the branching of the main axis of the flowering shoot, as in each case the branch arises in the axil of a subtending leaf.

Each bract is narrowly and sharply triangular in outline, and in general anatomy resembles the scale-leaves which form a covering over the rhizome, with the exception that here there is no lignified band of tissue connecting the midrib with the edges of the leaf. This is as one would expect, for it is unlikely that in sub-aerial organs of this type so rigid a central mechanical system would be required as in corresponding structures in the soil.

The narrow cortex of the peduncle appears to resemble closely the cortex of the aerial stem. Large-sized raphide sacs are distributed through the groundwork of smaller, loosely packed parenchyma cells.

The stele is bounded by a rather narrow ring of mechanical tissue

similar to that found in the stem (Plate CCXLIX, Fig. 6). The vascular tissue is composed of six separate bundles, three of which are distinctly larger than the other three. In each bundle the xylem presents two diverging arches, each of which terminates in one or more large vessels, and in the " bay " of which lies the phloem. In the three large-sized bundles the phloem is split into three distinct patches, while in the bundles of smaller size there are only two separate phloem groups. Owing to a tendency towards disintegration, it was impossible



2. Diagram to show arrangement of bracts and peduncles on flowering shoot. Br. 1–3, bracts in transverse section. P. 1–3, peduncles in transverse section. Pet., portion of cortex of petiole. (×40)

to obtain peduncles in which the structure of the phloem elements could be made out.

A feature of interest in the very young leaves surrounding the apex of the reproductive shoot is the great number of raphide sacs which are very conspicuous in the rather limited amount of parenchymatous tissue.

From these observations on the flowering shoot of *Trichopus* it is not possible to draw many conclusions that are of value from the standpoint of comparison with other members of the Dioscoreaceae. Attention has already been drawn to the fact that the inflorescence, consisting here of a fascicle of flowers borne on long filiform peduncles, departs far from the usual type of the family. No special features

occur here, apart from such as have been noted in the descriptions of other organs of the plant. However, the occurrence of raphide sacs in such large numbers in the young bracts about the apex of the floral axis is of some interest, in that it demonstrates the extremely wide extent of the occurrence of these structures throughout the whole plant.

(D) General Account of the Epidermal, Mechanical, Conducting, and Storage Systems of Trichopus zeylanicus as compared with other Dioscoreaceae.

It has been seen that the normal epidermal cells of the sub-aerial organs of *Trichopus* possess fairly thick cellulosic external walls, covered with a thin, corrugated cuticle. This type of epidermis is characteristic of many species of *Dioscorea* ; moreover, in its epidermal system *Trichopus* shows still more clearly a relationship with the Dioscoreaceae in the possession of the glandular, capitate hairs which were found to occur on the stems, and more particularly on the leaves of the plant. Finally, a large-celled epidermis of the type found in the leaves of *Trichopus*, and associated with the shady habitat of the plant, is known to be typical of many of the species of *Dioscorea*, so that this may be taken as furnishing still further evidence of the affinities of *Trichopus* with this group of plants.

The mechanical system, consisting in part of lignified parenchyma and in part of true sclerenchyma fibres, is strikingly developed throughout the organs of the plant. In the possession of a lignified pith in the root, and of a well-formed sheath of mechanical tissue around the stele of the stem, *Trichopus* conforms to the general plan of distribution of mechanical tissue in other genera of the family. The present species is exceptional, however, in the extreme thickness of the sclerenchymatous sheath around the vascular bundles of the leaf, a development which may perhaps be correlated with the sandy soil on which the plant normally grows.

In the general plan and arrangement of its vascular system, *Trichopus* has been seen to represent a somewhat isolated type. The variation in the extent to which the xylem arches penetrate in towards the centre of the root is of interest. In the roots of species of *Dioscorea* on which perennial swellings occur, the vascular tissue is distinguished in plan from those species where the swellings are annual, by the fact that it does not reach the centre of the root ; so that *Trichopus* may be taken as showing in this point a structure approaching more closely to what is seen in the *Dioscoreas* with perennial root swellings than to that occurring in those species in which these swellings are only annual. At the same time it has been shown that the extent of vascular tissue is not constant in the root of *Trichopus*.

In the arrangement of xylem in the individual stem bundles this plant conforms to the type of the family, and its affinities with the

Dioscoreaceae are further confirmed by the tendency of the phloem to become split into several distinct groups. Finally, it must be pointed out that one of the principal peculiarities of the conducting system of the Dioscoreaceae lies in the very few individual bundles in the aerial stem as compared with most other Monocotyledons; and the possession of still fewer bundles in the ring may be regarded as another important piece of evidence linking *Trichopus* with the Dioscoreaceae.

One finds in the storage system those features in which *Trichopus* departs most markedly from the type of the Dioscoreaceae. The presence of a prominent and well-developed tuber, frequently with accessory swellings on the roots, constitutes one of the most characteristic vegetative features of the family; and *Trichopus* was found to show no trace of any such tuber system.

This absence of externally conspicuous swellings is admittedly a departure from the normal organisation of the storage system in the Dioscoreaceae. Yet, in the wide stelar region of the rhizome, in the broad cortex of the root, and again in the pith cells of the aerial stem just below the node, very large quantities of starch are stored. And it seems, therefore, that the difference between this species and other members of the family is not so fundamental as it would at first sight appear. It lies rather in the fact that the storage system of *Trichopus* is diffuse instead of being concentrated in tuberous swellings, the products of metabolism being distributed throughout the extensive thin-walled tissue of attenuated organs rather than stored in structures developed specially for the purpose.

Throughout all the organs of the plant raphides of calcium oxalate have been found to occur. They were seen to be numerous in the root-cortex, in the swelling at the base of the petiole, and especially conspicuous in the immature bracts; while they also occur in a regular manner throughout the cortical tissues of the stem and the rhizome, and in the mesophyll of the leaf. Raphide sacs of this particular type are found widely in the family; and the fact of their being so plentiful here, together with the presence in *Trichopus* of a characteristic swelling at the base of the petiole, similar to that constituting the pulvinus in the leaves of many *Dioscoreas*, certainly may be taken as two further points to support the relationship of *Trichopus* with the Dioscoreaceae.

(E) Summary.

A detailed anatomical investigation of plants of *Trichopus zeylanicus* from Ceylon has enabled me to confirm and extend the work of Queva (1894) on this plant, and to establish a number of points of difference and at the same time many features of resemblance between the anatomy of this species and that of other Dioscoreaceae. These points may thus conveniently be summarised :—

1. Anatomical Features in respect of which Trichopus zeylanicus departs from the Type of the Dioscoreaceae.

(1) The absence of any form of swelling or spiny outgrowth on the root system.
(2) The presence of only a single endodermis in the root.
(3) The fact that the aerial stem consists of only a single internode.
(4) The absence of any tuber system associated with the stem.
(5) The fact that the arrangement, number, and course of the vascular bundles of the stem cannot be readily brought into line with the plan of organisation that is typical of the Dioscoreaceae.
(6) The absence of any large-sized sieve tubes in the phloem.
(7) The absence of any trace of the anterior arch of vascular tissue which is so characteristic of the leaves of most Dioscoreaceae.
(8) The absence of extra-floral nectaries in the tissues of the leaf.
(9) The greatly foreshortened floral axis on which the filiform peduncles are borne in a fascicle.

2. Anatomical Features in respect of which Trichopus zeylanicus shows Evidence of its Affinity with the Dioscoreaceae.

(1) The presence of thin-walled cells constituting passage areas in the pericycle occurring immediately internal to the passage cells of the endodermis of the root.
(2) The very wide distribution of raphides of calcium oxalate throughout the organs of the plant. Especially was a resemblance noted between the large raphide-sacs, circular in cross-section, appearing in the sub-epidermal collenchyma of the stem and the similar structures occurring in an exactly similar position in species of *Dioscorea*.
(3) The presence of a corrugated cuticle on the epidermis of a number of the organs of the plant.
(4) The wide distribution of glandular, capitate hairs over the surface of the sub-aerial organs.
(5) The small number of the individual vascular bundles as compared with the majority of Monocotyledons.
(6) The existence of large vessels of the xylem in a position external to the phloem in the individual stem bundles.
(7) The subdivision of the phloem into several distinct phloem groups. Especially characteristic of the Dioscoreaceae as a whole was found to be the existence in the vascular tissue of the midrib of the leaf of as many as seven individually distinct phloem groups.
(8) The fact that the vascular tissue destined for the reproductive shoot constitutes an inner ring of bundles in the stem.

(9) The shape and the venation of the leaf. The minute terminal acumen was a noteworthy feature too, since it is found also in a number of species of *Dioscorea*.

(10) The pulvinar swelling at the base of the petiole.

(11) The tendency for the development of collenchyma in the outer cortical layers which lie immediately beneath the ridges and prominences of the stem and the petiole.

(12) The arrangement of stomata and the type of epidermis characterising the leaf.

Conclusion.

Trichopus zeylanicus will always be recognised as an isolated and anomalous species, which departs in many respects very far from the normal habit of the family in which it is placed. Nevertheless, the present investigation has shown that, despite its many divergent features, it presents in the details of its anatomy a very considerable weight of evidence to support its inclusion in this family. Accordingly, I am led to the conclusion that its peculiarities are not quite so marked as would at first sight appear, and that the facts of its anatomy go far to establish the affinities of *Trichopus* with the Dioscoreaceae.

REFERENCES.

Beccari, O. Nota sul Trichopodium zeylanicum. Thw.; Nuov. Giorn. Bot. Ital. ii (1870), 13.

Beddome, R. H. Icones plantarum Indiae Orientalis (1868–9), t. 290.

Bentham, G., & Hooker, J. D. Genera plantarum, iii (1883), 745.

Endlicher, S. Genera plantarum (1836–40), n. 2165.

Gaertner, J. De fructibus et seminibus plantarum, i (1788), 44, t. 14.

Hooker, J. D. Flora of British India, vi (1894), 297.

—— Botanical Magazine, cxx (1894), t. 7350.

Knuth, R. Das Pflanzenreich. Dioscoreaceae (1924), 346.

Lindley, J. Botanical Register (1832), sub t. 1543.

Pax, F. Engler-Prantl: Pflanzenfamilien, ii, Abt. 5 (1888), 136.

Queva, C. Recherches sur l'anatomie de l'appareil végétatif des Taccacées et des Dioscorées (1894), p. 394.

Trimen, H. The Flora of Ceylon, iv (1898), 280.

Uline, E. B. Engler's Botanische Jahrbücher, xxv (1898), 155.

EXPLANATION OF PLATES CCXLVIII–CCLII

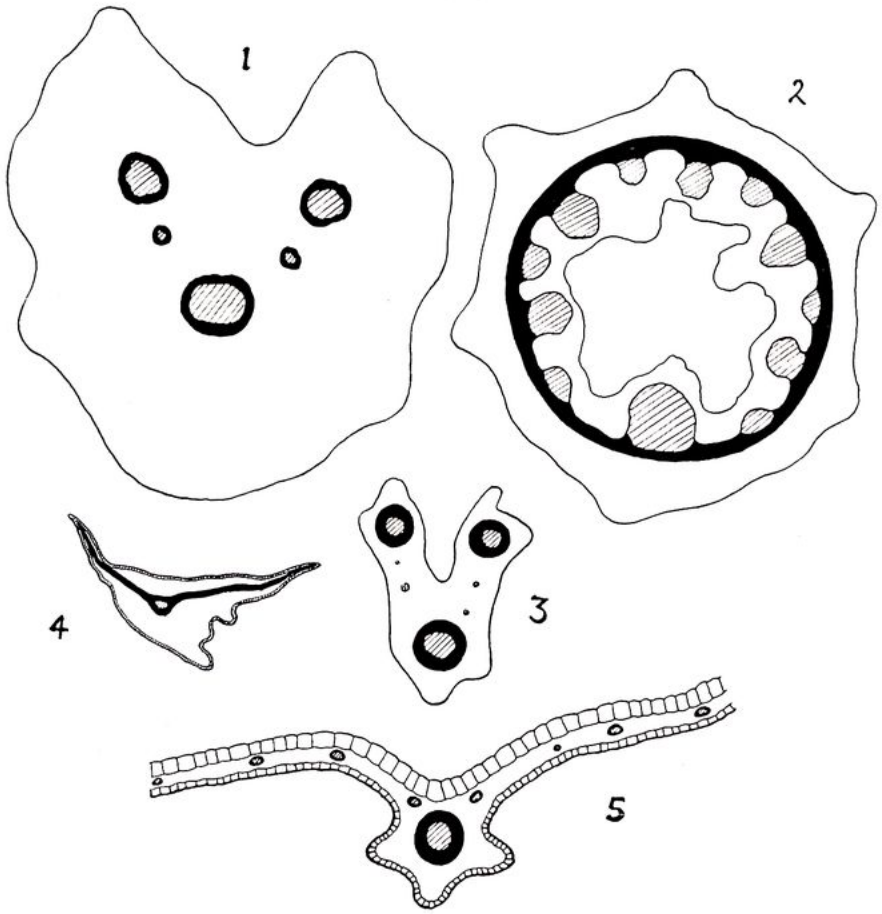
PLATE CCXLVIII.—Diagrams showing general arrangement of tissues. Mechanical tissue shown in black; vascular bundles shaded. Transverse sections of: (1) Base of petiole; (2) Stem; (3) Mid region of petiole; (4) Scale-leaf from rhizome; (5) Leaf, showing relative dimensions of cells of upper and lower epidermis. (2 and 4, ×52; 1, 3, and 5, ×26)

PLATE CCXLIX.—Diagrams showing anatomical details. Transverse sections of: (1) Midrib of leaf; (2) Part of stele of root; (3) Smallest type of vascular bundle found in stem; (4) Intermediate-sized vascular bundle of stem; (5) Largest vascular bundle of stem; (6) Mature peduncle, in which the cortex has disintegrated, and the position occupied by phloem is marked by gaps in the tissues. In 1–5 the phloem groups can be distinguished as patches of thin-walled tissue "stippled," and at *v* some of the large vessels can be seen. In 3–5 all the large vessels shown are thus marked. (×150)

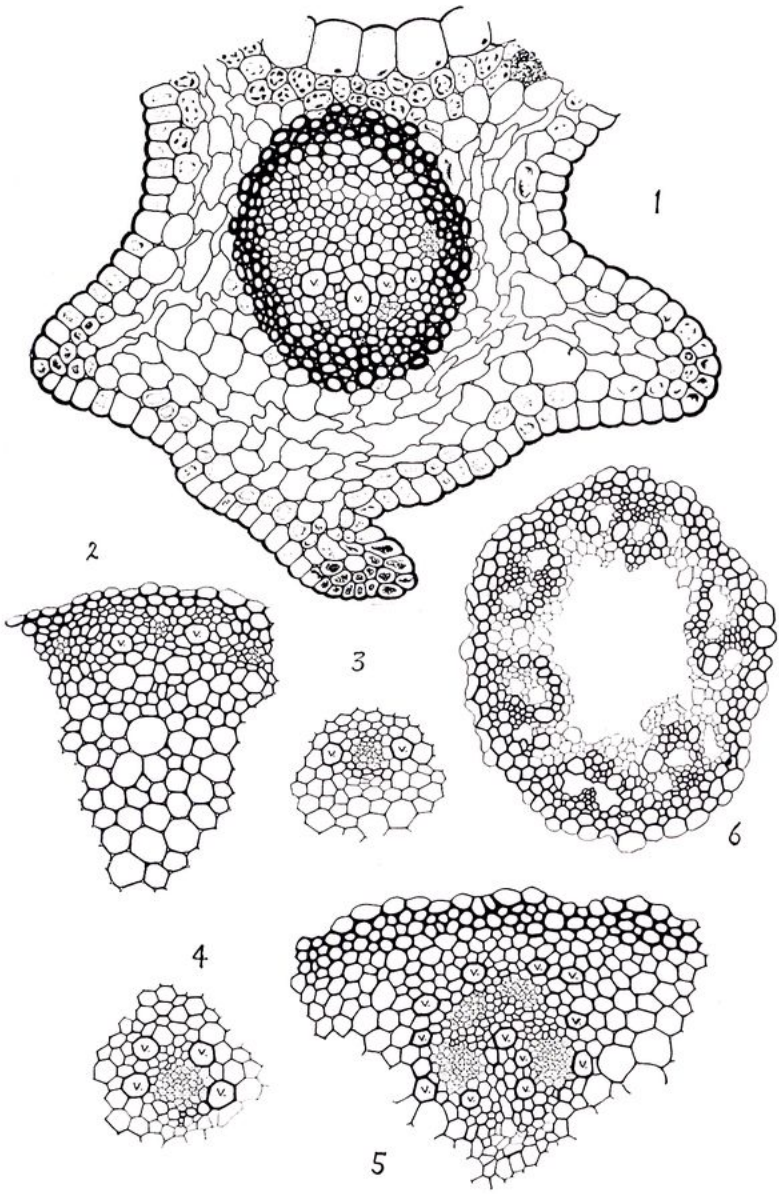
PLATE CCL.—Successive transverse sections of the rhizome, showing the mode of origin of the vascular tissue of the aerial stem. (For explanation see text.) (×20)

PLATE CCLI.—Successive transverse sections through node, showing transition from stem arrangement to petiole arrangement of vascular tissue. Mechanical tissue black; vascular bundles shaded. (×30)

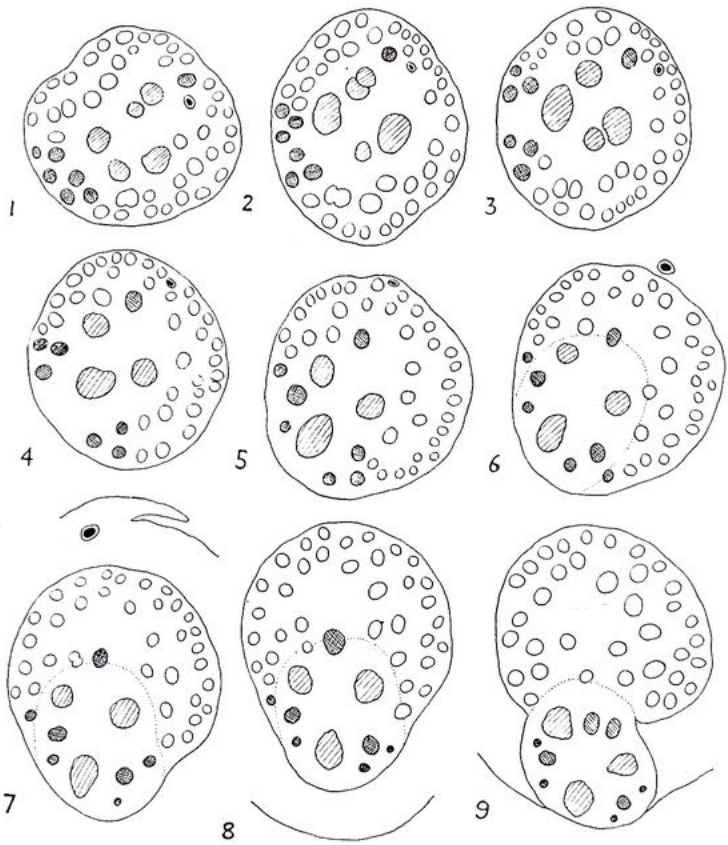
PLATE CCLII.—Successive transverse sections through the second type of node, showing the mode of origin of the vascular tissue of the reproductive shoot. Mechanical tissue black; vascular bundles shaded. Those of reproductive shoot "stippled." (×20)



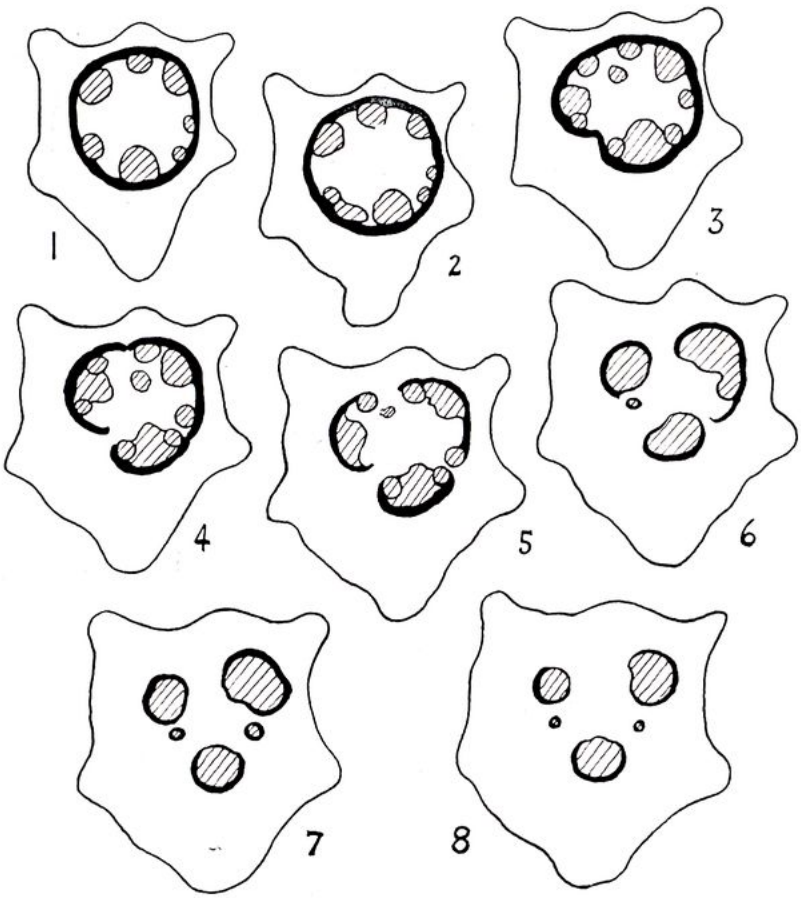
TRICHOPUS ZEYLANICUS GAERTN.



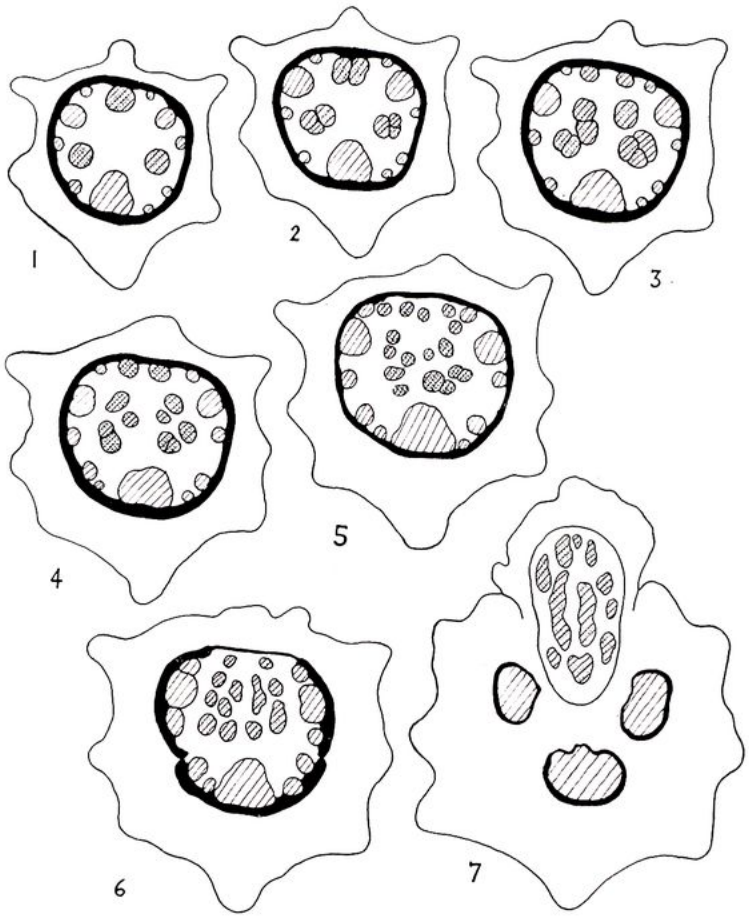
TRICHOPUS ZEYLANICUS GAERTN.



TRICHOPUS ZEYLANICUS GAERTN.



TRICHOPUS ZEYLANICUS GAERTN.



TRICHOPUS ZEYLANICUS GAERTN.