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On Tmesipteris Vieillardi, Dangeard, an Erect Terrestrial Species from New Caledonia

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IV. *On Tmesipteris Vieillardi*, DANGEARD, *an Erect Terrestrial Species from New Caledonia.*

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[PLATES 5 AND 6.]

CONTENTS.

Tmesipteris Vieillardi, DANGEARD,* is one of those rare plants from the Pacific region, of which our knowledge has remained comparatively incomplete, owing chiefly to the difficulty of obtaining adequate material.† As is well known, the genus *Tmesipteris* occurs under several forms, which DANGEARD described as so many distinct species, but which are generally grouped under the name *Tm. tannensis*, BERNH. The usual habit of plants belonging to this genus is that of semi-erect or pendulous epiphytes, although specimens are frequently seen growing on the ground.‡ But it is not commonly known that one of the forms is normally erect and terrestrial, only rarely growing as an epiphyte. In its external morphology and anatomy also *Tm. Vieillardi* shows some noteworthy points of difference from the remaining forms (*see* Plate 5, figs. 1, 5, 8 and 10),

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* DANGEARD (1890–91), p. 163 ff.

† The plant is said to be confined to New Caledonia; but see below, under Taxonomy.

‡ HOLLOWAY (1917), p. 3; LAWSON (1917A), p. 93.

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and it is not unlikely that it represents the parent type from which the other forms may have arisen.

The chief object of the present paper is to describe these distinctive features of *Tm. Vieillardi* and to discuss their bearing upon the affinities of this plant, both within the family Psilotaceæ and with other Pteridophytes. Advantage has been taken of this opportunity to publish photographs of the different "forms" of the genus, so as clearly to illustrate, for what they are worth, the individual differences in habit and external morphology.

The material on which this paper is based was collected in New Caledonia by Prof. R. H. COMPTON, who has recently published a taxonomic account of part of his collections.* Prof. COMPTON very kindly entrusted to me the anatomical investigation of his formalin† specimens of *Tmesipteris*, and it is with great pleasure that I record here my sincere thanks to him. I also wish to express my gratitude to Prof. A. C. SEWARD, F.R.S., in whose laboratory the research was originally begun,‡ for the interest he showed in the work during the early stages. Moreover, the fact that he very kindly undertook to revise the manuscript has now afforded me the benefit of his able criticism and valuable suggestions, for which also it is a genuine pleasure to me to offer my sincerest thanks to him.

TAXONOMY.

In the concluding chapter of BERTRAND's monograph§ there is an admirable critique of the earlier literature, so that we need not refer to it here. Among the dried specimens at his disposal BERTRAND could recognize only a single species. His description was based on a specimen from the Blue Mountains, identified as *Tm. tannensis* BERNH., which, as he himself stated (footnote p. 222), closely resembled a specimen from New Caledonia. I may point out here that the plant described by BERTRAND is specifically identical with that subsequently named *Tm. Vieillardi* by DANGEARD, and regarded by him as endemic to New Caledonia.

In 1890–91 DANGEARD,|| also working only with dried specimens, recognized as many

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* COMPTON (1922), p. 461.

† The material was subsequently transferred to alcohol.

‡ The work was started as early as November, 1915, at the Cambridge Botany School, but for various reasons could not be finished till quite recently. In the meantime several important memoirs bearing on the subject of the Psilotaceæ have appeared. The discovery of the prothalli (LAWSON, 1917, 1917A; HOLLOWAY, 1917, 1921; DARNELL SMITH, 1917) has filled up a serious gap in our knowledge of the group, while the epoch-making discoveries at Rhynie (KIDSTON and LANG, 1917–20) have thrown a welcome light not only on the affinities of the Psilotaceæ, but on questions of much wider significance. A brief preliminary account of the present work, so far as it had then progressed, was read before the Cambridge Philosophical Society (SAHNI, 1918), and further details, especially concerning the distribution of the phloem, and the theoretical considerations, were recently discussed before the Indian Botanical Society (SAHNI, 1923A).

§ BERTRAND, C. E. (1881), p. 319.

|| DANGEARD (1890–91), pp. 212–16.

as five species, and it is noteworthy that he based his diagnoses largely upon the anatomy. But the great majority of authors* recognize only the single species *Tm. tannensis* BERNH., with the remaining forms as varieties.

The recent discovery of the sexual generation† affords another character that may prove to be of taxonomic value, but the prothalli of only two of the forms have yet been described‡, and these do not appear to show any important differences.§

In dealing with closely allied plants, such as the different "forms" of *Tmesipteris* undoubtedly are, taxonomic distinctions are not easily defined, and they are not worth maintaining except when they carry a special interest. In the collection at my disposal four out of the five species recognized by DANGEARD were represented. As regards the form *Vieillardi* of DANGEARD, I have without hesitation followed this author in recognizing it as a distinct species: both in its habit and anatomy it appears to differ more from any of the remaining forms than the latter do among themselves. Moreover, one of the distinctive features in its anatomy, namely, the presence of medullary xylem, appears to deserve emphasis as carrying a phylogenetic value. All the remaining forms, on the contrary, have provisionally been grouped together under *Tm. tannensis*, but their varietal names have been retained.

DESCRIPTION.

Tmesipteris Vieillardi, DANG.

(Text figs. 1–4, 5 *a–g*, 6 *a*, 7; Plate 5, figs. 1–4, 7, 11–13; Plate 6, figs. 14–24.)

Tm. tannensis, 1881. BERTRAND, C. E., 'Arch. Bot. du Nord de la France,' vol. 1, pp. 252–598.

Tm. Vieillardi, sp. nov. 1890–91. DANGEARD, 'Le Botaniste,' vol. 2 (iv), p. 166 ff. Plate IX, figs. 1, 2.

Tm. tannensis, var. *Vieillardi*, 1914. DOMIN. 'Bibl. Bot.,' Heft 85.

Tm. Vieillardi, 1922. COMPTON, 'Journ. Linn. Soc. (Bot.),' vol. 45, p. 462.

Distinctive features.—Terrestrial plants with a stiff erect radially symmetrical shoot.

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* BAKER (1887), p. 80; JENNINGS and HALL (1891), pp. 2, 9; KLEIN (1891), p. 327; PRITZEL (1900), p. 618; CAMPBELL (1918), p. 504; CHEESEMAN (1906); SYKES, Mrs. THODAY (1908), p. 65; LUERSSEN (1879), pp. 638–39; BOWER (1908), p. 409; SEWARD (1910), p. 17; DOMIN (1914), p. 230.

† LAWSON (1917, 1917A); DARNELL SMITH (1917); HOLLOWAY (1917, 1921).

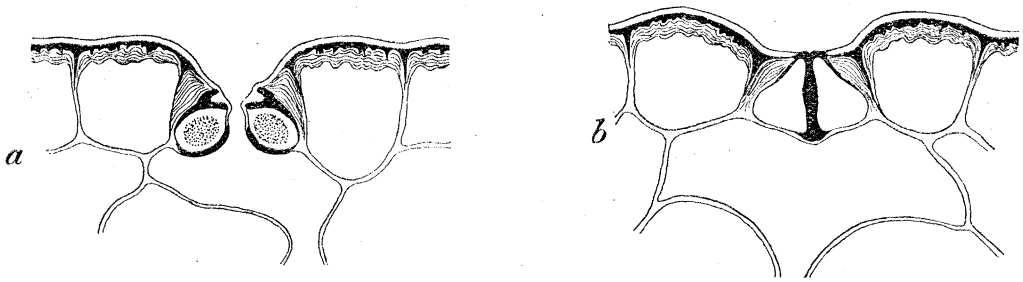
‡ LAWSON describes his prothalli as belonging to *Tm. tannensis*, but he apparently employs this name as a general designation and not as referring to any particular form. In the absence of data as to sporophytic characters, it is impossible to say which particular form is meant.

The form whose prothallus was discovered by HOLLOWAY was identified by this author as *Tm. lanceolata*; but the sporophyte shown in his photograph (Plate I, facing p. 3) does not agree with DANGEARD's original description and figure of this form (DANGEARD, 1890–91, p. 204, fig. 6, Plate XV). It appears to correspond rather to the *Tm. elongata* of DANGEARD (*loc. cit.*, p. 186, fig. 5, Plate XII; compare Plate 5, figs. 5 and 10 in the present paper). The discrepancy arises from the fact that DANGEARD's paper was not accessible to HOLLOWAY.

§ HOLLOWAY (1917), pp. 38–39, and Postscript, pp. 43–44.

Transition region comparatively long (up to 10 cm.), with numerous scale-leaves (up to 40). Foliage leaves isobilateral, narrow and strap-shaped, often strongly falcate, but with parallel margins. Pith normally containing one or more xylem strands and associated sieve tubes in the lower part of the shoot.

The normal habitat is terrestrial,* but Prof. COMPTON occasionally found the plant making its way up the stem of a *Lomaria*, where, however, it only produced small yellow shoots, apparently of a sickly nature. The axis is usually curved at the base of the transition region, where it changes from an apparently indifferent to a negatively geotropic organ.† At the same time, the diameter increases appreciably. The transition region in *Tm. Vieillardi* is considerably longer (reaching up to 10 cm.), and the number of scale-like leaves correspondingly larger (as many as 40) than in any other form of the genus. The difference is clearly beyond the observed range of variability.



TEXT-FIG. 1.—*Tm. Vieillardi.* Camera-lucida sketches of stomata. *a*, section across the middle of a stoma, showing the enormously thickened dorsal walls of the guard cells, each of which contains a large nucleus and has a dorsal and a ventral lignified lamella (black), the former with a peculiar process. *b*, section near one end of a stoma, showing the two guard cells separated by a lignified septum.

In the outer walls of the epidermal cells the cuticle has been left unshaded, the cellulose is shaded with wavy lines, and the lignified parts are shown black. (× 248.)

As text-fig. 2 *a* shows, the epidermal cells of the rhizome are not all alike: those giving off rhizoids are isodiametric and smaller than the others. On certain parts of the rhizome the rhizoids were much longer than on others, and sections invariably proved that the mycorrhizal fungus was confined to the regions with long rhizoids.

Pith and Medullary Xylem.—It is in the transition region and proximal part of the leafy shoot that the most notable feature in the anatomy of *Tm. Vieillardi* is seen. Text-figs. 2 *b–f* show, in addition to the normal ring, a variable number of xylem strands embedded in the pith. These will be described in detail presently, but the pith may first be disposed of.

The structure of the pith shows some variation; as a rule, it is composed of large cells with a collenchymatous tendency. Sometimes the walls are uniformly thickened

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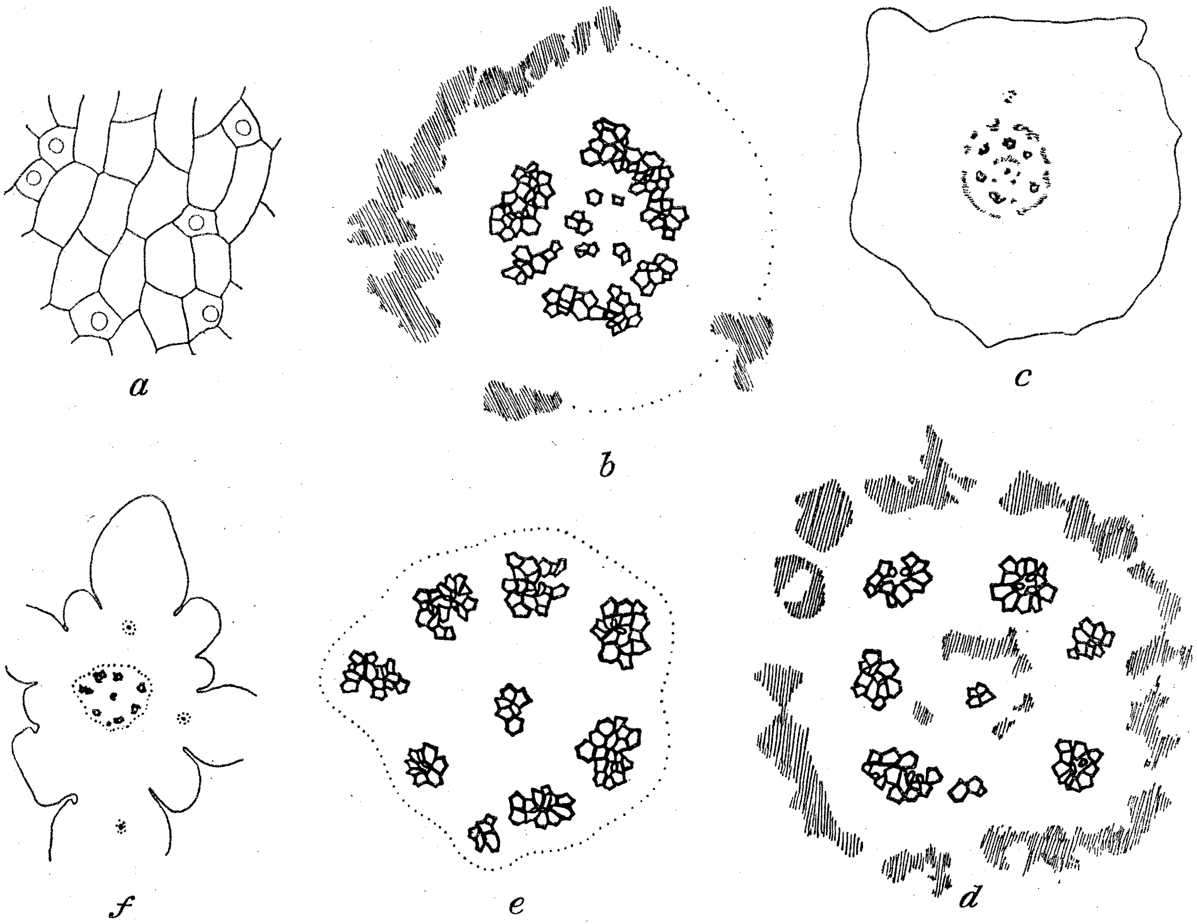
* As guessed by DANGEARD from clods sticking to the rhizomes of his herbarium specimens (DANGEARD, 1890–91, p. 168).

† Compare the restorations of *Rhynia* and *Asteroxylon* in KIDSTON and LANG's memoir (*loc. cit.*—Part IV, Plates I, II).

(Plate 5, fig. 11), but the thickening is never so pronounced as to give the appearance of fibres. The cells are prosenchymatous, the end walls being usually either transverse or slightly oblique (Plate 5, fig. 12; Plate 6, fig. 15). The longitudinal walls, moreover, show numerous fine pits of a round, oval or slit-like shape (Plate 6, figs. 19, 20, 23, 24).



Text-fig. 2.—*Tm. Vieillardi.* *a*, (× $46\frac{2}{3}$) epidermis of rhizome, showing small isodiametric cells with scars of rhizoids scattered among the larger hairless cells. *b*, (× $66\frac{2}{3}$) Part of a transverse section through the base of the transition region showing the relation of the medullary to the peripheral xylem. The surrounding shaded part represents the brown deposit in the inner cortex. *c*, *d*, Section through a more distal part of the transition region (from another specimen). *c*, (× $16\frac{2}{3}$) represents the entire section with a single leaf-trace in the cortex. *d*, (× $74\frac{2}{3}$) shows the xylem on a larger scale. The medullary xylem is here represented by a single strand surrounded by a ring of brown deposit. *e*, *f*, section through the leafy shoot (from a third specimen). *f*, (× $16\frac{2}{3}$) shows the general features of the entire section. *e*, (× $74\frac{2}{3}$) shows only the xylem on a larger scale. A single medullary strand is present.

All the drawings, including the outlines of the tracheides, are based on camera-lucida sketches.

The medullary xylem, when first observed, was taken to be an abnormal feature comparable to the tracheides found by Gwynne-Vaughan in the pith of *Osmunda regalis*.*

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* Gwynne-Vaughan (1914), p. 351.

But on examining further specimens it was found to be a normal occurrence, although variable in amount and distribution. Nine entire plants were carefully examined in serial transverse sections, and portions of several others were also investigated. Only in one case was medullary xylem absent. In the size of the tracheides and the form of pitting the medullary strands, as a rule, do not differ from the main bundles of the stele, but they are in all observed cases devoid of protoxylem elements. The section shown in Plate 5, fig. 13, is exceptional in having a medullary strand composed of such wide tracheides. The medullary strands are generally connected, at their origin, with the main stele. Distally they were usually seen to end blindly in the pith, rarely joining on to the main stele. In one case, the only one of its kind that came under my observation, a medullary strand when traced upwards gradually approached the periphery of the pith and ultimately became one of the bundles of the stelar ring. It may be added that in a few cases (text-fig. 2 *c*, *d*) the pith cells in the vicinity of the medullary strands were found impregnated with the same brown substance which is well known to occur in the inner cortex, especially in the rhizome and transition zone.* Associated with the medullary xylem there are usually some sieve-tubes, although I am unable to say whether they form a definite layer round it (Plate 6, figs. 16, 23, 24).

This is by no means the first time that medullary xylem has been recorded in *Tmesipteris*. On page 175 of his monograph, DANGEARD, while describing the anatomy of the transition region in *Tm. Vieillardi*, says " il arrive même que le centre de la moëlle se trouve occupé par un massif ligneux, dans lequel nous n'avons pas vu de protoxylème," and he figures one such bundle in his Plate XI, fig. 1. Before him BERTRAND had also figured a transverse section through the same region, showing an isolated bundle near the centre of the pith (*loc. cit.*, p. 248, fig. 215). This author traced the bundle in serial transverse sections and found it connected at both ends with one or other of the peripheral strands.† A more detailed investigation appears to have been precluded by the nature of the material at the disposal of the French authors : both of them apparently regarded the feature as a rare occurrence. At any rate, neither of them attached any significance to it, disposing of it in a passing reference.

As I am inclined to attach some importance to the medullary xylem in *Tm. Vieilliardi*, the distribution of this tissue may be described in a few actual specimens examined by me.

Specimen 1.—About two centimetres above the distal end of the rhizome one of the strands of the xylem ring gave off a small branch towards the pith. This internal bundle before long broke up into three. Of these three bundles one ended blindly in the pith, while each of the other two, on being traced upwards, merged into one or other of the main bundles. The medullary xylem in this specimen was small in amount, and confined to the lower portion of the transition region.

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* This substance is probably the same as that commonly seen in the inner cortex of many ferns and identified by WALTER (1890, p. 15) as phlobaphene.

† The presence of medullary xylem affords, among other points, strong proof that the plant described by BERTRAND was no other than *Tm. Vieillardi*, DANG.

Specimen 2.—Near the base of the transition region one of the strands of the xylem ring gave off a large bundle towards the centre. This ran up for about a centimetre and then ended blindly in the pith. Another bundle originated in a similar way near the top of the transition region, and could be traced along the pith for a distance of several centimetres into the base of the leafy region, where it ended blindly like the other bundle just described.

Specimen 3.—At two different levels in the base of the transition region two distinct strands appeared as islands in the pith, but on being traced upwards ended blindly after a course of a few millimetres. About half-way up the transition region another medullary strand was seen, also apparently unconnected at its basal end with the main stele. This strand soon became enlarged and then broke up into a number of scattered tracheides, which again became consolidated into one bundle. This strand could be traced far into the leafy shoot, ending blindly in the pith within six or seven centimetres of the apex of the plant.

Without entering into further detail the reader may be referred to the diagram in text-fig. 3 (below), which with the help of the account given above, will enable him to form an idea of the range of variation exhibited by the medullary xylem, both as regards distribution and extent of development. This diagram should, however, be regarded as only a generalized sketch, combined of several observed cases, rather than as representing a typical specimen: such an extensive development of medullary xylem as that shown in the sketch is the exception rather than the rule.

From the foregoing account it may be concluded that the presence of medullary xylem in the proximal part of the aerial shoot is a normal and characteristic feature of *Tm. Vieillardi*, and the variability of the tissue in this species, while it is entirely absent in the other forms, strongly suggests that even here it is on its way to extinction. The absence of protoxylem indicates that the medullary xylem represents only the cauline part of the stele and has nothing to do with leaf-traces; this is also shown by the fact that at their distal ends the medullary strands as a rule terminate blindly in the pith.

From an examination of a large number of sections containing medullary xylem it emerges that *in a general way* the quantity of the medullary xylem and its distribution (whether consolidated or scattered) roughly follows the total diameter of the stem. Thus, the section shown in fig. 2 *b*, with well-developed and scattered medullary xylem, was in total diameter more than twice as large as that in fig. 2 *f*,* in which only a single medullary strand is seen. That this rule does not always apply is, however, seen on comparing fig. 2 *c* in which the diameter of the stem was $1\frac{3}{4}$ as great as in fig. 2 *f*, but which actually carries a smaller medullary strand. Similarly, the section photographed in Plate 5, fig. 11 (devoid of medullary xylem) is very nearly equal to that in Plate 5, fig. 13, and almost $1\frac{1}{2}$ times that in fig. 2 *f*, both of which possess medullary xylem.

The importance of the size of an organ as a factor determining the configuration of its

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* Curiously enough, this proportion is by no means maintained in the *stelar* diameters, as the reader can judge from the magnifications given in figs. 2 *b* and *e*.

vascular supply, a line of enquiry which offers a fertile field for investigation, forms the subject of an able Address recently delivered by Prof. BOWER.* Still more recently the same subject has been treated with special reference to the Ferns in Prof. BOWER's valuable work on the Filicales† (see also p. 153 below).

Phloem.—The phloem of *Tmesipteris* is commonly described as occurring only on the outer side of the xylem, where it is said to form a continuous zone of sieve-tubes, both in the rhizome and in the aerial stem. But an examination of my sections of the aerial stem‡ of *Tm. Vieillardi* leads to the conclusion that the phloem is not so restricted. For I believe that the great majority, if not all, of the cells directly abutting on the xylem strands, both on their centripetal side as well as laterally, deserve the name of sieve-tubes equally with those surrounding the xylem ring. Except for their generally somewhat larger diameter—a difference which in any case is neither large nor constant—they do not show the least difference, either in general appearance, mode of pitting or staining properties, from the sieve-tubes of the outer phloem. Longitudinal microtome sections treated with gentian violet and orange G showed in both cases exactly the same kind of light-coloured granular patches (either left unstained or stained orange) in the apparently lignified walls, which took up the violet stain.

As this is a point of fact on which my conclusion was opposed to that arrived at by previous workers, I was at first inclined to hesitate in making a definite statement. But after carefully re-examining my earlier sections and also a dozen more paraffin series, stained in a similar way, I am able to say with confidence that my interpretation is correct: in addition to the outer phloem, undoubted sieve-tubes are present both internally to the xylem cylinder and occupying the "rays" between the xylem bundles. Moreover, in all my series of longitudinal sections, wherever medullary strands are present, sieve-tubes are seen in close association with them. I cannot say whether these sieve-tubes form a definite layer round the medullary xylem, but I think this is unlikely, for the longitudinal sections do not always show such elements on both sides of the medullary xylem.

In transverse sections the detection of the sieve-tubes (even of the outer phloem) is usually very difficult, or even impossible, and the boundary between the pith and the internal phloem may appear arbitrary. But when the pith cells have uniformly thickened walls, as in Plate 5, fig. 11, the distinction is not so vague. In this figure it will be noticed that the central group of about 26 cells with uniformly thickened walls (pith) does not occupy the whole of the space enclosed by the xylem ring, but that one or two layers of somewhat narrower collenchymatous cells are left between the pith and the xylem. Similar collenchymatous cells, moreover (oval in cross-section), compose the rays between the xylems, and pass quite insensibly into the tissue just outside the xylem ring, which

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* BOWER (1920A).

† BOWER (1923).

‡ Both in the transitional zone and in the leafy region.

all agree is phloem. The impression gained is that each xylem strand is more or less completely surrounded by phloem.

An examination of serial longitudinal sections cut with the microtome confirms this impression. Plate 5, fig. 12, represents an obliquely tangential longitudinal section, which in the upper part of the figure passes through the periphery of the pith (*p*) and happens to traverse, on both right and left sides, gaps between the xylem strands of the vascular cylinder. Confining our attention first to the upper part of the figure, it is not difficult to distinguish the central group of large thick-walled elements (*p*), about half a dozen cells wide, from the thinner-walled and, on the whole, narrower elements lying to right and left of them (*rph*). These lateral groups are composed entirely of typical sieve-tubes, which are provided with relatively large roundish, light-coloured patches (the sieve-plates), instead of the narrow and often slit-like perforations characteristic of the central group (well seen in the cell to the left of the straight transverse wall).

Let us now pass on to the middle part of the same figure. Owing to its obliquity the section here traverses different tissues to those in the upper part. In the first place one notices that in the downward continuation of each of the phloem groups a strand of xylem (x^1, x^2) appears along the middle of it so as to leave, in either case, a few sieve-tubes both to the right and to the left of the xylem. In the second place, the downward continuation of the pith is occupied by a number of cells exactly similar to those just described as sieve-tubes. These are, in fact, the sieve-tubes of the internal phloem (*iph*) *seen in tangential view*: the section in its oblique course has transgressed from the periphery of the pith to the phloem which immediately surrounds it and abuts on the inner faces of the xylem strands. Passing towards the bottom of the figure, we see even a third xylem strand (x^3) traversed *tangentially* by the same oblique plane; and between the three xylem groups are wedged in two narrow phloem rays (*rph* indicated by arrows), which are clearly in continuity above with the internal phloem.*

The figures reproduced in Plates 5 and 6 are also from untouched photomicrographs. They illustrate in greater detail and clearness the structure and position of the internal phloem, medullary xylem and its associated sieve-tubes. Since the full explanations are given on pp. 168–70 it is needless to say more than a few words here. Figs. 19, 20, 23 and 24 show very clearly the kind of difference in pitting that distinguishes the phloem from the pith. Figs. 19 and 20 show that there was some justification for the name "sieve-parenchyma," applied to the ground tissue by JENNINGS and HALL.† There is, however, no possibility of confusing the pith and the phloem immediately surrounding it, in preparations such as those here figured. Fig. 14, from the distal part of a rhizome, is notable because it shows a feature which as a rule does not appear below the transition region: the xylem is excavated, with the concavity filled up by a thin-walled tissue similar in appearance to that outside. As this was the only case of the

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* It is evident from an examination of the whole series that this is not a case of a medullary strand between two peripheral strands.

† JENNINGS and HALL (1891) pp. 3–4.

kind met with, it was impossible to ascertain by longitudinal sections the true nature of the central tissue.

The sieve-tubes of *Tm. Vieillardi* vary from narrow cells with uniseriate sieve-plates (Plate 6, fig. 22) to wider elements with the plates scattered, so that several may be met with in passing across a sieve-tube (Plate 6, fig. 24).

Pericycle.—Near the periphery of the stele there is an interrupted layer of narrow fibrous cells frequently squarish in cross-section (Plate 5, fig. 11), which BERTRAND* regards as belonging to the phloem, but which may perhaps with equal justification be described as a pericycle (DANGEARD, périphragme†).

Leaf-traces.—As already stated, the transition region in *Tm. Vieillardi* is better developed and the number of scale leaves much greater than in the other forms. Associated with this fact is the presence of a vascular supply in relation to many of these scale leaves. The earliest (lowermost) traces are merely strands of thin-walled cells, ending blindly in the cortex some distance below the leaf-base (text-fig. 3); higher up definite tracheides are present, but the trace invariably stops short at the leaf-base, never entering the free process.‡ Only when we come to leaves with a definite lamina do we find the bundle actually entering the free portion of the leaf, but it is noteworthy that even then it never penetrates the apiculus.§

There has been some controversy‖ as to whether the gaps in the stele of *Tmesipteris* are to be looked upon as true foliar gaps or only as " perforations " having no relation to leaf-traces. The discussion has some importance as bearing on Prof. JEFFREY'S classification of the vascular plants into the Lycopsida and Pteropsida. As *Tm. Vieillardi* is a favourable species for the investigation of this question, I microtomed several centimetres of the leafy stem after I had removed all appendages and then carefully shaved off the outer cortex to facilitate the paraffin process. In order to compare the vascular supply to the leaves with that of the sporangiophores I had selected different pieces of stem which bore, respectively,

(*a*) only sterile appendages (leaves).
(*b*) intermixed leaves and fertile appendages (sporangiophores).
(*c*) only fertile appendages (sporangiophores).

From the series of sketches in text-fig. 4 (which is fully explained in the legend) the reader can follow the behaviour of the stelar bundles and off-coming traces in a typical example. An examination of my sections reveals a rather peculiar state of affairs, which makes it impossible to give a categoric answer to the question: Are there foliar gaps in *Tmesipteris*? In the transition region as well as in the greater part of the

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* BERTRAND (1881), p. 247.

† DANGEARD (1890–91), p. 170.

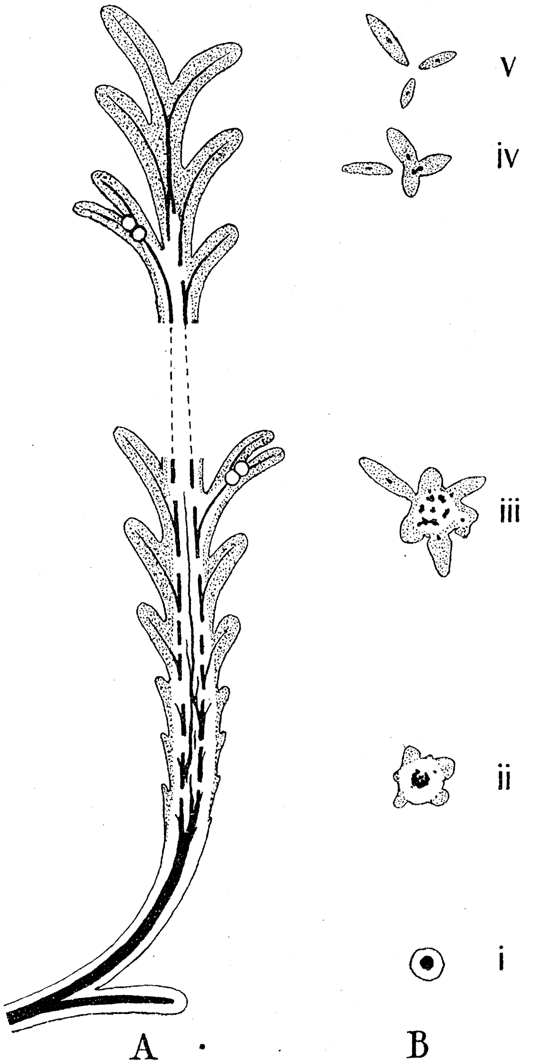
‡ It is noteworthy that the same peculiarity is shown by the leaf traces of *Asteroxylon* (see p. 161 below).

§ This fact might indicate that the scales on the transition region represent merely the apiculi of leaves that are for the most part coalescent with the axis.

‖ SYKES (1908); JEFFREY (1908); BOWER (1908), pp. 487–88.

leafy shoot the great majority of the gaps in the stele have no constant relation to the leaf-traces and must be regarded as "perforations." As Prof. JEFFREY has shown, the vascular supply to the leaves and sporangiophores (which he regards as sporophylls) is usually nipped off tangentially or almost tangentially from the stelar bundle,* and in such cases leaf-gaps are naturally out of the question. Moreover, in the stele of the transition region distinct gaps are already present, although here leaf-traces are either absent or too feebly developed to produce gaps (text-fig. 2 *b-d*; see also BERTRAND, 1881, figs. 215-16, pp. 248-49). In fact, gaps may appear in the xylem even in the region of the rhizome, as seen in fig. 14, Plate **6**, and in a transverse section of an unusually large rhizome figured by HOLLOWAY.† As this author suggests, the diameter of the rhizome probably has to do with the hollowed out or dissected nature of the xylem cylinder. The section photographed in fig. 14, Plate **6**, is of a size greater than the average for *Tm. Vieillardi*. In rare cases, however, owing to the crowding of gaps and traces it may so happen that a trace comes off from the base of a gap. (See text-fig. 4 *a*, *b*.)

But apart from these perforations in the stele, true leaf gaps also occur here and there, when an entire stelar bundle itself leaves the stele to supply a leaf.‡ Such cases appear to become more frequent as we approach the apex of the shoot, where the stele appears to be composed entirely of decurrent leaf-traces, and the axis of coalescent leaf-bases.§



TEXT-FIG. 3.—*Tm. Vieillardi.* Diagrams to illustrate the general organization. In both A and B the xylem is shown black, the pith and inner cortex white, and the leaves as well as their decurrent bases are shown dotted. The transverse sections (B i, ii, iii, iv, v) are from the levels at which they are shown. The diameter of the axis appreciably increases at the transition from the rhizome to the aerial stem, but as we approach the leafy region, it again diminishes gradually as far as the apex.

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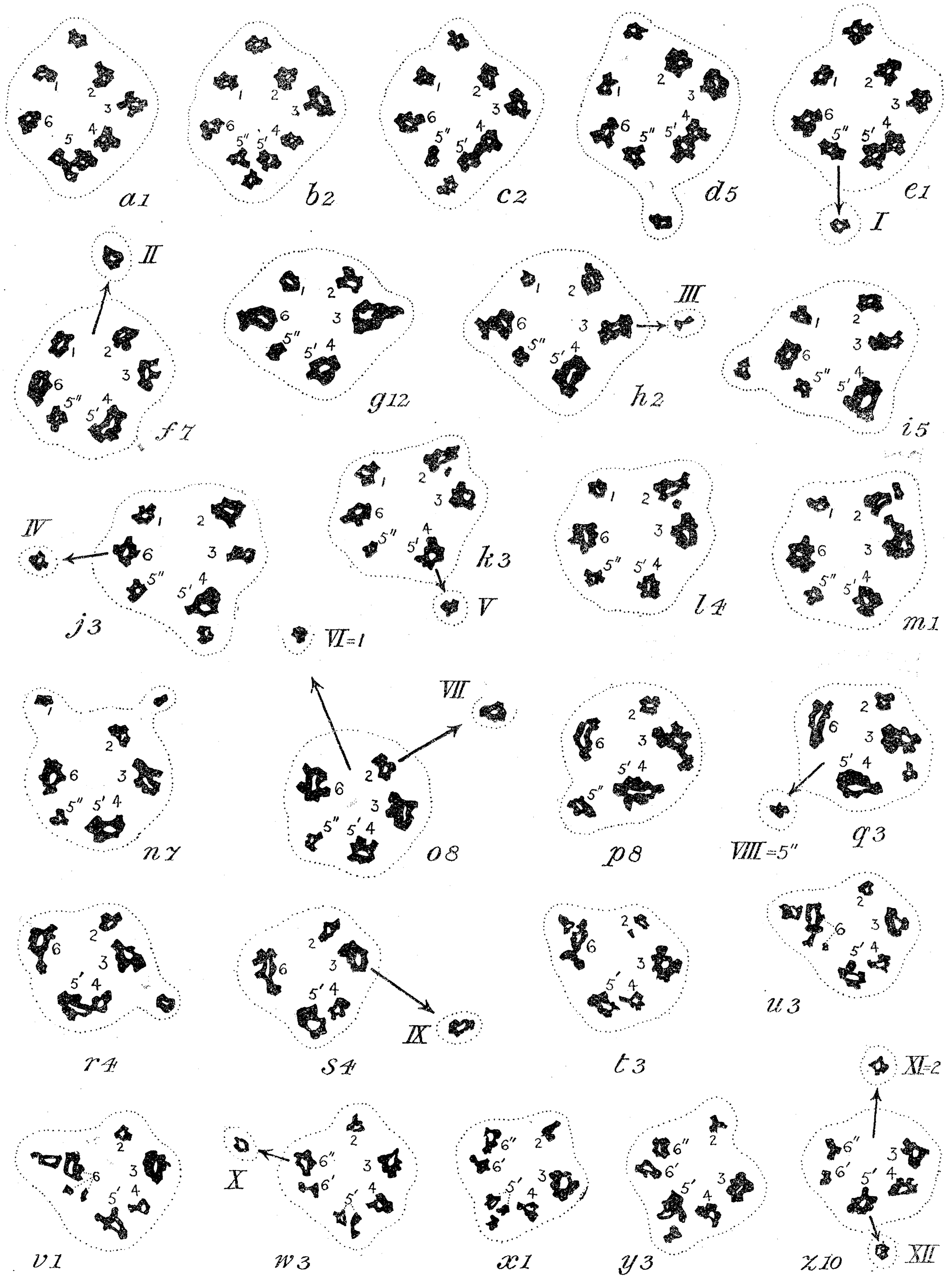
* JEFFREY (1908), pp. 246–48.

† HOLLOWAY (1917), fig. 83 on p. 32. See also BOWER (1920A) and p. 8 of the present paper.

‡ The same may happen in the case of a sporangiophore (text-fig. 4, traces vi, viii, xi).

§ DANGEARD (1890–91), p. 217.



TEXT-FIG. 4.—*Tm. Vieillardi.* Serial transverse sections through the leafy shoot, to show origin of vascular supply to twelve sporangiophores (I—XII). The sections are from a microtome series; the outlines of the individual xylem strands (black) were drawn roughly with the aid of a camera-lucida, the protoxylems being left blank. The behaviour of the stelar bundles can be traced with the help of the numbers attached to them. (× about 67.)

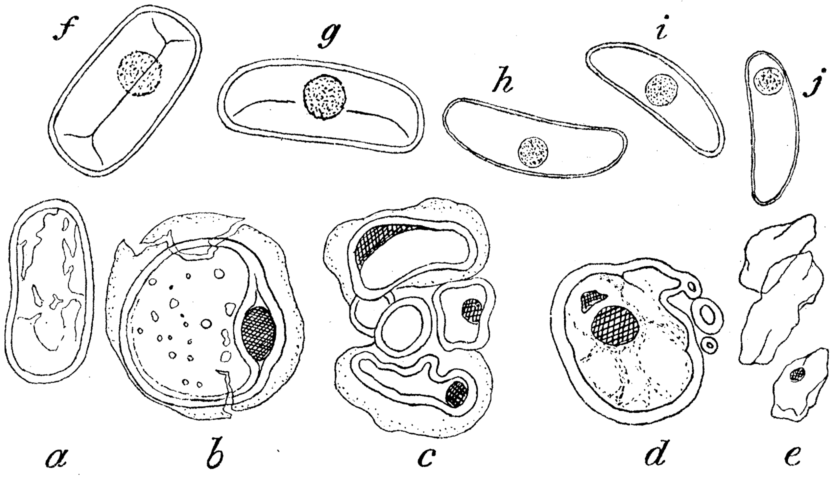
The numbers placed after each letter (*b* 2, *c* 2, *d* 5) representing a section denote, in tenths of a millimetre, the vertical distance between that section and the one preceding it. Thus *n* 7 means that the interval between the sections *m* and *n* is 0·7 mm. As the sections were cut of a uniform thickness, these figures could be determined with reasonable accuracy by counting the number of sections intervening between the sections figured.

BERTRAND* and SYKES† have discovered certain points of difference between the supply bundles of a sporangiophore and an ordinary leaf-trace. I carefully examined my serial sections containing intermixed traces of sporangiophores and leaves, and also compared the separate series of leaf- and sporangiophore traces; but I found no constant difference, whether in size, structure or relative time of departure from the main stele.

The general features of the vascular anatomy of *Tm. Vieillardi* are represented diagrammatically in text-fig. 3.

Sporangiophores.—The sporangiophores of *Tm. Vieillardi* are confined to the distal half of the shoot. The leaf-lobes are identical in all respects with the foliage leaves characteristic of this species, but there appears to be nothing distinctive in the shape or structure of the synangia. As described long ago by JURANYI‡ in "*Tm. tannensis*," the main synangial bundle runs a short distance into the septum. It gives off, right and left, the two girdle-like traces discovered by Miss SYKES§ in her New Zealand specimens; but in my specimens of *Tm. Vieillardi* these traces passed only about half-way round the septum.

In describing the spores of *Tm. Vieillardi* attention must be drawn to the fact that on many of the plants the synangia, although outwardly normal, invariably contained spores of several different shapes and sizes. Most of these were quite unlike those we are accustomed to associate with the Psilotaceæ (text-fig. 5 *a-e*). They are evidently abnormal and will be described later. In the same synangia there were also some others (text-fig. 5 *f-g*) which may perhaps be regarded as the normal ones for the species, for spores of only this size and shape were found in some plants from another locality



TEXT-FIG. 5.—Camera-lucida sketches of spores. *a–e*, abnormal spores of *Tm. Vieillardi*; *f*, *g* (? normal) spores of same; the rest are normal spores; *h*, from *Tm. tannensis* var. *lanceolata*; *i*, from *Psilotum triquetrum* (Roy. Bot. Gard. Calcutta); *j*, from *Tm. tannensis* var. *typica*. (× 367·5.)

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[*] BERTRAND (1881), pp. 250, 256–57.

[†] SYKES (1908), pp. 70–72.

[‡] JURANYI (1875).

[§] SYKES (1908), p. 74, fig. VIII F, and p. 75.

(Mt. Koghi), as well as in a dried specimen of *Tm. Vieillardi* in the British Museum Herbarium.* However, if these are the normal spores of this species it is rather surprising that they differ so much in size from those of the other forms of the same genus (text-fig. 5, *f*, *j*), when the latter so closely resemble those of *Psilotum* (text-fig. 5, *i*).

Prothallus.—The prothallus of *Tm. Vieillardi* is not known.

Tmesipteris tannensis, BERNHARDI.

With the exception of *Tm. Vieillardi*, all the "forms" of *Tmesipteris* may provisionally be placed in BERNHARDI's species *Tm. tannensis*.

So far as the histology of the stem is concerned the three forms *tannensis*, *elongata* and *lanceolata* are essentially identical with each other, so that one description will do for them all. The notable points of difference from *Tm. Vieillardi* lie in the absence of medullary xylem, the sclerenchymatous nature and pitting of the pith and, so far as observed, in the fact that the sieve-plates are always uniseriate.

Concerning the distribution of the phloem, my conclusions with regard to this species are the same as in the case of *Tm. Vieillardi*. Fig. 25, Plate 6, from a median longitudinal section through the leafy stem, shows clearly a sieve-tube (*iph*) abutting on the one side upon a xylem strand and on the other upon the pith (*p*). It is not possible to assert definitely that the phloem on the inner face of each xylem strand forms a complete and unbroken layer. In fact, sections have been met with in which pith-like cells were seen directly in contact with the xylem; but such cases are not common.

The number of stelar bundles is smaller than in *Tm. Vieillardi*, a fact evidently related to the less crowded leaves. The vascular supply to the leaves and fertile organs was carefully studied in paraffin sections, and on the question of leaf-gaps the conclusions drawn in the case of *Tm. Vieillardi* were fully confirmed.

Young Plant.—Among the much branched rhizomes I found a young specimen consisting of two leafy shoots arising from the same rhizome (Plate 5, fig. 9). The anatomy of this specimen was studied in microtome sections. As HOLLOWAY† has meanwhile published an account of the young plant, I need not go over the same ground, for my observations agree with his description. The main point is that the simple stele of the rhizome is continued unbroken into the aerial shoot.

The form *lanceolata* shows an even stronger contrast to *Tm. Vieillardi*, because of the "dorsiventral" structure of the distal part of the shoot, where the leaves are placed apparently in two series, although the leaf-traces arise spirally. The leaves are broadly lanceolate, with a slightly thickened‡ and reflexed margin. They have a leathery

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* I take this opportunity of expressing my hearty thanks to Dr. A. B. RENDLE for permission to examine specimens in this herbarium, and also to Dr. OTTO STAPF for a similar courtesy at the Royal Herbarium, Kew.

† HOLLOWAY (1917), p. 30.

‡ The dumb-bell shaped transverse section of a leaf, figured by DANGEARD (1890–91, Plate XV, fig. 10), is probably drawn from a desiccated specimen and gives an exaggerated impression of the marginal thickening.

texture and two well-marked surfaces, the stomata being confined to the lower (shaded) side. It is obvious, however, that these surfaces are not morphologically adaxial and abaxial, for the leaf is expanded in the plane of the axis itself.

Such modifications of the shoot, originally due, no doubt, to a unilateral external influence, are by no means a rare phenomenon. Perhaps the closest analogy is found in some species of *Lycopodium* (*L. complanatum*, *L. alpinum*, *L. volubile*) in which, as Prof. GOEBEL* has shown, the action of light is reflected in the "dorsiventral" organization of the distal branches. The same author describes similar adaptations in the conifers,† notably in *Thujopsis dolabrata*, and a striking instance was recently described in the podocarp genus *Acmopyle*.‡ It would be an interesting study, for those who have the opportunity, to observe the behaviour of some of these plants when cultivated on the klinostat.

One is tempted incidentally to cite a parallel from the animal kingdom, namely, the familiar flat-fishes of the order Pleuronectidæ§—animals with a primarily bilateral symmetry which becomes masked, during the early stages of development, by a false and superficial "dorsiventrality" along a plane at right-angles to the original median plane.

In the anatomy of the stem the form *lanceolata* is quite similar to the type, the *resemblance extending to the minutest details*. It would therefore be superfluous to describe it here.‖ The spores very closely resemble those of the type form (text-fig. 5 *h*).

PRITZEL's well-known figure of *Tmesipteris*¶ is based upon a specimen of the form *elongata*, which appears to attain a greater size than any other. The flaccid, occasionally forked, shoots hang vertically down. As in *Tm. Vieillardi*, the leaves are isobilateral and placed on all radii—features that may be related to the vertical posture of the axis, erect in the one case, pendant in the other.

It is common knowledge that the ripe synangium of *Tmesipteris* dehisces along a mid-ventral line. But I noticed that some empty old synangia taken from alcohol specimens and accidentally left to dry up had assumed the form shown in Plate 5, fig. 6; the synangial wall had divided into four valves, each of which had curled up, as shown in the photographs. Whether this is the normal state of affairs can only be decided by examining living specimens; if this is so, the curling up of the valves would be an effective method of emptying the synangium. By alternately wetting and drying a synangium the movement could be repeatedly seen in the same specimen. This shows

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* GOEBEL (1913), pp. 236–40.

† GOEBEL (1913), pp. 246–48.

‡ SAHNI (1920), p. 259, text-fig. 2.

§ COLE and JOHNSTONE (1901), p. 8.

‖ From the external characters I was originally led to regard this plant as a distinct species (see COMPTON, 1922, p. 461), but after a careful comparison of the anatomy I am inclined to place it as a variety of *Tm. tannensis*.

¶ PRITZEL (1900), fig. 381, p. 608.

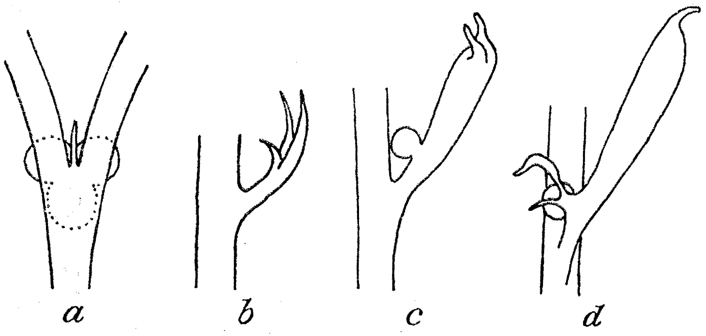
that it has a definite relation to the structure of the wall, as is the case with the fruit-capsules of many angiosperms. Between the two pairs of valves the septum is left intact, supported by a thickened rim which is produced at one point into two delicate horn-like processes, whose function is obscure (Plate 5, fig. 6 *c*, *d*).

I may add that while this hygroscopic movement was best seen in the form *elongata*, the same phenomenon was observed in the forms *tannensis* and *lanceolata*, and also in *Tm. Vieillardi*, but in the last-named plant the horn-like processes on the septum were much shorter than in the other forms.

Abnormalities.

The Psilotaceæ are well known for the frequent occurrence of abnormalities in their sporangiophores. These have been described from time to time by a number of authors* and interpreted in various ways. Although the real significance of most of these structures is obscure, it may be worth while to describe briefly a few more, which do not appear to have previously been recorded in *Tmesipteris*.

Tm. tannensis var. *typica*.—Text-fig. 6 *b-d* shows three structures differing only in details from others figure by Bower and Holloway. They are all apparently of a teratological nature.



Text-fig. 6.—Abnormal sporangiophores of *a*, *Tm. Vieillardi*; *b–d*, *Tm. tannensis* var. *typica*.

Tm. Vieillardi.—(*a*) Trilocular synangia are not uncommon in *Tmesipteris*, but the one shown in text-fig. 6 *a* differs in the position of the loculi and in the presence of a minute sterile lobe in the angle between the two normal lobes. It is noteworthy that the vascular supply is not (as might be expected) similar to that of a normal synangium of *Psilotum*, but that the main synangial bundle divides into three, one entering each septum (Plate 5, fig. 7).

(*b*) Text-fig. 5 *a-e* shows some of the abnormal spores found in many of the synangia. The majority of them are large and roughly circular, with very thick walls, and usually contain a large deep-staining nucleus. Sometimes several spores of very different sizes

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* Thomas (1902); Bower (1908), p. 410, fig. 228; Sykes (1908), p. 72, fig. VII; Sykes (1908a), p. 525; Goebel (1915-18); Holloway (1921), p. 417; Sahni (1923), pp. 185–91, fig. 2.

are found grouped together, and from fig. 5 *d* it appears as if small cells are being constricted off from a large one. In other cases, again, the shape is oval, with thin walls (*e*). I find it difficult to explain these unusual appearances. (See p. 155 above.)

THEORETICAL CONSIDERATIONS.

The aberrant family Psilotaceæ is one of those remarkable groups of living plants whose nearest known allies are not met with till we search far back in the geological record. Undoubted fossil Psilotaceæ are still unknown.* While resemblances with the Lycopods have long been recognized,† until recently the group to which we looked for the closest comparison were the palæozoic Sphenophyllales.‡ But ever since DAWSON§ gave the name *Psilophyton* to those obscure Devonian plants, which have recently risen into prominence, the Psilotaceæ have been vaguely suspected of having an even more ancient connection; and this suspicion has been confirmed in a striking manner by the work of KIDSTON and LANG|| on the Psilophytales. The far-reaching resemblances which the Psilotaceæ show to this archaic phylum, coupled with the peculiar combination of characters in their recently discovered prothalli, have enhanced the importance of this little family, already rich in theoretical interest.

(*a*) *General Organization.*

Even apart from its rootless character the genus *Tmesipteris* presents, in its general organization, features which mark it as an extraordinary type of plant. The peculiar mode of attachment of the leaves, appearing as prominent wings on the axis, each one decurrent through many internodes, imparts to the whole plant a strange appearance. Towards the apex of the plant, if there are no sporangiophores, the stem appears to be composed entirely of coalescent leaf-bases (Plate 5, figs. 8, 9, 10 and text-fig. 3) affording a very striking illustration of the phytonic theory.¶ As DANGEARD has already observed, the vascular anatomy confirms this impression. For, if we follow upwards the axial stele as it successively gives off leaf-traces, we find it steadily becoming thinner and finally resolving itself into the two or three terminal leaf-traces. After these traces have departed there is no indication left of a central axial cylinder or even a procambial strand. In specimens like those figured in Plate 5, figs. 8, 9, 10, there is no trace of an apical bud, and the most careful search in the angle between the terminal leaves (or even along their inner margins) does not reveal anything that might be construed as a meristematic cell. We are, therefore, justified in concluding that the growth of the

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* SEWARD (1910), p. 24; POTONIÉ und GOTHAN (1921), p. 189.

† CAMPBELL (1918), p. 485.

‡ SCOTT (1897), (1907), pp. 163–66; THOMAS (1902); BOWER (1908), p. 398. But see also SCOTT (1922), p. 639, and (1923), pp. 397–98.

§ DAWSON (1859), (1871), (1888).

|| KIDSTON and LANG (1917-20), part I, p. 776.

¶ DANGEARD (1890–91), p. 217.

shoot is limited, like that of most leaves. Indeed, in some forms of *Tmesipteris*, where the leaves are placed in two series (Plate 5, figs. 8–10), the resemblance to a pinnate fern leaf is very striking,* strongly recalling, as Prof. SEWARD has suggested to me, the habit of some fossil fronds, especially *Thinnfeldia*.

While at the apex of the plant the leaves are apparently all-important, they become relatively less so as we pass towards the base, for now the stem begins to assert itself as an entity distinct from the decurrent leaf-bases, and steadily gains in importance over the leaves, till in the rhizome it forms the entire axis by itself. (See the diagrams in text-fig. 3.) A similar relation between stem and leaf is shown by an examination of the anatomy, and this is specially clear in the case of *Tm. Vieillardi*. Whereas in the rhizome the stele is exclusively cauline, in the terminal region of the plant it is entirely made up of leaf-traces. Between the two regions the stele is of a dual nature, consisting centrally of cauline medullary xylem (a distal continuation of the rhizome stele), and peripherally of a ring of anastomosing bundles, each of which may be partially or entirely foliar.

It will thus be seen that, even in its vegetative anatomy, *Tmesipteris* is an aberrant type, difficult to place definitely either among the Lycopsida or among the Pteropsida.

The structure of the outer cortex presents another feature which is of some theoretical interest. As is well known, in the region of the shoot densely covered with leaves, the outer cortex consists entirely of the same kind of tissue as the mesophyll of the leaf, and there is apparently nothing to contradict the view that here it is in reality a sheath formed of coalescent leaf-bases. This genus therefore affords a remarkably good illustration of the "leaf-skin" theory of the stem.†

(*b*) *Anatomy of the Aerial Stem.*

The so-called medullary xylem of *Tmesipteris Vieillardi* may be directly compared to the central (cauline) part of the xylem in *Asteroxylon* and *Lycopodium*. In each case it is devoid of protoxylem, and takes no direct share in the formation of the leaf-traces. As seen in transverse section, the usual solid cauline strand of the

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* I may mention here that Prof. COMPTON remarked that the whole aerial shoot of *Tmesipteris* might really be a leaf bearing so many pinnæ. To the casual observer, such a view might perhaps appear to deserve serious consideration, especially in the case of these heterodox plants whose morphology is still so obscure. But there are some obvious objections to this view. In the first place, there is no known parallel in which a leaf normally arises as a direct continuation of the axis on which it is borne. Secondly, the comparison that it is possible to make between the sporangium-tipped shoots of the Rhyniaceæ and the sporangiophores of the Psilotaceæ seems to rest on a real homology. Lastly, as already pointed out, the distichous arrangement of the leaves is only superficial, for the leaf-traces arise in a spiral sequence. However, it would not do to lay much stress on the third objection, for, as suggested by LIGNIER (1903; 1908, p. 279), the dorsiventral pinnate leaf, such as that of a fern, may itself have originated from a system of branched axes, and a possible method is suggested by the way in which the dorsiventral "shoots" of *Tm. tannensis* var. *lanceolata* have probably arisen from the radial shoots of *Tm. Vieillardi*.

† SAUNDERS (1922).

Asteroxylon stele may sometimes be replaced by small groups of tracheides scattered in a thin-walled tissue (? presumably phloem). A similar reduction in the central xylem may be noticed within the genus *Lycopodium*. In this genus, although the central (cauline) xylem is usually well developed, in many species it is represented by a single strand, which in some transverse sections may appear as an isolated group of tracheides. Thus a section closely similar to fig. 13, Plate 5, of the present paper has been figured by Miss WIGGLESWORTH* in the young sporophyte of *L. complanatum*, and I have myself seen the same feature in the adult stems of two Indian species, namely, *L. Hamiltonii* and *L. setaceum*.†

So far as the distribution of the xylem is concerned, a section such as that shown in Kidston and Lang's fig. 52, Plate 7,‡ bears a close comparison with text-fig. 2 *b* of the present paper. As these authors point out, the mesarch protoxylem of *Tmesipteris* finds its counterpart in *Asteroxylon*, and the same feature has been demonstrated by Sinnott§ in some species of *Lycopodium*. The resemblance is increased by the fact, now demonstrated, that in the genus *Tmesipteris* the stele of the aerial stem is not ectophloic, as generally described, but that phloem also occurs laterally and centripetally to the bundles of the ring. The lateral phloems would correspond to the phloem which occupies the bays between the xylem salients of *Asteroxylon* and *Lycopodium*.

The facts before us appear fully to warrant the suggestion that the scattered medullary strands of *Tm. Vieillardi* are the vestiges of a once continuous axial column running presumably through the whole length of the stem. In the retention of medullary xylem and of its erect terrestrial habit *Tm. Vieillardi* has apparently lagged behind the other forms of the genus, which seem to be gradually relinquishing their primitive terrestrial home. It is tempting to trace the elimination of medullary xylem in *Tm. tannensis* BERNH. to the mechanical requirements of a pendulous habit, but it must be remembered that this elimination has already been largely carried out in *Tm. Vieillardi* itself; moreover, *Tm. tannensis* is not always pendulous, and even when it is pendulous its pith is composed of sclerenchyma, a tissue with mechanical properties similar to those of xylem.

The leaf-traces of *Asteroxylon* follow a very oblique—nearly vertical—course through the cortex, and terminate in the leaf-base, never entering the free portion.|| The vascular supply to the scale-leaves of *Tm. Vieillardi* shows the same peculiarities. As in *Asteroxylon*, too, the more proximal scale-leaves are devoid of a vascular supply. The general structure and mode of origin of the leaf-trace is also very similar in the two genera, at the same time recalling that in *Lycopodium*.

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* WIGGLESWORTH (1907), Pl. 22, fig. 14.

† I am very grateful to my friend Prof. N. K. TIWARY for material of these plants, collected by himself in the Nepal Himalayas.

‡ KIDSTON and LANG (1917–20), Memoir No. 3.

§ SINNOTT (1909).

|| KIDSTON and LANG (1917–20), Part III, p. 650; SCOTT (1922), p. 607.

(*c*) *Anatomy of Young Plant.*

In its simplicity of structure the young plant of *Tmesipteris* reveals, as HOLLOWAY has also pointed out,* a further basis for comparison with the Psilophytales. The simple stele of the rhizome is continued unbroken into the aerial axis in the same way as in *Rhynia*. In this respect, therefore, *Tmesipteris* quickly passes over during its ontogeny a feature which was permanent in the Rhyniaceæ.

(*d*) *Sporangiophores.*

The anatomical resemblances between the Psilophytales and the Psilotales are accompanied, as KIDSTON and LANG have shown, by a general agreement in the sporangiferous organs. In the fossil group the sporangia are clearly terminal on shoots, but it is possible to interpret in the same way the clustered sporangia (synangia) of the Psilotaceæ, especially as we know that in the Rhyniaceæ the branching of the sporangiferous axis was sometimes shared by the sporangium itself.† The sterile leaf-like lobes of the Psilotaceæ, identical in structure and appearance with the vegetative leaves, would be strictly homologous with them, but whatever their exact morphological nature may be,‡ it would not affect the general conclusion that the organ on which they are borne is of an axial and not foliar nature.§ The fact that the vascular supply to a sporangiophore originates in the same way as an ordinary leaf-trace, while going in support of the foliar theory, is not inconsistent with an axial nature of the organ. The usual presence of a pair of leaves on the sporangiferous axis was largely responsible for the comparison with the forked sporophylls of the Sphenophyllales, but the Rhynie discoveries have shown that this comparison, though fully justified on the evidence then available, was probably based on a superficial resemblance.

Before concluding, attention may be drawn to another aspect of the sporangiophore of the Psilotaceæ which, while consistent with their axial nature, suggests that these organs are built on an essentially verticillate plan. This hypothesis was suggested by two abnormalities observed in *Tm. Vieillardi*.‖ In their essential features these abnormalities looked like the diagrams in text-fig. 7. On this hypothesis the sporangiophore of *Tmesipteris* would be an axis bearing a whorl of two sterile lobes (which may be either leaves or modified branch axes) succeeded by a whorl of two fertile lobes (sporangia) alternating in position with the sterile lobes. The sporangiophore of *Psilotum* would be similar to that of *Tmesipteris*, except that the whorls are trimerous instead of dimerous.

The normal sporangiophore of *Tmesipteris* could easily be derived from fig. 7 *a* by a

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* HOLLOWAY (1917), p. 43.

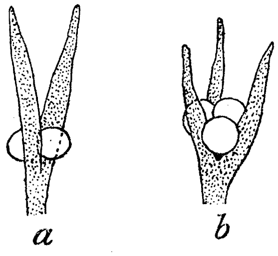
† KIDSTON and LANG (1917–20) Pt. IV, p. 851, and Pt. II, Pl. IX, figs. 58, 60, 63 (*Hornea Lignieri*).

‡ This has been ably discussed by LIGNIER (1903), (1908), p. 278.

§ JURANYI (1871), (1875) ; STRASBURGER (1873) ; GOEBEL (1881), pp. 688-89 ; BERTRAND (1881) ; SYKES (1908), (1908A).

‖ These have been described in a separate paper (SAHNI, 1923), in which their theoretical bearings have also been more fully discussed.

slight bend in the synangial stalk, tilting the synangium from its terminal position into an "adaxial" one. As Prof. GOEBEL* has shown, such a bend actually takes place during the development. The normal sporangiophore of *Psilotum* differs from fig. 7 *b* chiefly in its sessile character and in the absence of a leaf-lobe on the stem side. But we have only to imagine a sporangiophore of the type here figured attached in a sessile manner, as in *Psilotum*, with the synangium reclining against the stem, and the disappearance of the extra leaf-lobe (which would lie wedged in between the stem and the synangium) would not be difficult to account for.



TEXT-FIG. 7.

If the suggestion here put forward is justified, at least a distant comparison† of the Psilotales with the Sphenophyllales would still be possible, although not in the same sense as the forked sporophyll theory would imply. The sporangiophores of the Psilotales, while in a general way resembling those of the Equisetales and Sphenophyllales, would be unique among Pteridophytes in the possession of sterile lobes below and alternating with the individual sporangia of the fertile whorls. At the same time this suggestion of a verticillate organization for the sporangiophores of the Psilotales need not seriously conflict with their obvious affinities with the Psilophytales, as expressed in their vegetative structure: for it is possible‡ to look upon the verticillate arrangement as a sort of condensed repeated dichotomy.

Taking the sum-total of the evidence into account, the Psilotales seem to approach even nearer to the Psilophytales than has hitherto been suspected, while the old-fashioned theory of the lycopod alliance, recently revived by the discovery of *Asteroxylon*, gains further support from the structure of *Tm. Vieillardi*. At the same time, an affinity with the Sphenophyllales (and Equisetales), although by no means a close one, may yet be recognized, in the light of the suggestion that the sporangiophores of the Psilotales are built upon a fundamentally verticillate plan.

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* GOEBEL (1881), p. 693.

† I also take this opportunity of correcting a regrettable mistake in my paper just cited. On p. 187, line 22, after the word "Psilotaceæ," the sentence should read, "which lends countenance to a comparison with the Sphenophyllales." There can, of course, be no question of including the Psilotaceæ within the Articulatæ.

‡ SAHNI (1923), p. 190.

SUMMARY AND CONCLUSIONS.

1. This paper is based on an investigation of alcohol material of the following forms: *Tm. Vieillardi*, DANG., *Tm. elongata*, DANG., *Tm. lanceolata*, DANG., and the form described by DANGEARD as *Tm. tannensis*, BERNH. Two species of *Tmesipteris* are recognized :—

(*a*) *Tm. Vieillardi*, DANG.

(*b*) *Tm. tannensis*, BERNH. (including the forms *lanceolata* and *elongata* provisionally as varieties).

The form *truncata* of DANGEARD has not been examined, but to judge from the published description and figures, it may also be included as a variety of *Tm. tannensis*.

2. *Tm. Vieillardi* differs from *Tm. tannensis* (in the wide sense) in (1) its erect terrestrial habit and narrow strap-shaped leaves with parallel margins, (2) the greater length of the transition region with its very numerous scale leaves, many of which receive a distinct vascular supply, (3) the presence of cauline medullary xylem in the lower part of the aerial shoot, (4) the structure of the pith and sieve-tubes, (5) the (? normally) larger and thicker-walled spores.

3. The erect habit, terrestrial mode of life and the medullary xylem mark this plant as an archaic form of the genus, facilitating the comparison of the Psilotaceæ with the Psilophytales, already established on more important grounds by Dr. KIDSTON and Prof. LANG.

4. This species may represent the parent type that gave rise to the usually pendulous and epiphytic forms grouped under *Tm. tannensis*, BERNH. *Tm. Vieillardi* also appears to have made unsuccessful attempts towards adopting an epiphytic habit. Indeed, the whole genus may be said to be gradually relinquishing its primitive terrestrial home, *Tm. Vieillardi* being one of the stragglers. The absence of roots in this primitive form is a further indication, if such is needed, that the rootless habit of the genus preceded the adoption of an epiphytic mode of life, and is not a reduction phenomenon.

5. The medullary xylem in the aerial shoot of *Tm. Vieillardi* may be directly compared with the central cauline xylem in the stele of *Asteroxylon* and *Lycopodium*.

6. In *Tm. Vieillardi* most of the scale-leaves on the transitional region of the axis are supplied with leaf-traces, and these resemble the leaf-traces of *Asteroxylon* in the fact that they stop short at the leaf-base, never entering the free portion of the leaf.

7. In the aerial shoot of *Tmesipteris* the phloem is not confined to a layer outside the xylem ring, as commonly described, but more or less completely surrounds each individual bundle of the ring. In longitudinal sections, not only in *Tm. Vieillardi* but also in *Tm. tannensis* (vars. *typica*, *elongata*, *lanceolata*), the histological distinction between the pith and the phloem abutting on its periphery is clear and unmistakable in the author's preparations, stained in Gentian Violet and Orange G (Plate 5, fig. 12; Plate 6, figs. 1–25).

8. The distribution of the phloem in the aerial stem of *Tmesipteris*, considered along with the rest of the stelar anatomy, facilitates the comparison of *Tm. Vieillardi* with *Asteroxylon* and with *Lycopodium*.

9. The sporangiophores of the Psilotales are not forked sporophylls but, as KIDSTON and LANG have suggested, axial organs, in a general way comparable with the branched sporangium-tipped axes of the Psilophytales. There are indications that in their mode of branching they reveal an essentially verticillate organization, a whorl of two (*Tmesipteris*) or three (*Psilotum*) sporangia succeeding an alternating whorl of sterile lobes, of which there are two in *Tmesipteris* and two (reduced from three) in *Psilotum*.

10. The evidence now brought forward tends to bring the Psilotales (or especially the genus *Tmesipteris*) even nearer to the Devonian genus *Asteroxylon* than has hitherto been suspected, at the same time supporting the old view that the Psilotales are related to the Lycopods.

11. Further, if the verticillate hypothesis suggested above is justified, a distant comparison may also be made with the other Pteridophytes (Sphenophyllales and Equisetales), in which the sporangia occur in whorls. The sporangiophores of the Psilotales, while in a general way resembling those of the Sphenophyllales and Equisetales, would differ in the possession of whorls of sterile lobes, below and alternating with the whorls of sporangia.

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EXPLANATION OF PLATES.

PLATE 5.

(*All the figures, except fig.* 7, *are from untouched photographs.*)

FIG. 1.—*Tm. Vieillardi*, DANG. The sporangiophores are seen towards the distal end in two zones separated by a sterile region (Mt. Mou, 18.3.1914). About $\frac{2}{3}$ nat. size.

FIG. 2.—*Tm. Vieillardi*, DANG. Rhizome and lower part of transitional regions of two aerial shoots. About $\frac{2}{3}$ nat. size.

FIG. 3.—*Tm. Vieillardi*, DANG. Transitional region and lower part of leafy shoot. In the lower half of the figure are seen about a dozen minute processes (scale-leaves) each of which terminates a distinct ridge (decurrent leaf-base). Nat. size.

FIG. 4.—*Tm. Vieillardi*, DANG. Leafy region of shoot, bearing sporangiophores. The minute white dots on the leaves are air bubbles held at the stomatal depressions. The specimen was photographed while immersed in alcohol. Nat. size.

FIG. 5.—*Tm. tannensis* var. *elongata*, DANG. Showing the pendulous habit; the transition region is much shorter and the scale-leaves very much fewer than in *Tm. Vieillardi* (Tonine, 2.10.1914). About $\frac{1}{2}$ nat. size.

FIG. 6.—*Tm. tannensis* var. *elongata*, DANG. Different views of sporangiophores showing the mode of dehiscence: *a*, back view; *b*, front view showing the four valves and the septum with its two triangular tooth-like processes in the median plane; *c*, *d*, side views showing the same processes. All × $2\frac{1}{2}$ diams.

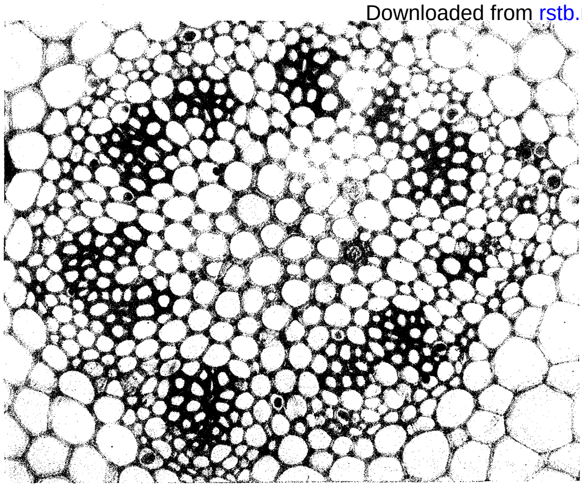
FIG. 7.—*Tm. Vieillardi*, DANG. Transverse section of an abnormal trilocular synangium, showing a vascular bundle in each of the three septa. The tracheides were dotted with indian ink on the print, to make them prominent. × abt. 10 diams.

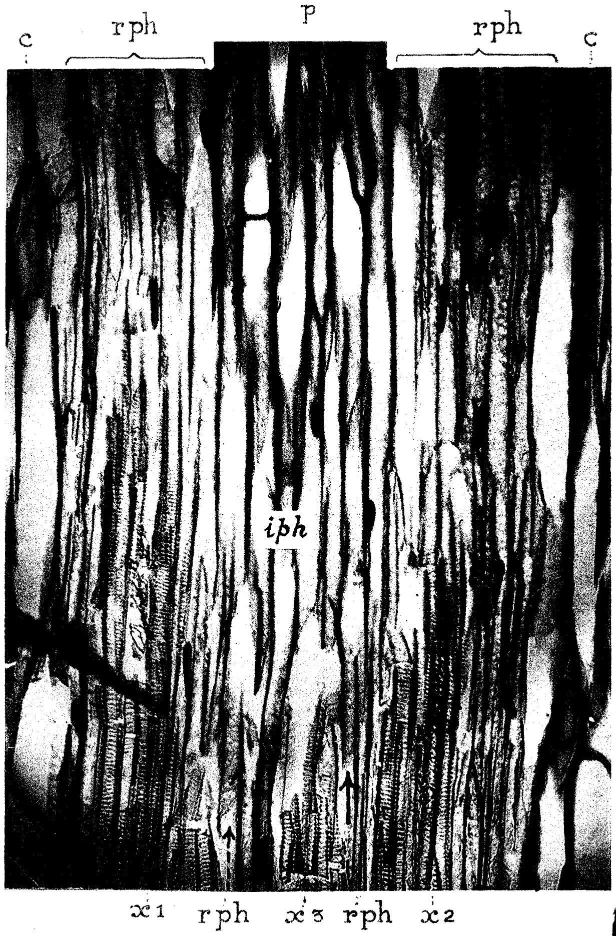
FIG. 8.—*Tm. tannensis* (typical form). Note the short transition region and few scale leaves. The distal part of the shoot was twisted through 90° to show the biseriate arrangement of the leaves (Mt. Mou, 8.3.1914). About $\frac{1}{2}$ nat. size.

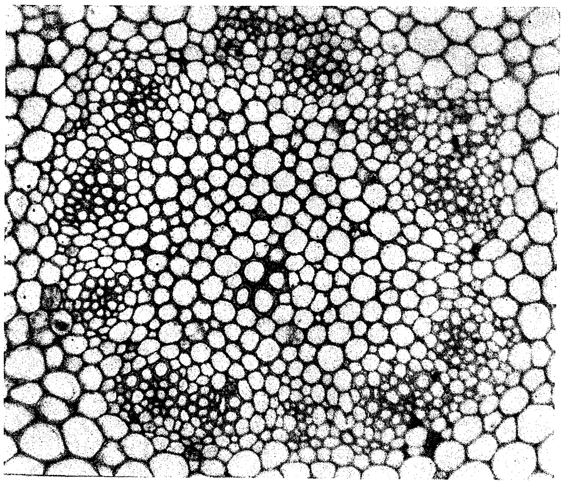
FIG. 9.—*Tm. tannensis* (typical form). A young plant found among the adult specimens of this form. × $2\frac{1}{2}$ diams.

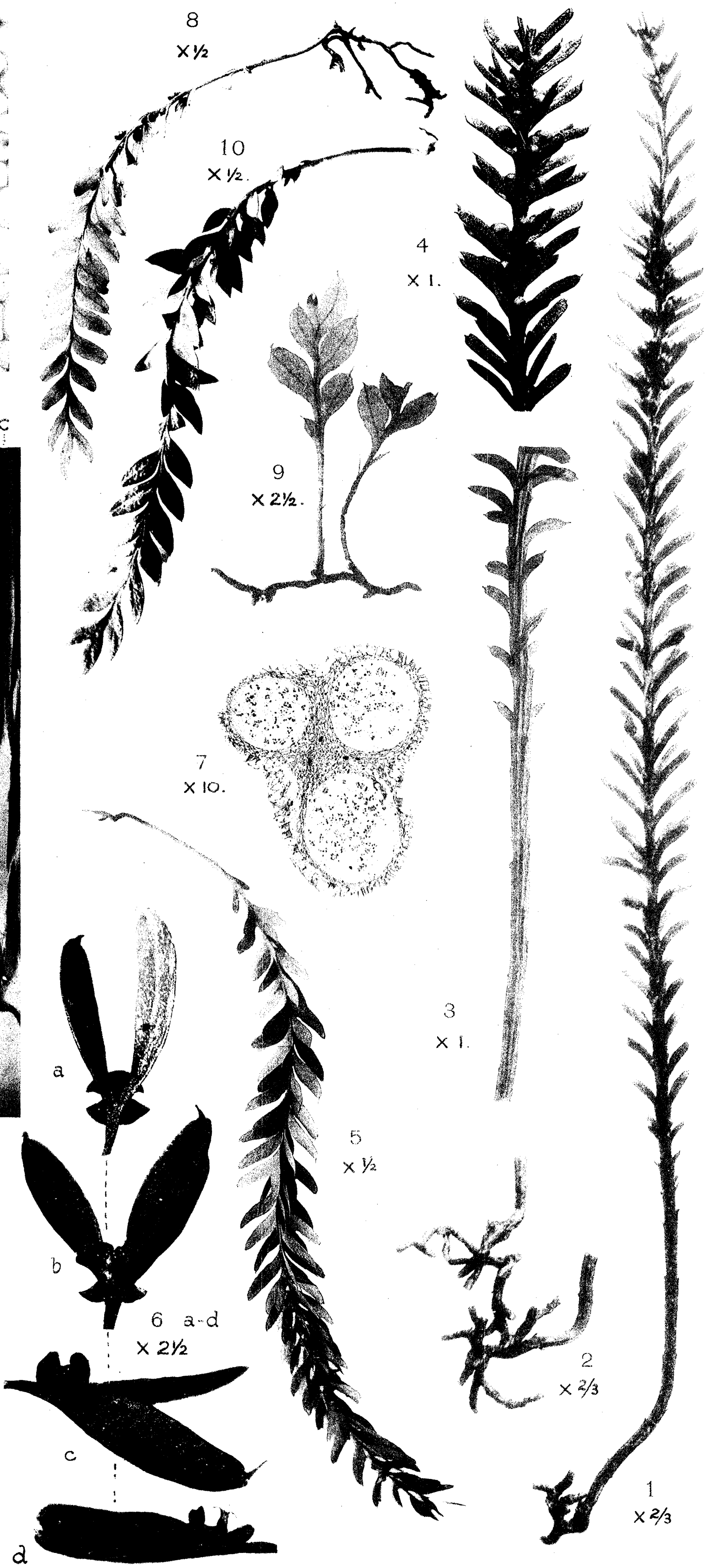
FIG. 10.—*Tm. tannensis* var. *lanceolata*, DANG. The distal part of the shoot was twisted through 90° to show the biseriate arrangement of the leaves. The leathery texture of the leaves (contrast fig. 8) is well brought out in the photograph. The distal (biseriate) leaves are seen from their upper surface which is slightly convex (Mt. Canala 13.6.1914). About $\frac{1}{2}$ nat. size.

FIG. 11.—*Tm. Vieillardi*, DANG. Photomicrograph of a transverse section of the stem (leafy region) showing a central group of about 25 uniformly thick-walled cells (pith) surrounded by a layer or two of smaller collenchymatous cells (internal phloem) connected, round each xylem strand, with the outer phloem. Along the periphery of the stele there is a broken layer of small thick-walled cells. An endodermis is not distinguishable. × 100.









B. Sahni. phot.

Zinco Collotype Co., Edinburgh.

Tmesipteris.

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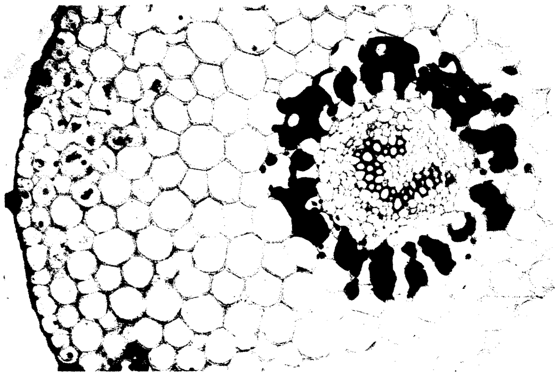
14 ×38



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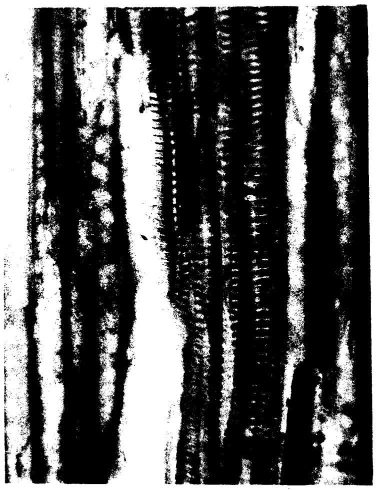
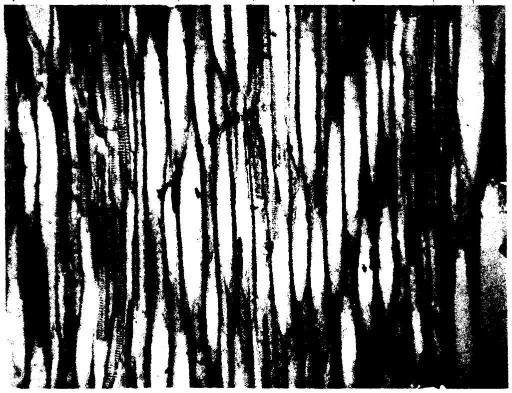




15 ×60

24 ×240.

25 ×240

21 ×60

20 ×240

22 ×240

B Sahni phot.

Zinco Collotype Co., Edinburgh.

Tmesipteris

FIG. 12.—*Tm. Vieillardi*, DANG. Photomicrograph of an oblique longitudinal section of the stem (leafy region) showing the same tissues as above ; x_1 x_2 x_3, xylem ; *c*, cortex ; *p*, pith ; *rph*, phloem in the region of the ray ; *iph*, internal phloem *in tangential section*. In the cell containing the letter *h* sieve-plates are clearly seen in the original section. This section is specially instructive on account of its slight obliquity (further explanation in text, p. 151). × 100.

FIG. 13.—*Tm. Vieillardi*, DANG. Photomicrograph of a transverse section through the leafy stem, showing an eccentrically placed strand of medullary xylem. The tracheides of the medullary xylem are normally of the same average size as those of the main stele, but in this section they are abnormally wide. The pith, too, is unusually large. (Compare Plate 5, fig. 11.) × 69.

PLATE 6.

(*All the figures are from untouched photomicrographs.*)

Tm. Vieillardi, DANG.

FIG. 14.—Transverse section through the distal region of a rhizome. The xylem has already become horse-shoe shaped, while a thin-walled tissue not distinguishable, at least in transverse sections, from that immediately outside the xylem, occupies the concavity. A deposit of phlobaphene surrounds the whole stele. The presence of rhizoids and of mycorrhiza shows that the section is not from the transitional region, as might be inferred from the configuration of the xylem. × 38.

FIG. 15.—Median longitudinal section through the leafy stem showing a medullary strand (*mx*) embedded in the pith (*p*) and two opposite strands of the xylem ring right and left (*x*, *x*) ; *c*, cortex. × 60.

FIG. 16.—Part of the same section (centre and left) further enlarged to show the presence of phloem internally (*iph*) to the xylem as well as externally (*oph*). A sieve-tube (*mph*) is also seen in association with the medullary xylem (*mx*). × 160.

FIG. 17.—Part of the same section. The light patches, best seen when viewed at arm's length, are the sieve-plates. × 240.

FIG. 18.—Radial section through the " ray " between two strands of the xylem ring, showing typical sieve-tubes, one of them containing a large nucleus. × 240.

FIG. 19.—Median longitudinal section through the leafy stem, showing on the left a xylem strand with typical sieve-tubes both centripetally (*iph*) and centrifugally (*oph*) to it. On the extreme right is a portion of the xylem strand of the opposite side (*x*), the corresponding inner phloem (*iph*) being indistinctly seen. Between the internal phloems of the two sides are about nine cells of the pith (*p*), some of them clearly showing the characteristic pits, quite distinct in appearance from sieve-plates. × 160.

FIG. 20.—Part of the same section further enlarged to show the structure of the internal phloem (*iph*) and pith (*p*). × 240.

FIG. 21.—Median longitudinal section through the leafy stem, to show especially the internal phloem (*iph*) on the lower right-hand side, photographed on a larger scale in the next figure. The arrow on the left indicates the phloem internal to the xylem of the opposite side. × 60.

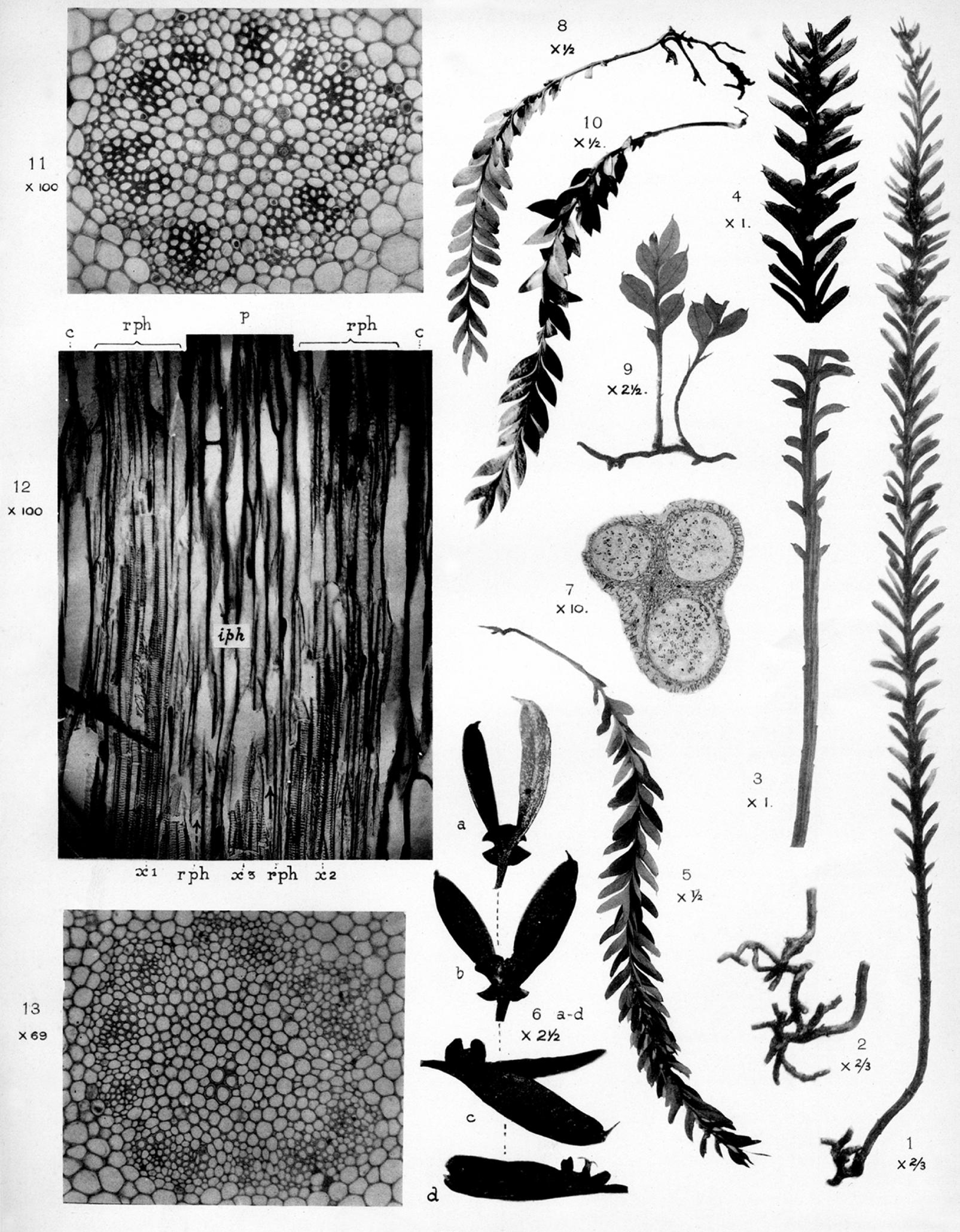
FIG. 22.—Part of the above section, showing sieve-tubes (*iph*) between the pith and xylem. × 240.

FIG. 23.—Longitudinal section through a strand of medullary xylem and an associated sieve-tube. To the right a thick-walled pith cell with characteristic round and slit-like perforations, and towards the upper end a slightly oblique end wall. × 240.

FIG. 24.—Another section through the same medullary strand. The sieve-tube is wider and shows multiseriate sieve-plates; the pitting of the pith cell in its upper part is in the form of vertical slits. × 240.

Tm. tannensis var. *typica.*

FIG. 25.—Median longitudinal section through the leafy stem. *On the left the section passes through a xylem strand, on the right through a "ray" between two xylem strands.* The ray is composed of sieve-tubes (*rph*) with circular uniseriate sieve-plates. The xylem not only has sieve-tubes on its outer side (on the left, out of focus) but a definite sieve-tube (*iph*) is also seen abutting on its pith side. There are five pith cells (*p*), one of them clearly showing some *oblique* slit-like pits. × 240.



Tmesipteris

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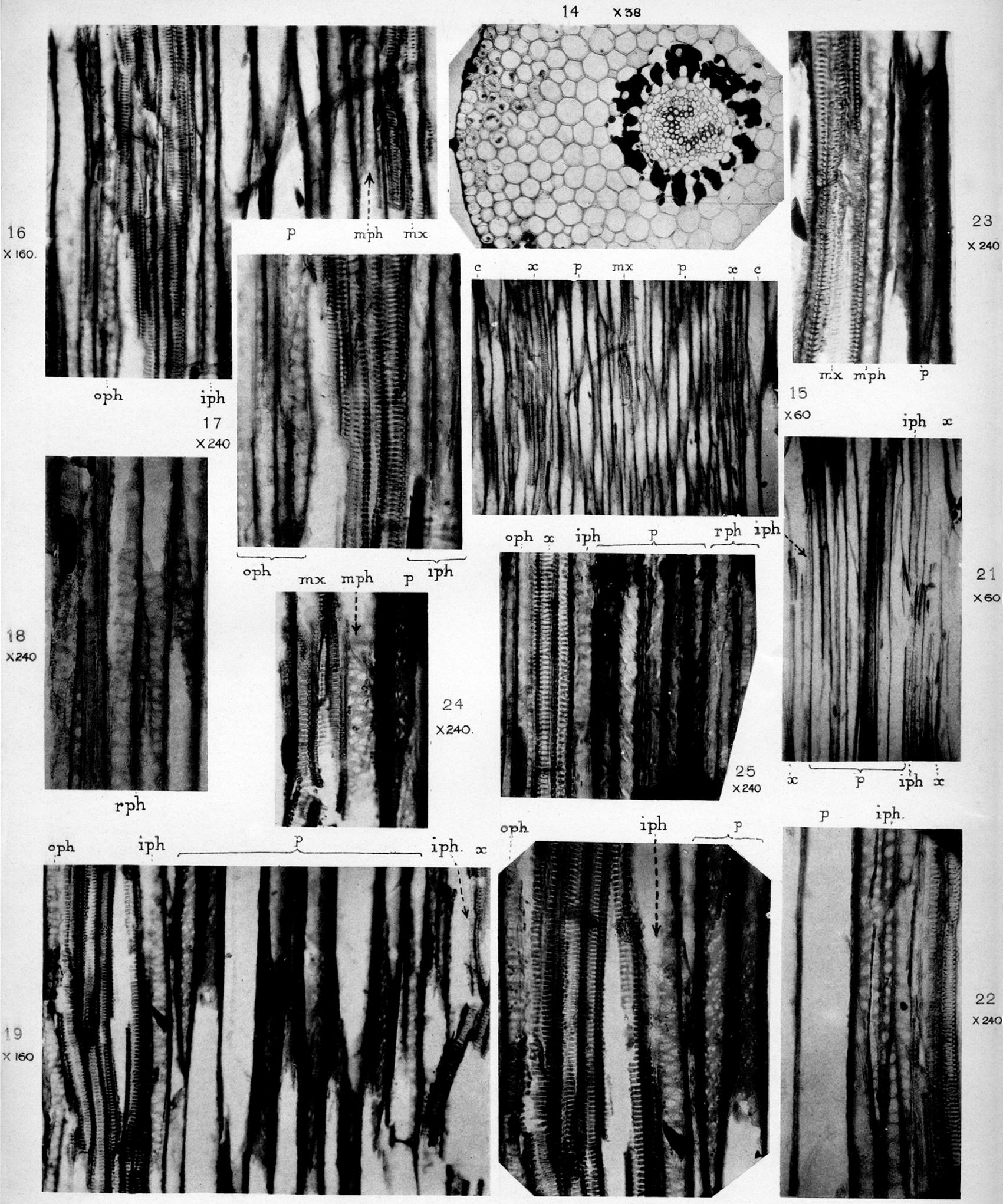

Tmesipteris

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Tm. Vieillardi, DANG.

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