The Anatomy of *Psilotum triquetrum*.

BY

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With Plate XXXIX.

THE genus *Psilotum* is represented by four species, *P. triquetrum*, *P. flaccidum*, *P. complanatum*, and *P. capillare*. Baker¹, however, gives only two distinct species, *P. triquetrum* and *P. complanatum*, regarding *P. capillare* as merely a variety of *P. triquetrum*, and, similarly, *P. flaccidum* of *P. complanatum*. Of these, *P. triquetrum* appears to be the most frequent in occurrence, being reported from practically all the warmer regions of the world². The plant is found growing in the humus at the base of trees, amongst the roots of tree-ferns, and in the crevices of rocks. It is generally regarded as an epiphyte; but as young plants which had developed from bulbils, and also portions of the underground rhizome which had been broken off from the main plant, have been known to vegetate underground for a considerable length of time³, the plant may also be regarded as being saprophytic in nature. A small, but well-developed, specimen grew for some time in the soil amongst the roots of *Norantea guianensis* in one of the tropical houses at the Cambridge Botanic Garden. It was unknown how the plant originally came there⁴.

EXTERNAL MORPHOLOGY.

The plant consists of a much-branched, green, aerial stem bearing the sporangia and small reduced leaves, and a brown underground rhizome, which is likewise much branched. There are no roots.

¹ Baker ('87), p. 30. Willis ('97), p. 314.

² Spring ('49), p. 269, *et seq.* Bertrand ('81), p. 257.

³ Solms-Laubach ('84), p. 141.

⁴ Mr. Lynch tells me it is probably due to small pieces of the rhizome being broken off during potting, and one of these may have been unintentionally mixed with the soil in the pot of the *Norantea*.

The Aerial Stem.

The aerial stem forms externally the most noticeable part of a *Psilotum* plant. At its base, where it issues from the soil, it is smooth, brown, and circular in outline, but higher up it gradually becomes green in colour, and the surface is conspicuously ribbed. Branching is apparently dichotomous, the first bifurcation occurring as a rule near the base of the stem, and is repeated many times. Here and there trichotomy may occur, not only in the lowest portion of the stem, as Solms-Laubach¹ states, but also at the second, third, or fourth level of forking. Prantl² states that the branching of *Psilotum* cannot be regarded as dichotomous, for one of the branches arises in the axil of a leaf, whilst the other continues the growth and the phyllotaxis of the main shoot. In the case of *P. flaccidum*, however, in which the leaf-insertion is much clearer than in *P. triquetrum*, and is represented by the fraction $\frac{1}{2}$, Solms-Laubach³ has shown that the position of the leaves is not altogether regular in regard to the branching, whilst the phyllotaxis of the two branches points to dichotomy of the main shoot. As a rule, in *P. flaccidum* a leaf is found below each bifurcation. The first few leaves belonging to the two resulting branches continue the distichous arrangement as if no forking had occurred; thus, the first of these leaves is found on the outer side of the branch which is furthest away from the leaf below the bifurcation, whilst the second leaf is immediately above the latter and on the nearer branch. Higher up each branch assumes the usual distichous arrangement. It may, however, occasionally happen that the leaf usually found below the bifurcation is carried up, and is therefore situated on one of the two resulting branches. Judging from external appearances only, the branching would seem to be, as a rule, a regular dichotomy, although at times, especially towards the apex, branches of unequal size may be found. The question, however, will be referred to later in discussing the internal anatomy.

Leaves are present as small, scale-like structures. The phyllotaxis cannot be represented by a fraction which is constant throughout the plant. As Solms-Laubach⁴ has pointed out, in the smaller, three-angled branches near the apex the leaf-insertion is easily ascertained, and is clearly represented by the fraction $\frac{1}{3}$; but in lower and stouter regions of the plant, owing to a certain extent to the twisting of the stem which often occurs, the leaf arrangement is much less clear and cannot be definitely or satisfactorily determined.

The sporangia occur, as a rule, on the later-formed branches, but they may be found on older branches near the base of the stem. The sporangial

¹ Solms-Laubach ('84), p. 163.

² Prantl ('72), p. 92.

³ Solms-Laubach ('84), p. 165. Pl. XXIII, Figs. 10 and 11.

⁴ Solms-Laubach, loc. cit., p. 164.

leaves are bi-lobed, a feature which makes it easy to locate even very young sporangia. The sporangia themselves are for the most part trilocular, but bilocular ones are occasionally found.

The Rhizome.

The much-branched rhizome of *Psilotum* bears no leaves or roots. In texture it is much softer than the aerial stem, and the surface is generally covered with fine, brown hairs, though these may be better developed in some regions than in others. The apices of the branches are white and naked, and the whole rhizome forms a somewhat confused mass of branches, which cannot be disentangled without breaking. Small circular, or oval, white spots occur at intervals on the branches; these are destitute of hairs, and may be sunk or slightly raised above the surface. They represent dormant lateral buds which are capable of resuming growth under favourable conditions.

Here and there some of the rhizome-branches assume a vertical, instead of a horizontal, position, and grow upwards towards the surface of the soil; these are future aerial branches. As they develop, the superficial hairs disappear and the surface becomes smooth and hard, and small scale-like leaves shortly make their appearance.

Before passing to the internal anatomy, reference must be made to Professor Bertrand's¹ detailed account of *Psilotum*. In regard to the external structure, Professor Bertrand has described the aerial stem under the heads of 'cladodes "souches,"' 'cladodes of the first, second, third, &c. order,' 'terminal and sporangiferous cladodes,' and 'simple, aerial branches,' the last being only occasionally found. Similarly, the underground portion has been subdivided into 'simple subterranean branches' and 'sympodia' of these, and 'subterranean cladodes' and 'sympodia of cladodes'.² These structures have not the same morphological value. The 'simple branches' are to be considered as such, whilst the 'cladodes' and 'sympodia of cladodes' are to be regarded as consisting of two or more stems which are united throughout the greater part of their course. At the apex, however, their real nature may be detected, this being shown by the presence of two or more 'centres of growth' being always found, each of which may possess a distinct apical cell. The first elements of the xylem-strand to be differentiated below the apex consist of two or more separate groups of spiral tracheids, each group corresponding to an apical 'centre of growth.'

¹ Bertrand ('81), p. 252, *et seq.*

² It is of course open to question whether the term 'cladode' can rightly be used in regard to the rhizome; cf. Goebel's definition of the term, viz. 'a branch consisting of one internode counterfeiting a leaf.' The branches of the rhizome of *Psilotum* are brown, and destitute of chlorophyll; they fulfil the functions of roots, and have not the slightest resemblance to leaves.

In the case of the aerial stem the branching, as a rule, is fairly regular, and it might for some purposes be convenient to term the series of bifurcations as branches of the first, second, third, &c. order. Taking Professor Bertrand's sub-divisions as a whole, there is nevertheless some doubt whether such detailed and often confusing distinctions are satisfactory. In regard, however, to the rhizome of *Psilotum*, it must be stated that the above sub-divisions¹ have not been confirmed, although it may possibly be due to less well-developed material. The branching in the rhizome is as a rule very irregular, although here and there dichotomy may be found. In other cases, judging by the external appearance, ordinary lateral branches are found; these are generally smaller than the main branch from which they are given off, or again they may remain as dormant lateral buds, which may develop under suitable conditions.

Seeing that the apices of the branches are naked, they are in consequence easily injured. When this occurs, microscopical, as well as superficial, investigation shows that the apex itself is black and discoloured, whilst one of the lateral buds lying in its neighbourhood frequently exhibits distinct signs of renewed activity.

The question as to the presence of Professor Bertrand's centres of growth, as shown by the existence of the apical cells and the distinct protoxylem-groups, will be referred to later in dealing with the anatomy of the plant.

ANATOMY.

The Aerial Stem.

Psilotum possesses a single central stele (Pl. XXXIX, Fig. 1). The stem is ribbed in the stouter parts of the plant; towards the apex it is triangular in outline. The epidermis is cuticularised, and stomata are present in fairly large numbers lying in the grooves of the stem between the ridges (Fig. 1, *st*). The guard-cells are slightly sunk below the level of the other epidermal cells, and the outer walls are cuticularised. The cortex is composed of three zones, an outer, which is parenchymatous and assimilating, a middle sclerenchymatous, and an inner parenchymatous surrounding the stele. The outer parenchymatous zone (Fig. 1, *pa*) is composed of peculiar cells, the structure of which is best seen in longitudinal sections (Fig. 3). The lateral walls bulge out at regular intervals, each cell having 2-4 such swellings. The swellings of adjacent cells touch each other, and in consequence a conspicuous row of intercellular spaces is formed. The cells themselves are nucleated and contain chlorophyll. The sclerenchymatous zone (Fig. 1, *sd*) consists of thick-walled fibrous elements with pointed ends, and the walls are perforated by small slit-like pits. Towards the centre this sclerenchymatous zone passes gradually into the inner

¹ Solms-Laubach ('84), p. 158.

parenchymatous region (Fig. 1, *p'a*) immediately surrounding the stele. The cell-walls of this tissue are perforated by numerous oval or circular pits, which vary in size. Starch is generally found in the cells, and in the lower and older parts of the plant conspicuous nodules of varying shape and size (Fig. 1, *n*) are also present. These nodules are unaffected by acetic and nitric acids, and the fact that they are left as an insoluble residue after several days' maceration and boiling in Schulze's macerating fluid suggests the presence of silica.

The endodermis, which Bertrand describes as a badly defined layer, is however clearly recognizable, after suitable treatment or after staining, when the thickenings on the radial walls stand out very distinctly (Fig. 2).

The centre of the stele is occupied by a group of sclerenchymatous fibres (Fig. 1, *f*); the walls of these have numerous, small, simple pits. In the stouter parts of the plant the fibres form a conspicuous group; higher up the number gradually decreases until only two or three, and finally none at all, are present. The xylem surrounds the central group of fibres with a star-like outline, the projecting points marking the position of the protoxylem-groups, the number of which varies with the size and region of the stem. In stouter branches nine or ten may be found, in the small apical branches two or three only may be present. In the latter case the xylem may be present as a small central strand, or it may form two small masses lying close together, each containing one group of protoxylem. The xylem is made up of ordinary scalariform tracheids, the protoxylem of spiral elements.

Between the endodermis and the xylem a mass of tissue is found which is very difficult to differentiate. Seen in transverse section, there is no clearly defined pericycle, the tissue consisting of a mass of parenchymatous elements of varying size. Treatment with aniline chloride gives signs of lignification¹ in some of the cells, especially at the corners; and this is more noticeable in the tissue lying outside the projecting tips of protoxylem (Fig. 2). In longitudinal sections the main mass of the tissue is seen to be composed of elongated parenchymatous cells (Fig. 4, *pa*) with conspicuous nuclei. Staining with chlor-zinc-iodide shows that the walls of these cells are covered with numerous small oval or circular pits or pores. Besides the nucleated parenchyma, long tube-like elements (Fig. 4, *st*) occur singly, or occasionally one or two together, which may possibly be regarded as sieve-tubes. These tube-like elements are frequently crowded with granules which stain yellow with chlor-zinc-iodide. With Delafield's haematoxylin the walls stain a deeper blue than in the case of the ordinary parenchymatous cells, and scattered globular masses are found of varying size (Fig. 4, *m*) which stain very deeply. These are probably of the same nature as the

¹ Vaughan Jennings and Hall state that in *Tmesipteris* they failed to find lignification of the phloem, but the material at my disposal showed it far more noticeably and clearly than in *Psilotum*.

refractive spherules described by Poirault¹ as occurring in the sieve-tubes of many ferns. No nuclei could be found in these tubes, and no trace of callus could be demonstrated by treatment with coralline soda or with a watery solution of aniline blue. The phloem, or phloem tissue, is not stained blue by iodine as in the case of *Lycopodium*. Owing to the fact that no definite pores or sieve-plates have been observed in this tissue, it is of course open to question whether in *Psilotum* the term sieve-tube can be applied. It has been likewise impossible to locate any definite tissue corresponding to the protophloem, although Russow² in 1872 figured and described such elements as forming regular groups alternating with the protoxylem masses. Later, however, he modified his earlier view, stating that the protophloem (defining this as the first of the sieve tissue to be differentiated) consisted of numerous groups, each of which was composed of two or three elements lying at the periphery of the vascular strand.

Bifurcation of the stem is very simple (Fig. 1). The stele widens horizontally and new protoxylem-groups make their appearance (Fig. 1, $p'x'$). The central mass of fibres with the surrounding xylem splits into two approximately equal halves, and new tracheids arise so that each of the two resulting groups of fibres are surrounded as before by xylem, though for a short time they touch the phloem tissue directly. The two strands become further apart, the endodermis then breaks and closes up round each. This process is repeated at each level of bifurcation.

Unlike *Tmesipteris*, in which each leaf receives a small vascular strand from the stem, the leaves of *Psilotum* have no vascular bundle.

In regard to the region in which the sporangia occur, each sporangio-phore receives a small vascular strand from the main stem. In stouter branches this strand is much the smaller, but towards the apex, where the stem branches are slighter, it is frequently equal in size to the main stele left in the stem.

The Leaf.

The leaf of *Psilotum* has a very simple structure (Fig. 5), the outermost parenchymatous zone and the epidermis of the stem alone being continuous with the tissues of the leaf. Externally the leaf is covered by a typical epidermis with cuticularised outer walls, but no stomata are present. The centre of the leaf is occupied by parenchymatous tissue; near the apex this consists of elongated, nucleated cells, which, lower down, gradually pass into the parenchyma of the stem with its characteristic intercellular spaces.

The Apex of the Aerial Stem.

The apex of an aerial branch of *Psilotum* ends in a conical prominence, at the summit of which a three-sided apical cell³ is found. In the smaller

¹ Poirault ('93), p. 139.

² Russow ('72), Taf. XI, Fig. 30; also ('75), pp. 20 and 40.

³ Strasburger ascribes an apical cell only to the underground stem. Solms-Laubach has

branches the whole apex is surrounded by two or three foliaceous leaves, which serve as a protection, but it is easily recognized in longitudinal sections. In the stouter shoots, especially in those bearing the branches with fertile leaves and sporangia in all stages of development, the apex is much hidden. It is often difficult to distinguish from the leaves, each of which arises as an outgrowth of the apical tissues, and at an early stage may show considerable resemblance to the stem apex. The presence of an apical cell in the young leaf, however, cannot be stated as constant, though at times it appears to be present. Professor Bower¹ has also pointed out that it is often impossible to say at an early date whether a leaf will be a fertile one or not.

The apical cell of the stem (Figs. 6 and 7) has a large nucleus and granular protoplasmic contents. It has been termed by Professor Bertrand² a 'dermatogen' apical cell; but the subsequent divisions in the cells which are cut off from it do not appear to bear out this statement, other layers being derived from these divisions besides the dermatogen itself. It has not, however, been possible to trace the connexion between the cells cut off from the apical cell and the developing stele. Each cell which is cut off from the apex appears to divide by a tangential wall into an inner and outer cell (Fig. 7), and the inner again divides so that three result, an outer, middle, and an inner. A vertical wall also arises at an early stage, but it has not been possible to determine satisfactorily any of the subsequent divisions. The outermost of the three cells resulting from the tangential divisions forms one of the cells of the dermatogen layer, which passes over into the epidermis of the stem.

The stele in the stem branches ends in an apical meristem of undifferentiated elements with conspicuous nuclei. Between this meristem and the apex itself is a mass of tissue, the product of the subsequent divisions of the segments cut off from the apical cell; the tissue is composed of irregular cells with comparatively large nuclei.

In regard to the dichotomy of the aerial shoot it is difficult to make any definite statement. As Solms-Laubach³ has pointed out, the behaviour of the apical cell, if present, is an important factor in such a question. In dichotomy the single apical cell may on the one hand divide medianly into two, or again it may disappear altogether before bifurcation occurs, two new apical cells being differentiated in the two resulting branches. The nature of the apparent dichotomy would be open to doubt if it was shown that the single original apical cell continued to exist as the apical cell of one of the branches, a new one being cut off laterally for the second branch. It has been impossible to say definitely what occurs in *Psilotum*. The

confirmed this view, and is inclined to agree with Strasburger in regard to the absence of a distinct apical cell in the aerial stem, although he finds one to be present in the fruiting branches.

¹ Bower ('94), pp. 42 and 49; also Juranyi ('71), p. 177.

² Bertrand ('81), p. 441, *et seq.*

³ Solms-Laubach ('84), p. 170.

apical cell has never been observed dividing into two. On the other hand, radial sections of bifurcating branches have never shown an apical cell to be present at the summit of either branch, although we have seen that it is generally found in older ones. From this we might then conclude that a new apical cell arises later in each resulting branch in place of the original single one which was present below the level of forking.

The Subterranean Stem.

In accordance with his definitions of the external structure, Professor Bertrand has described in some detail the anatomy of the rhizome of *Psilotum*. The structure of a simple branch and of the various 'cladodes' is given, and more or less hard and fast rules laid down as to the appearance presented by the stele in each sub-division. As already stated in this paper, it has been impossible to distinguish satisfactorily these various underground structures from their external appearance; and investigation of the anatomy, moreover, has not led in any way to their confirmation. The structure of the stele depends, for the most part, on the size and development of the branch in question, and not on the position it occupies in regard to the main mass of the rhizome. According to Bertrand, the typical structure of the stele in a simple branch consists of a diarch band of xylem, with spiral protoxylem-elements at the two extremities of the band. The present investigations have not confirmed this as being in any way constant or typical. The xylem-strand varies considerably in size and shape (Figs. 8, 9 and 10); in smaller branches two or three tracheids alone may be found, in stouter and more mature regions of the rhizome an irregular mass (Fig. 8) or a band-shaped strand¹, or again a central group of xylem more or less circular in outline may be found. The tracheids are scalariform, with no parenchyma interposed, and the spiral protoxylem elements of Bertrand appear to be generally absent. Both in transverse sections and in series of longitudinal sections cut on a microtome no trace of spiral or annular elements are often found, the first elements to be differentiated at the apex being as a rule of the ordinary scalariform type². These results therefore agree with the earlier researches of Russow³, who came to a similar conclusion in regard to the absence of typical spiral or annular elements in the protoxylem.

A similar absence of typical protoxylem also occurs in the rhizomes of *Loxsoma*, and of some species of *Schizaea* and *Anemia*⁴.

Figs. 10 and 11 represent the xylem of a branch of a rhizome below

¹ See also Boodle ('04), p. 500, Fig. 46.

² In some cases transverse sections have given one or two tracheids of smaller size than the rest, which might be taken for protoxylem. Further investigation of sections belonging to the same series have almost invariably shown that these elements merely represent the narrow pointed ends of scalariform tracheids of ordinary size.

³ Russow ('75), p. 21.

⁴ Gwynne Vaughan ('01), p. 79; Boodle ('01), pp. 375, 381.

the level of bifurcation. In neither case is the bifurcation quite equal. Fig. 10 shows a fully developed and fairly stout branch, whilst the section given in Fig. 11 was taken a little below the apex of a rhizome branch. The main stem has only three tracheids lignified; whilst the smaller branch, which in this case ended in a dormant lateral bud, contains but two lignified elements separated from each other by parenchyma.

Surrounding the xylem is the phloem tissue, which is similar in general respects to that found in the aerial stem, but is less well developed. The so-called sieve-tubes and nucleated parenchymatous cells are present, but the pitting on the walls is less noticeable, and there is practically no lignification of the sieve-tubes. The endodermis has its usual features, although not so easily distinguishable as in the aerial stem, and the thickenings often extend to the tangential walls (Fig. 8 a).

The main mass of the cortex is composed of large thin-walled cells containing starch. The two or three layers, however, lying next to the endodermis, have their walls coloured a dark brown; the coloration being due, according to Bertrand, to 'gélification' and 'humifaction' of the cell-wall. Investigation of this brown substance, however, shows that, whilst unchanged by the action of acids, it is slightly soluble in eau-de-javelle, but dissolves in potash, after which the cell-walls give the usual blue coloration on treatment with chlor-zinc-iodide. It is probably of the same nature as that described by other writers¹ as occurring in Ferns, and which has been termed 'phlobaphene.'

Many of the cells of this outer thin-walled cortex are crowded with filaments of the Fungus which occurs so noticeably in the rhizome of *Psilotum* and *Tmesipteris*. The filaments in some cases form a thick mass in the centre of the cell, in which it is impossible to distinguish individual threads; in other cells, in which the mycelium is actively living, the coils of threads are loose, and by staining with alum and Haidenhain's haematoxylin it is possible with an oil immersion lens to make out distinct nuclei. Globular or pear-shaped swellings occur often very abundantly on the mycelial threads; as many as thirteen were counted on one occasion in one cell alone. The walls of these structures, which according to Bernatsky² are aborted sporangia or 'sporangoïds,' also show nuclei with Haidenhain's haematoxylin. Bernatsky also states that he has obtained successful cultures of this Fungus, which he ranks as *Hyphomyces*.

The cells of the outermost cortical layer grow out into absorptive hairs. Each hair is composed of two cells, a basal cell and the main mass of the hair itself. The walls are coloured brown.

¹ Poirault ('93), p. 127. Boodle ('01), p. 361. Yapp ('02), p. 194.

² Bernatsky ('99).

The Apex of the Subterranean Stem.

The apex of an underground branch of *Psilotum* is terminated, as in the aerial branches, by a three-sided apical cell. The walls, too, arising in the segments cut off from this apex appear to be similar to those in the aerial part of the plant; and again no connexion has been traced between the apical meristem, in which the stelar tissue ends, and the apical cell itself.

The first xylem tissue to be differentiated and lignified appears to be often a single, ordinary, scalariform tracheid (Fig. 12); but in other cases two tracheids may appear at approximately the same time, lying either side by side, or separated from each other by one or more parenchymatous cells.

The presence of one of Professor Bertrand's 'cladodes' is said to be marked by more than one 'centre of growth' being found at the apex, each of which has a distinct apical cell. The apical cells in question may lie in the same or different planes. It is certainly true that towards the apex of a branch the lateral buds may often be present in large numbers, and these may either grow out directly into ordinary branches, or again may remain dormant, becoming more widely separated from each other by the subsequent increase in length of the branch. Transverse and longitudinal sections cut on a microtome do not, however, seem to show at any time that more than one apical cell is present at the actual apex itself, although a somewhat lateral cell may at times be found belonging to a dormant bud. It is often impossible to detect an apical cell or cells in a branch which is about to bifurcate, although after forking these may make their appearance in the two resulting branches. This may point, as in the case of the aerial stem, to the fact that the cells in question are developed secondarily from the apical meristem of their respective branches. In no case has an apical cell been observed which is dividing medianly into two, this fact agreeing with the investigations of Solms-Laubach¹.

The Intermediate Region.

This region includes the base of any aerial stem, from the level at which the external appearance gradually changes from the green ribbed surface to the smooth brown exterior, down to the point of insertion of this vertical stem on the rhizome.

At the extreme base the stele of the stem possesses more or less the structure found in an ordinary rhizome branch, viz. a central strand of xylem of varying size and shape, with no clearly defined protoxylem, and surrounded by phloem-tissue. The walls of the two or three cortical

¹ Solms-Laubach ('84), p. 171.

layers next to the endodermis have deeply coloured brown walls. Passing gradually up the stem, it is seen that the superficial hairs have disappeared, and the whole thin-walled cortex is gradually replaced by the brown-walled tissue. The xylem increases in amount, parenchymatous cells may be present scattered irregularly amongst the tracheids, but the protoxylem is often hard to determine, although further up the stem two and then three or more groups make their appearance. The secondary tracheids, which were first observed and have recently been described by Boodle¹, appear in this region. Higher up, the stele passes through an interesting stage (Figs. 13 and 14). The amount of xylem increases in extent, the three or four protoxylem-groups can be readily distinguished, and the parenchyma, instead of being scattered amongst the tracheids, lies in the centre as a more or less distinct pith (*pa*). In Fig. 13 it is seen that one tracheid (*t*) alone is left in the centre, whilst the xylem forms a ring broken only at one point (*g*). Further up again, the xylem forms for a short time a complete, unbroken ring round the central pith. This tissue is composed of nucleated elements, with thin areas on their walls, but no sieve-tubes have been observed, nor has any internal endodermis been detected. A few sections higher up, the first of the central fibres makes its appearance (Fig. 14, *f*) in the pith, the number then gradually increases, until the typical central mass is formed, surrounded by the xylem with its radiating points of protoxylem. The cortex gradually changes from the uniform mass of brown-walled cells to the usual arrangement of parenchymatous and sclerenchymatous zones found in the aerial stem.

THE REPRODUCTIVE ORGANS.

The nature of the sporangial apparatus in the Psilotaceae has given rise in the past to much controversy. The researches and results of Professor Bower² seem, however, to be conclusive in ranking the sporangium itself, not as a terminal outgrowth of a reduced axis which bears two leaves, but as an outgrowth from the sporangial leaf, which is bi-lobed possibly for a protective purpose. The whole sporangiophore is then a single foliar member. Investigations on the origin of the sporangium during the work on this paper have led to similar conclusions.

With the exception of the vegetative reproduction by means of bulbils, described by Solms-Laubach³, and the prothallus found and described by Lang⁴ as possibly belonging to *Psilotum*, nothing is known of the development of either *Psilotum* or *Tmesipteris*. Attempts have

¹ Boodle ('04), p. 499.

² Bower ('94), loc. cit.

³ Solms-Laubach ('84), loc. cit. 139.

⁴ Lang ('01), p. 405. See also Dr. Lang's paper in the present number of the *Annals of Botany*, 'On a Prothallus provisionally referred to *Psilotum*.'

been made to germinate spores of *Psilotum*, but without success. The spores have been sown in ordinary soil, in sterilised soil and sand, with varying conditions of heat, light, and moisture, at the base and in the crevices of tree and fern trunks in the tropical houses at Cambridge. Spores also have been sown in hanging-drop cultures, in water, and in different solutions of salts. Cultivations of the Fungus have also been made, and either the soil in which the spores were sown or the spores themselves were infected with portions of Fungus, but with no success. At the time of writing more attempts are being made under different conditions, though it seems improbable that any favourable results will follow.

THEORETICAL CONCLUSIONS.

Psilotum is generally regarded as representing an ancient type, which has retained to a certain extent some of its primitive features, whilst showing at the same time modifications due to its manner of life. Mr. Boodle¹ considers that the secondary tracheids in the stem probably represent a more normal secondary thickening, the reduction being in correlation with that of the leaves. Prof. Lignier², however, regards the Psiloteae as a very ancient type, this being shown by the primitive nature of the leaves.

In relation to the foliar structure the question as to the origin of the pith in *Psilotum* is of interest. If the small scale-like leaves with no vascular supply are to be regarded as primitive, then there is no doubt as to the stelar nature of the pith, for unlike other Pteridophyta there are no leaf traces to be considered, and the branching is not altogether constant at this level and cannot be taken into account. There are, therefore, no obvious points at which any continuity can be traced and any intrusion of the cortical into the stelar tissues can be observed. The protostele in the lower part of the stem is therefore succeeded by a medullated condition, and no further stage is found except the substitution, for a purely mechanical reason, of sclerenchymatous fibres for the parenchyma in the aerial stem. As each aerial branch from the rhizome turns to grow vertically upwards above the soil, cortical as well as stelar tissues undergo considerable change. More mechanical support is needed by the plant, and this for a short time is undertaken by the whole brown-walled cortex. Later the stele increases somewhat in size, though the xylem remains approximately the same in amount, and parenchyma replaces the conducting tissue of the stele for a short distance. Sclerenchyma, however, soon takes the place of this thin-walled pith, and in correlation with the necessary increase in the assimilating tissue of the stem the cortical sclerenchyma decreases.

¹ Boodle ('04), p. 505.

² Lignier ('08), p. 106.

It seems, however, to be more likely that the leaves of *Psilotum* represent reduced, and not primitive, structures, for in *Tmesipteris* the leaves and leaf traces are well developed. In this case a suggestion, which has been given by Tansley and Chick¹ in their paper on *Schisaea Malaccana*, may be also made for *Psilotum*. The stele remains the same in size, but the demand for water conduction is less, and hence tracheids, which originally occupied the centre of the stem, are no longer developed and their place is taken by ordinary parenchyma. The great reduction of the leaves in *Psilotum* is a point in favour of this suggestion.

The position of the Psilotaceae amongst the Pteridophyta is not very clear. The family was formerly placed as a sub-group of the Lycopodineae, but of late this affinity has been regarded as being somewhat remote, whilst a stronger relationship has been shown to exist with the fossil group of the Sphenophyllales. Anatomically, however, the Psilotaceae show certain Lycopodinean features. Professor Bower in 1893² drew attention to the resemblance between the central stele of the Psilotaceae and that found in the axis of *Lepidostrobus Brownii*. He enumerates the four chief points of resemblance, the crenulated margin of the xylem, the definite layer of endodermis as in *Psilotum*, the slight bulk of phloem tissue and absence of distinctive characters in it, and lastly, the presence of a parenchymatous pith in *Lepidostrobus* which resembles that 'well known to occur in *Tmesipteris*, though its place is taken in *Psilotum* by thick-walled sclerenchyma.' The presence, therefore, of a central thin-walled pith in the stem of *Psilotum* helps to strengthen the possible relationship.

There is again a strong resemblance between the aerial and intermediate regions of the stem of *Psilotum* and the fossil stems of *Lepidodendron mundum*³. Some sections of the latter in the Manchester Museum show a distinct medulla of varying size, the xylem forming a definite ring which may be broken at some levels. Other sections, again, show this parenchymatous pith replaced by thick-walled tissue as in *Psilotum*.

The 'secretory' zone⁴ of some Lepidodendroid stems is absent in *Psilotum*, but the somewhat unsatisfactory nature of the phloem may possibly be another link, though a slight one, between the two forms.

The affinity of the Psilotaceae with the Sphenophyllales is based not only on anatomical grounds, but also on the nature of the sporangial apparatus⁵. From the anatomical point of view, the characteristic triangular mass of primary wood, which is so noticeable in the stem of *Sphenophyllum*, recalls the structure of the smaller branches of an aerial stem of *Psilotum*, and the discovery of secondary tracheids serves to strengthen this

¹ Tansley and Chick ('08), p. 499.

² Bower ('93), p. 337.

³ Williamson ('89), p. 197, Pl. 6, Figs. 7-14.

⁴ Seward ('00), p. 155; ('02), p. 38. Weiss ('01), p. 3.

⁵ It has already been stated in this paper (p. 599) that in the Psilotaceae the synangium and its axis are to be regarded as the product of a single fertile leaf.

resemblance¹. In his account of the structure of *Cheirostrobis* in 1897², and again later in 1900, Dr. Scott has compared the synangium and its axis in the Psilotaceae to the ventral sporangiophore of the Sphenophyllales, regarding the vascular supply of the leaf and synangium in *Tmesipteris* as comparable to that found in the bract and sporangiophore of a *Sphenophyllum*. A still closer affinity between the Psilotaceae and the Sphenophyllales was suggested by Thomas³ in 1902, and based largely upon certain variations commonly met with in the fertile structures of *Tmesipteris*. Dichotomy may occur in some of the sporophylls, accompanied by an increase in the number of synangia; and this condition, which is also found, but less frequently, in *Psilotum*, is regarded by Thomas as an ancient feature of the Psilotaceae. Again, the synangium in *Tmesipteris* may be raised on a stalk or pedicel, and this is compared to the sporangiophore of *Bowmanites Römeri* with its two sporangia. Whether we accept such variations as representing normal conditions or otherwise, there nevertheless seems to be little doubt that a strong resemblance exists between the Psilotaceae and the Sphenophyllales in regard to the sporangial structures.

Professor Bower⁴ has adopted Thomas's view as to the close relationship of the two groups, and would include the Psilotaceae and the Sphenophylleae together in the Sphenophyllales. The two series are regarded as being related, but as having at the same time two distinct lines of evolution. Whilst admitting with Professor Bower the great importance of the spore-producing members in plants, nevertheless other considerations must also be taken into account. The structure and development of the young sporophyte, the anatomy of the mature plant, and again, the nature of the gametophyte, are points which must be considered, even though they may be ranked as secondary in importance. Dr. Scott⁵ has suggested that the Psilotaceae may be allied, though very remotely, to the Lycopodiaceae, having perhaps branched off from the main line of Lycopod descent very far back, at a point where some of the characters common to the Sphenophyllales were still retained; a knowledge therefore of the gametophyte and of the young sporophyte might throw fresh light on this possible relationship. As matters stand the affinity of the Psilotaceae with the Sphenophyllales is clearly the most marked, but until a further knowledge of the development of the living genera of *Psilotum* and *Tmesipteris* is known it would seem a little premature to assign to them a definite position in a group which hitherto has only included fossil forms.

In regard to the rhizome of *Psilotum*, a considerable similarity in structure has been found to exist with the fossil root or rhizome recently described and figured by Professor Weiss⁶. The structure of the two

¹ Boodle ('04), p. 506.

² Thomas ('02), p. 342.

³ Scott ('00), p. 499.

⁴ Scott ('97), p. 27; ('00), p. 499.

⁵ Bower ('08), p. 229.

⁶ Weiss ('04), p. 255.

groups of xylem with the somewhat irregular protoxylem, and again the whole appearance of the cortex with its absorptive hairs and cells with clearly defined fungal filaments and probable reproductive bodies, recall very forcibly some sections of *Psilotum*. As Professor Weiss has pointed out, it is impossible to decide the systematic position of this fossil root or rhizome until more is known of the whole plant to which it belongs; too much stress, therefore, must not be laid on these resemblances to *Psilotum*, however strongly marked and interesting they may be.

SUMMARY.

1. *Psilotum* possesses a much-branched aerial and subterranean stem, and greatly reduced leaves with no vascular supply. There are no roots.

2. The plant is monostelic throughout. A protostele is found at the base of the aerial stem, and this is often succeeded by a medullated stage. In the aerial branches a central core of sclerenchymatous fibres is found.

3. The protoxylem is often absent in the underground branches. The phloem throughout is poorly developed, though elements resembling sieve-tubes are present. Lignification of the phloem tissue may occur in the aerial stem.

4. Owing to its saprophytic manner of life, *Psilotum* probably represents a much reduced form, which may have retained some primitive characters. The relationship to any of the living Lycopodiaceae is somewhat distant, but the structure of the aerial stem shows resemblance to the fossil Lycopod *Lepidodendron mundum*, as well as to the axis of the cone of *Lepidostrobus Brownii*. On anatomical grounds, as well as on the nature of the sporangial structures, the Psilotaceae appear to be somewhat closely allied to the fossil group of the Sphenophyllales.

In conclusion, I must add that this paper was begun at Cambridge at the suggestion of Mr. Seward, but was continued and completed at the Owens College, Manchester. To Mr. Seward, to Professor Weiss, and to Dr. Scott I owe my warm thanks for suggestions and advice given me throughout. My thanks are also due to Mr. Lynch for the material and information with which he has so often supplied me.

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EXPLANATION OF PLATE XXXIX.

Illustrating Miss Ford's paper on *Psilotum triquetrum*.

- Fig. 1. Transverse section of an aerial shoot of *Psilotum* below a bifurcation. *st*=stomata, *pa*=outer assimilating layer of parenchyma, *scl*=sclerenchymatous zone, *p'a*=inner parenchymatous zone, *n*=siliceous nodules, *px*=protoxylem, *x*=xylem, *ph*=phloem, *f*=central fibres, and *p'x*=secondary protoxylem. × 34.
- Fig. 2. Transverse section of portion of aerial stem, showing lignification of phloem tissue. *px*=protoxylem, *st*=phloem tissue, *en*=endodermis. × 250.
- Fig. 3. Assimilating cells from the outer cortex in longitudinal view. × 150.
- Fig. 4. Longitudinal section of phloem tissue from an aerial shoot. *st*=sieve-tubes, *pa*=parenchyma, *m*=globular deeply staining masses of substance. × 300.
- Fig. 5. Longitudinal section of a leaf of *Psilotum*. × 40.
- Fig. 6. Transverse section of the apex of an aerial shoot, showing the apical cell. × 300.
- Fig. 7. Longitudinal section of the same. × 300.
- Fig. 8. Part of a transverse section of an underground stem of *Psilotum*. *en*=endodermis, *ph*=phloem tissue.
- Fig. 9. Transverse section of a branch nearer the apex. × 195.
- Fig. 10. Transverse section of a branch below bifurcation. × 180.
- Fig. 11. Ditto, but near the apex and showing tracheids passing off to a lateral bud *l*. × 173.
- Fig. 12. Transverse section below the apex of an underground branch, showing a single lignified tracheid. × 215.
- Fig. 13. Transverse section of the intermediate portion of the aerial stem. *ph*=phloem tissue, *x*=secondary xylem, *pa*=central parenchyma, *t*=single central tracheid. At *g* the break in the xylem ring is seen. × 90.
- Fig. 14. Ditto, higher up. *en*=endodermis, *f*=central fibres. × 42.