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for the Degree of Ph.D. in the University
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A CRITICAL EXAMINATION OF THE VITTARIEAE

WITH A VIEW TO THEIR SYSTEMATIC COMPARISON.

INTRODUCTION.

The Vittarieae, as described by Christensen (1), comprises five genera, viz. Vittaria, Monogramma, Antrophyum, Hecistopteris, and Anetium, all of which are epiphytic forms growing in the damp forests of the Old and New World Tropics. All of them possess creeping rhizomes on which the fronds are arranged more or less definitely in two rows on the dorsal surface. The fronds are simple in outline with the exception of those of Hecistopteris which are dichotomously branched. The venation of the fronds is reticulate except in Hecistopteris where there is an open, dichotomous system of veins, and in Monogramma, in some species of which the venation consists simply of a mid-rib. An interesting feature, which has proved to be valuable as a diagnostic character, is the presence of "spicule cells" in the epidermis. These "spicule cells" are elongated cells containspicules of silica and their presence appears to be universal in the Vittarieae. The sporangia are fairly constant in form throughout the group but their distribution is extremely varied. The roots are characteristically provided with very numerous reddish-brown root hairs, a character shared with other epiphytic Ferns. The Gametophyte is divergent from the common cordate type in all cases where it has been investigated. Such are the main external characteristics of the group under consideration.

The five genera at present included in the Vittarieae have had an extremely varied systematic history, a fact which indicates at once that there is likely to be very considerable difficulty

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1. Christensen, Index Filicum, 1906.

in any attempt to consider their systematic relationships. The grouping of the genera under the name Vittarieae is of comparatively recent date, and prior to that time the various genera received very varied treatment at the hands of the systematists. Presl, in his Tentamen Pteridographiae (1836), placed Vittaria and Prosaptia (now Davallia) in the Tribe Vittariaceae. A number of Antrophyum species and Monogramma were placed in §1 Grammitideae of the Tribe Grammitaceae, while the remaining species of Antrophyum and Hemionitis spatulata (now Anetium citrifolium) were placed in §2 Hemionitideae of the same Tribe. Hooker(Synopsis Filicum, 1868) placed all five genera in the Tribe Grammitideae (Hecistopteris being included under Gymnogramme), without, however, grouping the genera in any way as separate from the other forms included in the Group. In the Historia Filicum (1875) of J.Smith , Vittaria, Pteropsis angustifolia , and Dictyoxiphium are placed in his Tribe Vittarieae. Monogramme, Diclidopteris (now included in Monogramme), Pleurogramme and Hecistopteris are placed in the Tribe Pleurogrammeae. Antrophyum is placed in the Tribe Grammitideae , although the author states that "The general aspect and mode of growth indicates the affinity of this genus to be with Vittaria." Goebel (1) suggested in 1896 that the five genera should be placed together in the Vittarieae. This suggestion was based on the characters of the Gametophyte and on certain characters of the Sporophyte, chiefly the presence of spicule cells in the epidermis of the fronds. Goebel's

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1. Goebel,"Hecistopteris, eine verkannte Farngattung",Flora,1896

suggestion was followed by Christ (Die Farnkraute der Erde, 1897) and Diels (Nat.Fam.,1899-1902), and is now gwnerally accepted.

Goebel (1) has recently published an account of the Vittarieae, examining in particular the relationships of the genus Pleurogramme, included by Diels and other systematists as a section of the genus Monogramme. This account is by no means complete and takes little or no account of a number of important criteria, such as the vascular anatomy and the origin of the sorus, which have proved themselves to be extremely useful when making systematic comparisons. The only other general account of the Vittarieae of which I am aware is dne by Benedict (2), which, on the author's statement, deals "almost entirely with the comparative external morphology and venation of the genera and the probable relationships indicated by these characters." Although Goebel and Benedict, together with other writers who have described features of interest in single species, have given a considerable body of facts with regard to the Vittarieae, it has been thought worth while to give a connected account of this group in the present memoir ; and especially since the conclusions here reached do not agree with those of previous writers. The present account is based on a critical examination of a wide range of species, particular attention being paid to the vascular structure and other points previously neglected. The material for this investigation was kindly handed over to me by Prof.F.O.Bower in 1923,

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1. Goebel,"Vittariaceen und Pleurogrammaceen." Flora,1924.
2. Benedict," The Genera of the fern tribe,Vittarieae." Bull.Torrey Bot.Club, Vol.38.

and to him my best thanks are due. The material for the most part was collected in Jamaica by Prof.Bower ; the remainder was from the Calcutta Botanic Gardens, kindly sent to this Department by Mr.Burkhill. In addition to the above, Herbarium specimens have been used where no preserved material was available, and I am greatly indebted to Prof. Wright Smith for Herbarium material of the rare fern, Hecistopteris pumila.

A detailed description of the various genera will now be given, after which the general affinities of the group will be discussed together with certain stelar problems which are raised by the anatomical construction of the forms examined.

Vittaria, J.Smith (1793).

The genus Vittaria. along with Prosaptia (=Davallia), formed the Tribe VII Vittariaceae of Presl. J.Smith included Vittaria together with Pteropsis (=V.angustifolia) and Dictyoxiphium in his Tribe 10, Vittarieae. Hooker (Syn.Fil.) placed it between Antrophyum and Taenitis and divided the genus into two sections, § Euvittaria,Hk. and §§ Taeniopsis,J.Sm., the former having the "sori sunk in a two lipped marginal groove" and the latter with the "sori in a slightly intramarginal line, with the unaltered edge of the frond produced beyond and often rolled over it." This subdivision is accepted by Christ and Diels in their classification of the genus. In Hooker's arrangement the § Euvittaria contains only a single species, V.elongata whereas §§Taeniopsis has a comparatively large number of ill defined species differing only in detail from one another. Hooker gives only eight species with the remark that "the species are very difficult of discrimination and we have admitted here considerably fewer than M.Fee." Christensen, on the other hand, includes over forty species.

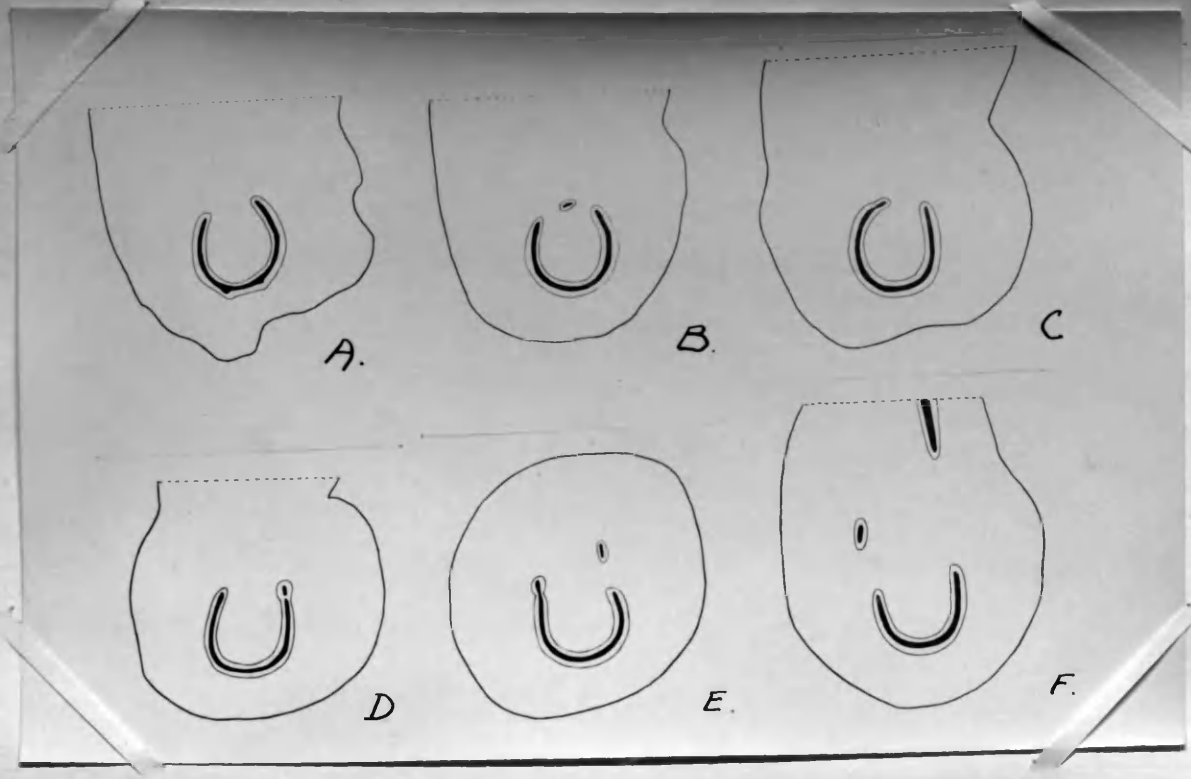
Benedict (1) has more recently divided the genus into two sections which do not coincide with those of Hooker. These are : Euvittaria, which appears to include most of the species of both of the sections of Hooker and Radiovittaria, which contains a small number of species previously included in §§Taeniopsis of Hooker. The same writer (2) has recently described the external morphology and a few points in the anatomy of the species of the latter

1. Benedict, l.c. p.166

2. Benedict, "A Revision of the Genus Vittaria.", Bull. Torrey Bot. Club,41, 1914.

section, the type species of which is V.remota Fée. Whereas all the species in Benedict's section Euvittaria have dorsiventral rhizomes and distichous phyllotaxy, the species in the section Radiovittaria are stated to have radial stems and polystichous phyllotaxy.

The following account is based on species from both of Hooker's sections but, unfortunately, I have not as yet had an opportunity of examining any species belonging to Benedict's new sub-genus Radiovittaria.



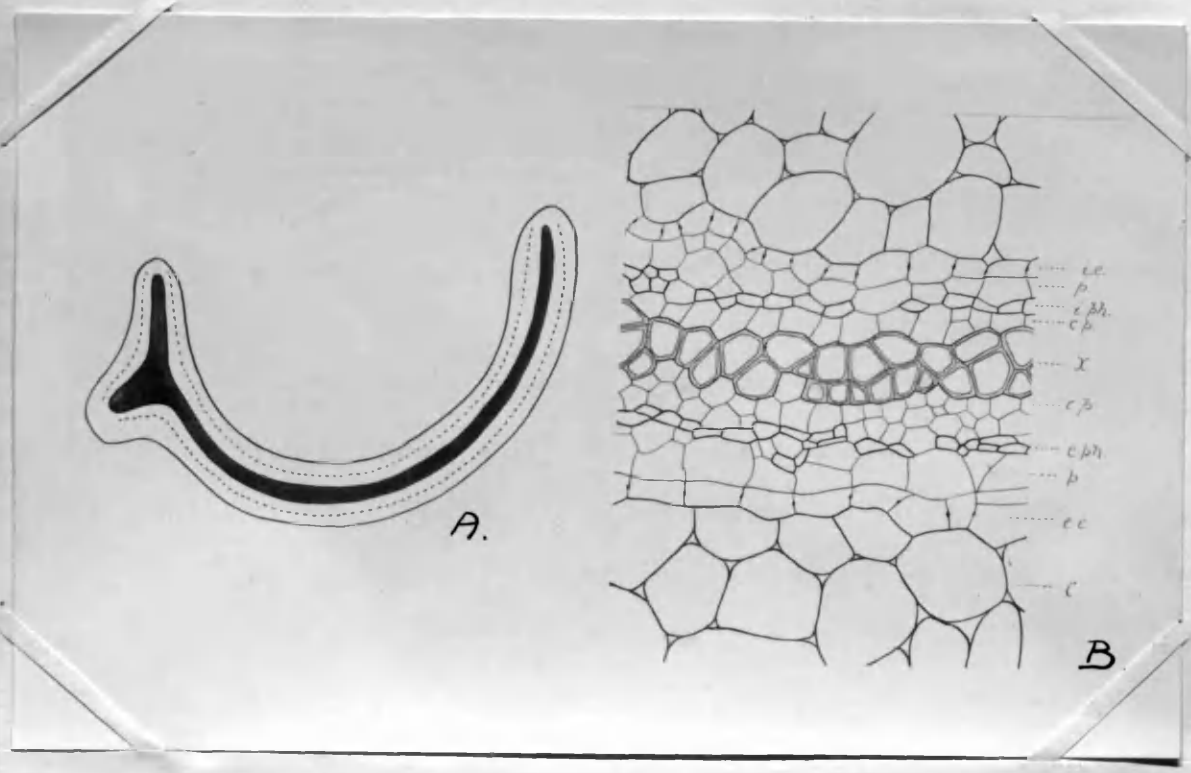


Fig.1. Vittaria lineata. A-F, series of transverse sections of the mature rhizome. X 13

Fig.2. Vittaria lineata. A, diagram of ventral meristele ; xylem, black; phloem,dotted; endodermis,plain line. X 55 . B, portion of ventral meristele. i.e.,internal endodermis; p,pericycle; i.ph.,, inner phloem; c.p.,conjunctive parenchyma; x,xylem; e.ph.,external phloem; e.e.,external endodermis; c,cortex. X 260

Vittaria lineata (L) J.Smith.

Vittaria lineata (Plate 1, 9) has a wide distribution in the tropics and sub-tropics of both hemispheres. The creeping rhizome bears the long, linear fronds in two ranks on its dorsal surface. The fronds are stated to be pendulous so that the plants look like"bunches of grass".

Together with a number of similar species V.lineata was originally described by J.Smith under the separate genus Taeniopsis but this latter genus was subsequently given up and re-united by the same writer with Vittaria. The name Taeniopsis is retained by Hooker (Syn.Fil.) as a sectional name and V.lineata may be taken as a typical example of this section. The material on which the following account is based was collected at Hollymount, Jamaica.

Anatomy.

The stele of the mature rhizome is a dorsiventral dictyostele, very similar to the examples of this type of structure described by Gwynne-Vaughan (1). Since dorsiventral dictyosteles are frequently present in the rhizomes of the Vittarieae a short description of this type of stelar structure may be given here. In the short internodes there is present a single horse-shoe shaped ventral meristele.(Fig. 1,A and Fig. 2, A,B.) The xylem is here in the form of a band about two tracheids in thickness and completely surrounded by a sheath of conjunctive parenchyma. Both

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1. Gwynne-Vaughan,"Observations on the Anatomy of Solenostelic Ferns,Part II." Ann. Bot.,Vol.XVII.

internal and external phloem are present as a single, or in places double, layer of small, protophloem like elements, the walls of which stain deeply with haematoxylin. External to the phloem there is a well marked pericycle of large elements and surrounding the entire meristele is an endodermis. This latter, it may be noted, is in the primary condition and shows a clearly defined Casparian Strip.

The method of leaf trace departure (Fig.1, A-F.) is as follows. As the node is approached a small meristele becomes detached from one of the arms of the horse-shoe and moves across to the other arm. The leaf trace then becomes separated from the axial stele as two strap shaped strands, one from each side of the leaf gap. This type of stelar structure, as Gwynne-Vaughan has pointed out, is not far removed from solenostely and results from the fact that the leaf gaps only overlap very slightly.

The rhizomes occasionally branch ina a dichotomous manner and there is in such examples an equal division of the vascular tissue, each arm having a structure similar to that described above. The growing point of the rhizome is described by Britton and Taylor(1) as " a fleshy green bulbous formation with a conical apex, completely enveloped in long brownish scales.Glands, similar to those of the leaves and hairs, resembling those of the root are present. The apical cell is wedge shaped and the differentiation of tissues follows quite closely the advance of the apical meristem."

The Frond.

The linear fronds attain a length of 18 ins. and a breadth of $\frac{3}{8}$ ins. There is a distinct mid-rib and on either side of it

1.Britton& Taylor,"The Life History of Vittaria lineata." Mems.Torrey Bot.Club.Vol.8.

there is a single line of much elongated, almost rectangular areolae. The venation of the fronds of young plants has been described and figured by Britton and Taylor, the stages passed through resembling those figured for Antrophyum species and Anetium (Figs. 22-36) The first formed fronds have a single vein. The next stage shows a single mesh and subsequent stages show the establishment of the reticulate venation characteristic of the fronds of mature plants.

At the base of the petiole of mature fronds of mature plants there are two strap shaped strands of the Adiantum type. These divide dichotomously at a higher level and the two inner shanks unite to ~~give~~ form the mid-rib which traverses the length of the frond. Spicule cells are present in the epidermis of the laminal portion. The stomata are mostly confined to the sides of the sporangial grooves and on the epidermis lining the latter simple glandular hairs are present.

Superficial Appendages.

The surface of the rhizome and leaf bases is clothed with clathrate scales of very characteristic structure, which holds with small, but from the taxonomic point of view important, variations throughout the genus (1). The characteristic appearance of this type of scale is due to the localisation of the thickening to the anticlinal walls, the superficial walls remaining thin and transparent. This differential thickening

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1. See Benedict, " A Revision of the Genus Vittaria J.E.Smith." Bull.Torrey Bot. Club, Vol.41, and the older, but apparently less reliable, statements of Muller, Bot.Zeit. 1854.

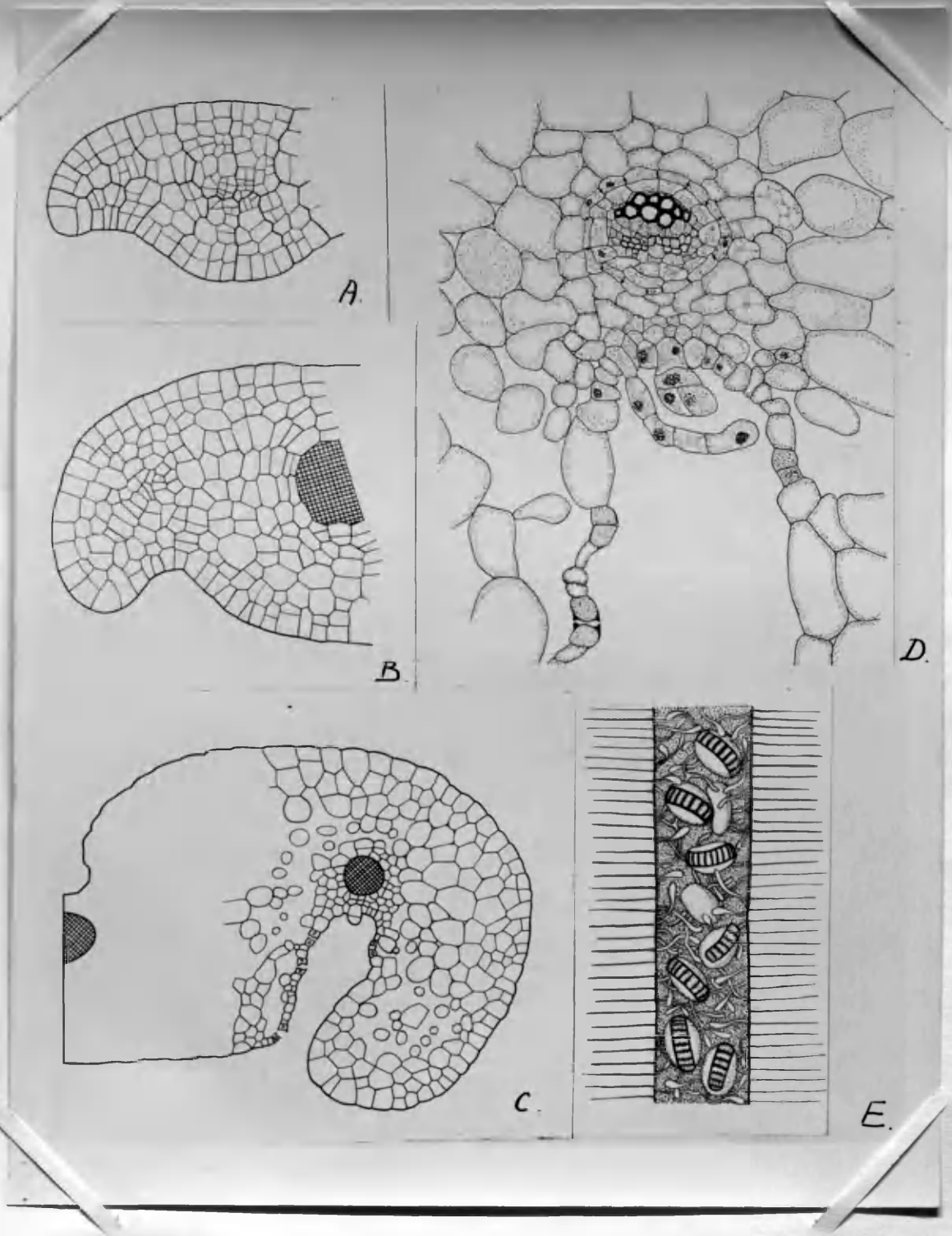

Fig.3. Vittaria lineata. A,B and C from unpublished drawings by Prof.Bower showing the origin of the sorus. X . D, portion of the sporangial groove showing stomata and a young sporangium protected by a paraphysis. X260 . E, sporangial groove in surface view. X 55 .

gives a lattice like appearance to the whole scale.

Sporangia.

The sporangia are borne in two deep grooves over the marginal commissural veins. The arrangement of the sporangia is very irregular but they are so placed that the annulus of each is able to function without interference from neighbouring sporangia (Fig. 3, E) Intermingled with the sporangia are very numerous paraphyses with club shaped end cells. These paraphyses apparently serve to protect the sporangia in the earlier stages of their development (Fig. 3, D), but it is not known whether they have any function at a later stage. The development of the sorus is indicated in Figs. 3, A-C which are from unpublished drawings kindly handed over to me by Prof. Bower. These show very clearly that the origin of the sorus is intramarginal, the true margin of the leaf forming the outer flange of the sporangial groove. The development of the sporangia appears to follow the usual course followed by the higher Leptosporangiate Ferns. The sporangium is marked by a number of features which are common to all the forms of the Vittarieae examined by me. The capsule has vertical annulus of fifteen or more cells. The stomium is four celled and the epi- and hypostomium each consist of two cells. The spores are reniform in shape and have a smooth surface. Spore counts yielded the numbers 52 and 61 indicating that the typical number for each sporangium is probably 64. The stalk of the sporangium is peculiar ; it is single celled at its base but a little below the capsule it consists of several cells. (Fig. 4, A) The curious nature of the stalk has a definite relation to the dehiscence of the sporangium, which has been studied in living material by Britton and Taylor.

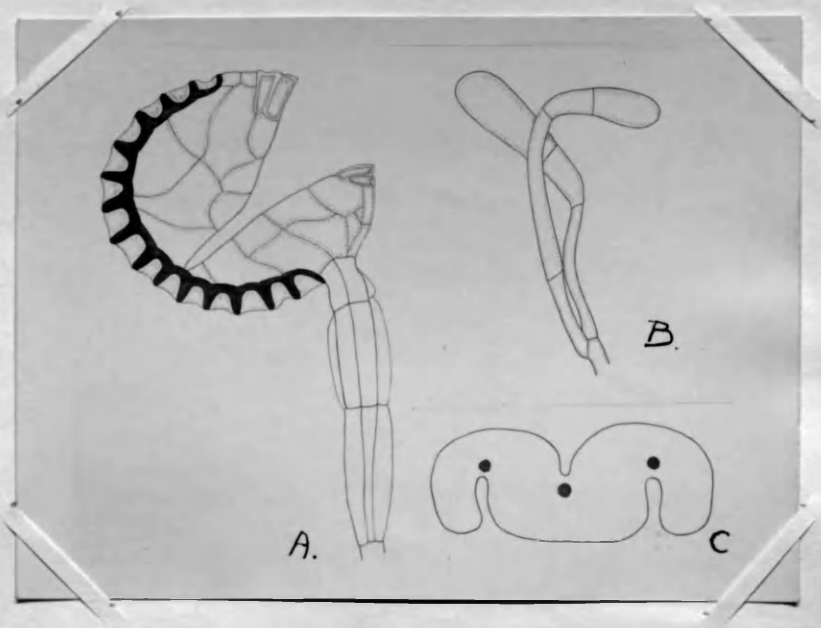

Fig.4. Vittaria lineata. A, sporangium. B, paraphysis. X 185 .
C, transverse section of mature fertile frond. X 20 .

They state that " As the sporangium ripens all the cells of the upper part of the pedicel become inflated and throw the sporangium back, so that when the split occurs, and the lip cells open by the everting of the annulus, the spores have a less interrupted access to the opening of the groove, their original position being such that did they keep it during the discharge of the spores many of them would become entangled among the branches of the paraphyses from which they would be powerless to escape."

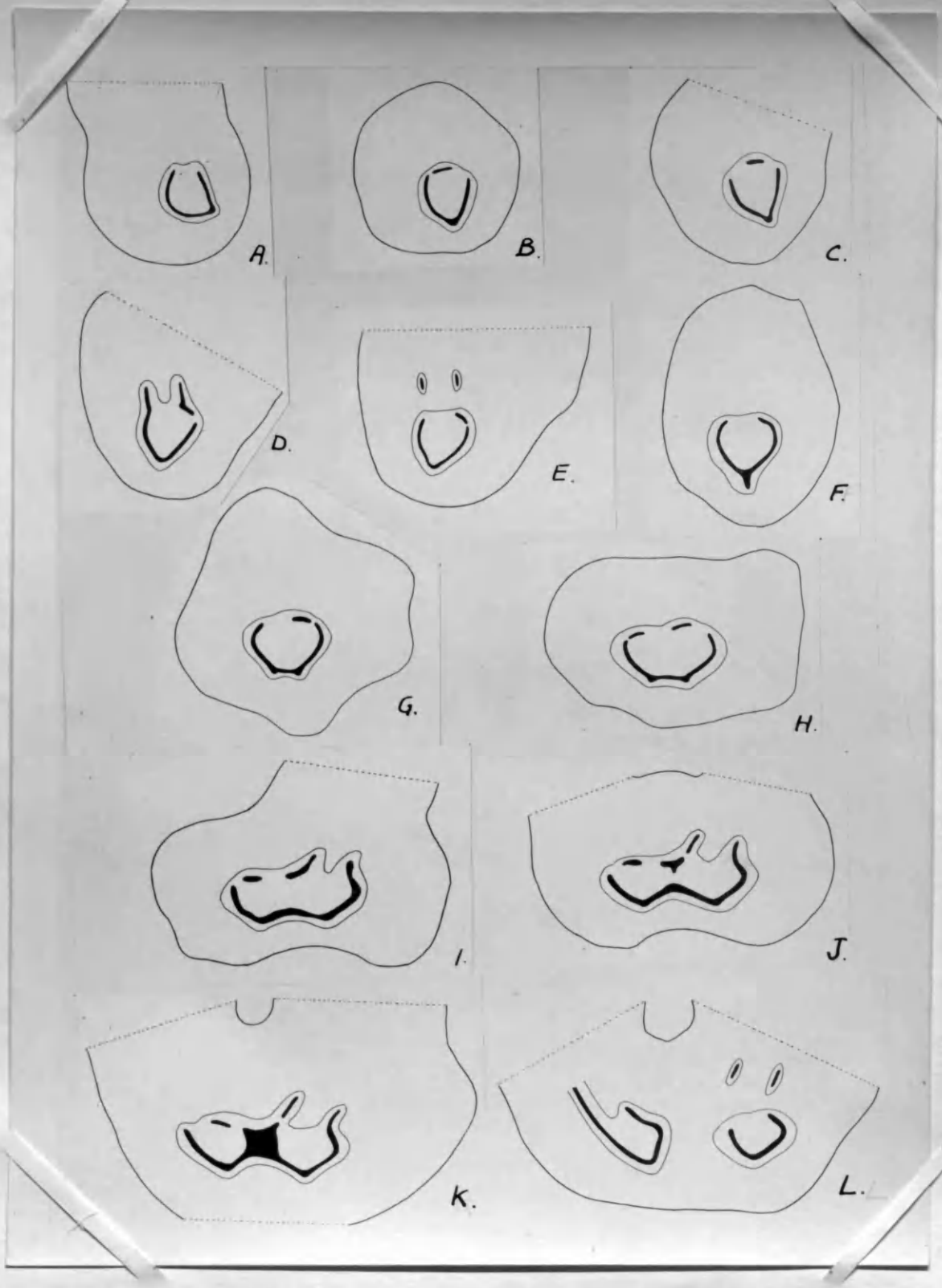

Fig.5. Vittaria elongata. Series of transverse sections of a mature rhizome showing the departure of leaf traces and a dichotomy of the rhizome. X 13 .

Vittaria elongata, Sw..

(Plate 1, B)

V.elongata is the only species included in the Section Euvittaria by Hooker (Syn.Fil.). In general habit it closely resembles V.lineata but it appears to be confined to the Eastern Tropics. The material upon which the following account is based was obtained from the Botanic Gardens of Calcutta in 1915.

Anatomy.

In the internode of the mature rhizome the stele appears as a more or less cylindrical structure (Fig. 5, A.). The xylem is in the form of a U-shaped curve, two or three tracheids in thickness, with the opening of the curve facing the dorsal side of the rhizome. Phloem is present both internally and externally as a layer of small elements. Surrounding the stele is an endodermis composed of relatively small elements showing a well defined Casparian strip. No internal endodermis is present (1) and the centre of the stele is occupied by parenchyma. A several layered pericycle is present on the outside of the external phloem but is not distinguishable opposite the xylic gap.

As the node is approached a strand of xylem becomes detached from one arm of the U-curve and moves across, inside the stele, to the other arm. Two strands, each surrounded by an endodermis, then become abstricted from the axial stele, and pass through the cortex into the base of the petiole (Fig. 5, B-E). Nowhere

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1. Jeffrey (Trans.Roy.Soc.London, B,Vol.195,p.132.) states that there was an internal endodermis in material from Buitenzorg. This was not the case in any of the material examined by me. Gwynne-Vaughan (l.c. p.719) has also briefly described the anatomy of this species. Some of his specimens agreed with the above description ; others he found to be typically dictyostelic, but he remarks that " it is quite possible that some of the specimens examined were wrongly named."

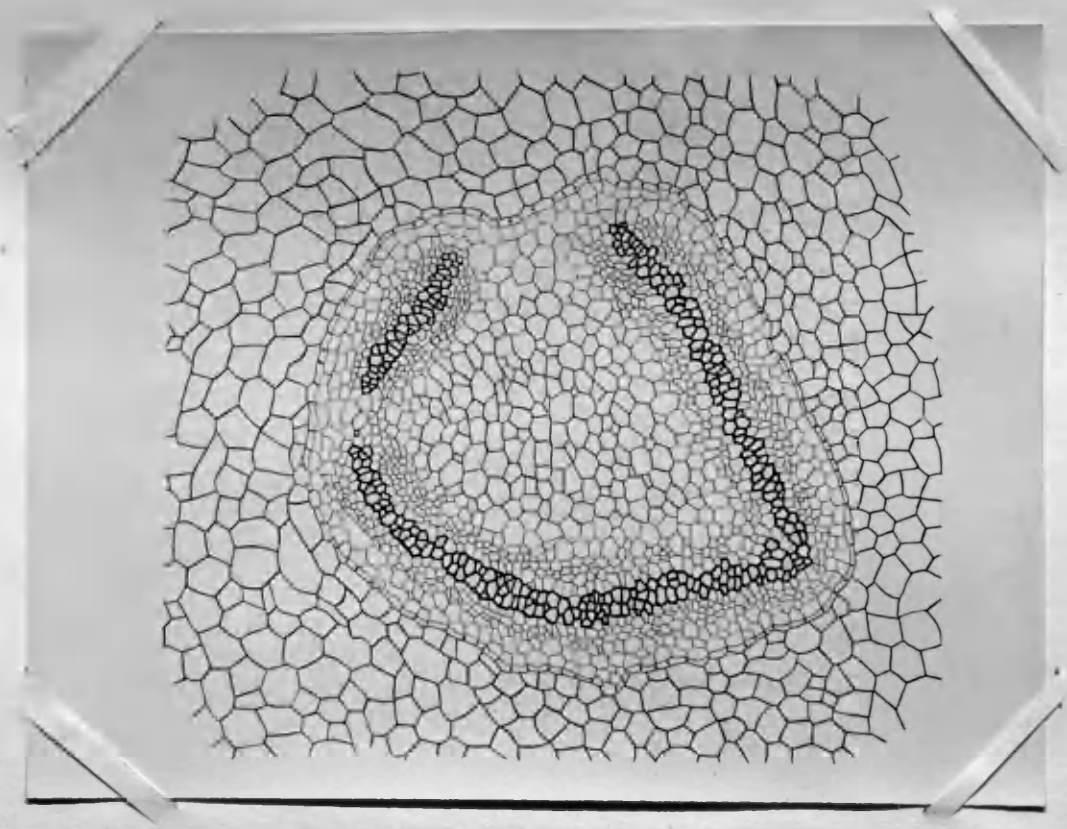

Fig.6. Vittaria elongata. Detailed structure of the stele at the level of B in Fig.5. X 75.

during the departure of the leaf trace does the cortex become continuous with the medulla, the endodermis remaining unbroken throughout. Branching of the rhizome frequently occurs. The branching is dichotomous and does not appear to be related in any way to the leaf insertion. The details of one such branching are shown in Fig. 5, F-L. In this particular example a leaf is given off from each branch immediately after the bifurcation has taken place and the changes leading up to the departure of these leaf traces are initiated before the actual branching occurs. As a result of the changes in the conformation of the stele leading up to the branching each shank is supplied with a stele essentially similar to the parent one. At no level of the branching is there a gap in the endodermis.

The Frond.

The fronds resemble those of V.lineata in general appearance, though in the specimens available for examination they are considerably broader. The venation of a sterile frond is indicated in Fig. 7, F. Spicule cells are present in the epidermis.

Superficial Appendages.

The surface of the rhizome and leaf bases is covered with clathrate scales very similar to those of V.lineata.

Sori and sporangia.

V.elongata (together with V.Sikkimensis and sulcata according to Christ) is characterised by the fact that the sporangia are situated in a marginal groove. It was unfortunately impossible to determine whether the origin of the sorus is truly marginal or not. In the youngest fronds available for examination (Fig.7, C) the sporangial groove is already clearly defined and it is impossible to determine the origin of the two flanges of the

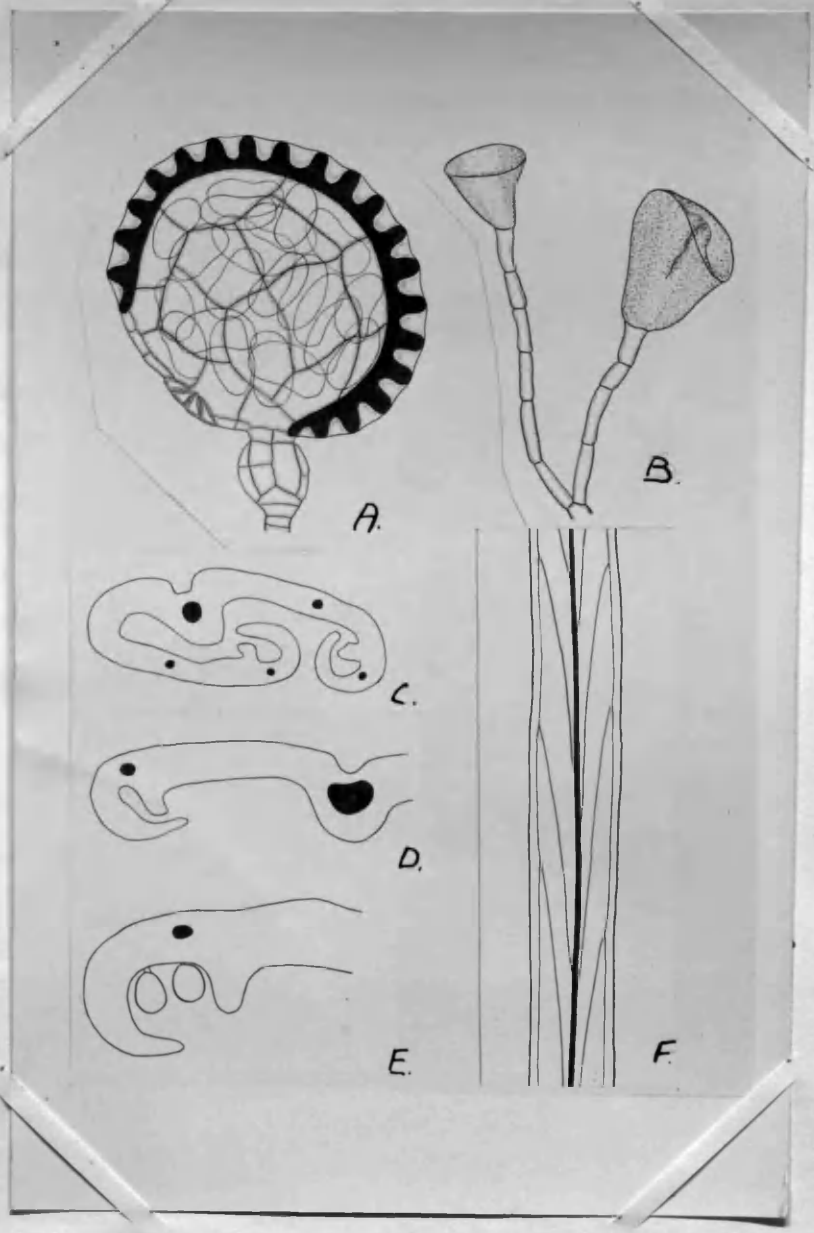

Fig.7. Vittaria elongata. A, sporangium. X185. B,paraphysis. X185. C-E, transverse sections of fertile fronds of different ages. X20. F, venation of sterile frond. X1/2

groove. It seems possible from comparison with V.lineata that the outer flange is formed by the true margin of the leaf and that the origin of the sorus is therefore slightly intramarginal. As the frond matures the sporangial groove widens somewhat and the sporangia arise at its base in a "mixed" condition.(Fig. 7, D,E.) The sporangia (Fig. 7, A.) are associated with branched paraphyses the end cells of which have a very curious and characteristic shape (Fig. 7, B.) The annulus is generally vertical though in some examples it appears to extend a little beyond the stalk. The stomium is composed of four cells somewhat narrower than those of V.lineata and there is an epi- and hypo- stomium each consisting of two or three cells. The stalk of the sporangium is single celled at its base but, as in the sporangia of V.lineata, it becomes several celled immediately below the capsule. It appears probable that the dilation of the cells below the capsule in this species, as in V.lineata, will throw back the mature capsule in such a way that the dispersal of the spores will be rendered more effectual than would otherwise be the case. The spores themselves are reniform and spore counts yielded the numbers 54,58,59 and 60, indicating that the typical number for each sporangium is probably 64.

Vittaria angustifolia,(Sw.) Bak.
(= Ptesopsis angustifolia (Sw.) Desv.)

The habitat of V.angustifolia is stated by Christ to be from the Antilles to South Brazil. It is a form which is intermediate in many of its characters between Vittaria and Antrophyum. This intermediate character is seen most strikingly in its venation

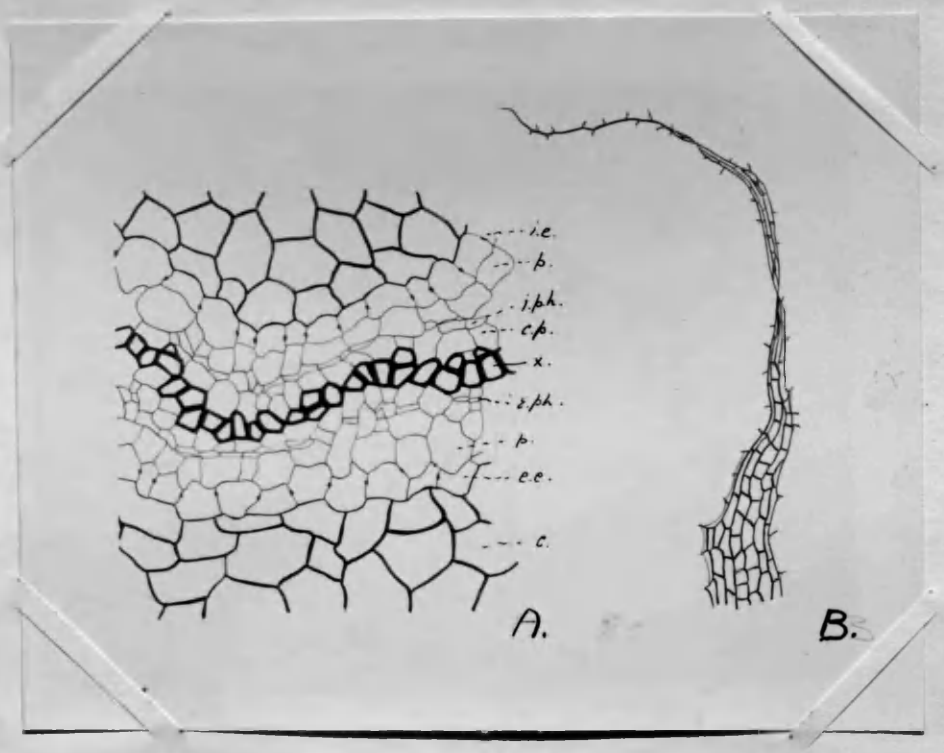

Fig.8. Vittaria angustifolia. A, ventral portion of the meristele; lettering as in Fig.2. X260. B, clathrate scale. X 15 .

and soral arrangement. There are several lines of areolae on either side of the mid-rib - a condition similar to that present in Antrophyum; and, on the other hand, the sporangia are arranged in two definite, slightly intramarginal lines as in Vittaria. This combination of characters has resulted in this form having a very varied systematic history. It was originally described by O.Swartz in 1788 as Pteris angustifolia. Since then it has been placed in a number of different genera by various systematists. Desvaux (Prod.de la famille des Fougères, 1827) and Presl (Tentamen,1836.) described it along with other species under Pteropsis. In 1827 Sprengel included it in the genus Taenitis, and Hooker did the same in the Synopsis Filicum (1868). J.Smith (Hist.Fil.,1875) retained Pteropsis,Desv. for the single species,P.angustifolia and this arrangement has been followed by Christ (Die Farnkrauter der Erde). Benedict (l.c.) also retains this form as a separate genus, Ananthacorus,Underwood and Maxon, a generic name which does not appear to have been generally accepted.Christensen and Diels have, however, included it in the genus Vittaria, the latter writer making a separate section for it,viz. Section III, Pteropsis, and it is the opinion of the present writer that this last arrangement is probably the best one, having regard to the facts which will now be described. The description is based on a specimen collected by R.H.Schomburgk in British Guiana in 1836.

Anatomy.

The mature rhizome has a typical dorsiventral dictyostele. In the internode the stele is in the form of a single U-shaped strand with the xylem forming a narrow band one or two tracheids in

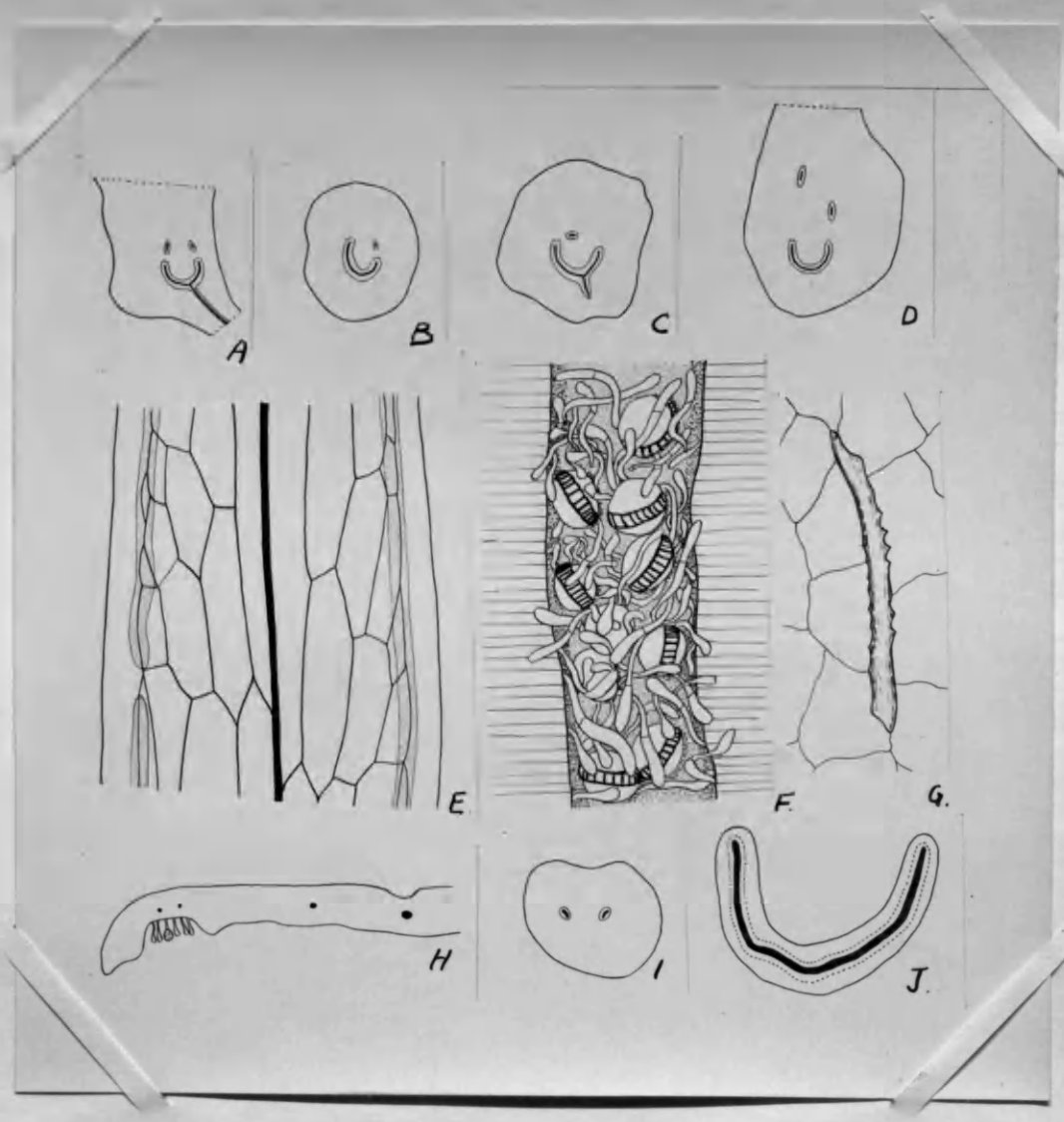

Fig.9. Vittaria angustifolia. A-D, series of transverse sections of mature rhizome. X 13 . E, venation of fertile frond ; soral lines stippled. X 4 . F, sporangial groove in surface view. X 40 . G,spicule cell. X 185. H, transverse section of fertile frond. X 13 . I, T.S.petiole. X 13 . J, diagram of meristele. X 60 .

thickness. Both internal and external phloem are present as a practically complete band of small, protophloem like elements. The endodermis is in the primary condition and the pericycle consists of a single or double row of relatively large elements. The method of leaf trace departure is indicated in Fig. 9, A-D; it is similar in all essentials to that described for V.lineata.

The Frond.

The fronds which are 12-18 ins. long and about half an inch broad are inserted somewhat irregularly in two rows on the creeping rhizome. The laminal portion shows a very distinct mid-rib and on either side of it there are three or four rows of elongated hexagonal meshes (Fig. 9, E.), thereby differing very markedly from all other Vittaria species. There are no points of particular interest in the structure of the lamina except that spicule cells of large size are present in the epidermis.(Fig. 9, G)

Superficial Appendages.

The rhizome and bases of the petioles are covered by clathrate scales. These approximate in their structure much more nearly to those of Vittaria than to those of Antrophyum, the rhizoid like structures, so characteristic of the latter, being entirely absent. (Cf. Fig. 8, B)with Fig\\\\\

Sori and Sporangia.

The sori form almost continuous lines in a submarginal position (Fig. 9, E). The sporangia are inserted in a broad groove over the marginal vein, although the groove may extend over the whole of the marginal mesh where the latter is small. Intermingled with the sporangia, which are inserted in the groove in two or three irregular rows (Fig. 9, F.), are numerous paraphyses with club shaped end cells. The sporangia are very

similar to those of the other Vittaria species. The material did not permit of any spore counts being made.

MONOGRAMMA, Schkuhr.

The limits of the genus Monogramma, which was founded by Schkuhr in 1799, have varied considerably in the hands of different systematists. Hooker divided the genus into two sections : § Eumonogramme, having the"frond with central vein only" (1), and §§ Pleurogramme, having " fronds with indistinct simple lateral veins in addition to the mid-rib." In 1893 Poirault (2) pointed out that spicule cells were absent from the fronds of one or two of the species in the Pleurogramme section and in 1911 Benedict made the general statement that the species in the section Pleurogramme were so unlike those of the section Eumonogramme that they would be better separated as a distinct genus. Goebel(l.c.1924) has recently emphasized this point, demonstrating that the Pleurogramme types possess no spicule cells, have sporangia with a two celled stomium, possess sclerenchyma in their rhizomes, and that clathrate scales are absent from their rhizomes and leaf bases. It is clear therefore that Benedict was correct in stating that "There is ample evidence to show that they are not only not to be included in Monogramma but they may not even be retained in the tribe Vittarieae." Pleurogramma must then be reinstated as a substantive genus (with affinities elsewhere than with the

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1. This diagnosis is incorrect since there are lateral veins in a number of the species included under Eumonogramme. This inaccuracy is probably due to the difficulty with which the venation is made out in such extremely narrow fronds. It only appears clearly after treatment of the frond with Eau de Javelle and staining with safranin or better still with Ammoniacal Fuchsin.
2. Poirault, Ann.des Sc.Nat.,1893, p.208.

Vittarieae) and Monogramma limited to the Eumonogramme types. This confirms the arrangement of Presl who not only recognised the two as separate genera but placed them in different tribes. Christ (1897) also recognised the two as separate genera, but he included both of them in the Vittarieae, a course which does not appear to be justified. Goebel (l.c.1924) holds the view that the Eumonogramme species would be better separated into two genera, namely Monogramme and Vaginularia,Fée. The former genus would contain those species not possessing lateral veins, the latter those possessing lateral veins. Going along with this difference of venation are differences in the detailed structure of the paraphyses and in the type of stomata. These differences appear to the present writer too small to justify generic separation of forms which are almost identical in their anatomical construction, in the struct- of their sporangia and in the form of their clathrate scales. Moreover the species of the Eumonogramme section show a gradual transition from forms almost identical with Vittaria species to the extreme simplicity of the M.graminea type. For the purpose of this memoir then the species will be described under the genus Monogramma,Schkuhr, this genus being now limited to those forms included by Hooker and other systematists in the section Eumonogramme. The number of species included in this latter section varies considerably in the different systematic works owing to the fact that the delimitation of the species, as in Vittaria, is a matter of considerable difficulty. The species which will now be described illustrate, however, the extremes of variation to be found within the genus.

Monogramma paradoxa,(Fee) Bedd..
(= M.Junghuhnii,Hk..)

M.paradoxa is a relatively small, grass like plant (Plate II, A) found in Ceylon, Java, Philippines and Polynesian Islands. It has a very slender rhizome on which the fronds are arranged in two rows on the dorsal surface. The fertile leaves possess lateral veins and on account of this feature Goebel places this species in the genus Vaginularia,Fee. The following account is based on Herbarium specimens collected by Lobb in Java.

Anatomy.

The anatomy of the rhizome is very similar to that of M.graminea and as the material of the latter species was more suitable for examination the detailed description of the anatomy will be given for that species. It may be briefly stated that the stele is protostelic with a V-shaped xylem mass and that the leaf traces depart as single strands from the two arms of the V-shaped mass alternately. As in M.graminea an occasional equal dichotomy of the axis sometimes occurs. The structure of the root is almost identical with that figured for M.trichoidea.

The Frond.

The fronds of the specimens available for examination were 12-15 cms. long. In the lower sterile portion of the lamina only the mid-rib is present but in the fertile region there is a single lateral vein which runs parallel to the mid-rib for a considerable distance and then, after converging towards the mid-rib, dies out without actually coming into contact with the latter (Fig. 10, E). In small specimens examined by Benedict the lateral vein is shown as uniting with the mid-rib and so forming a single areola (Fig. 10, A). In larger specimens examined by the same writer the fronds reach a length

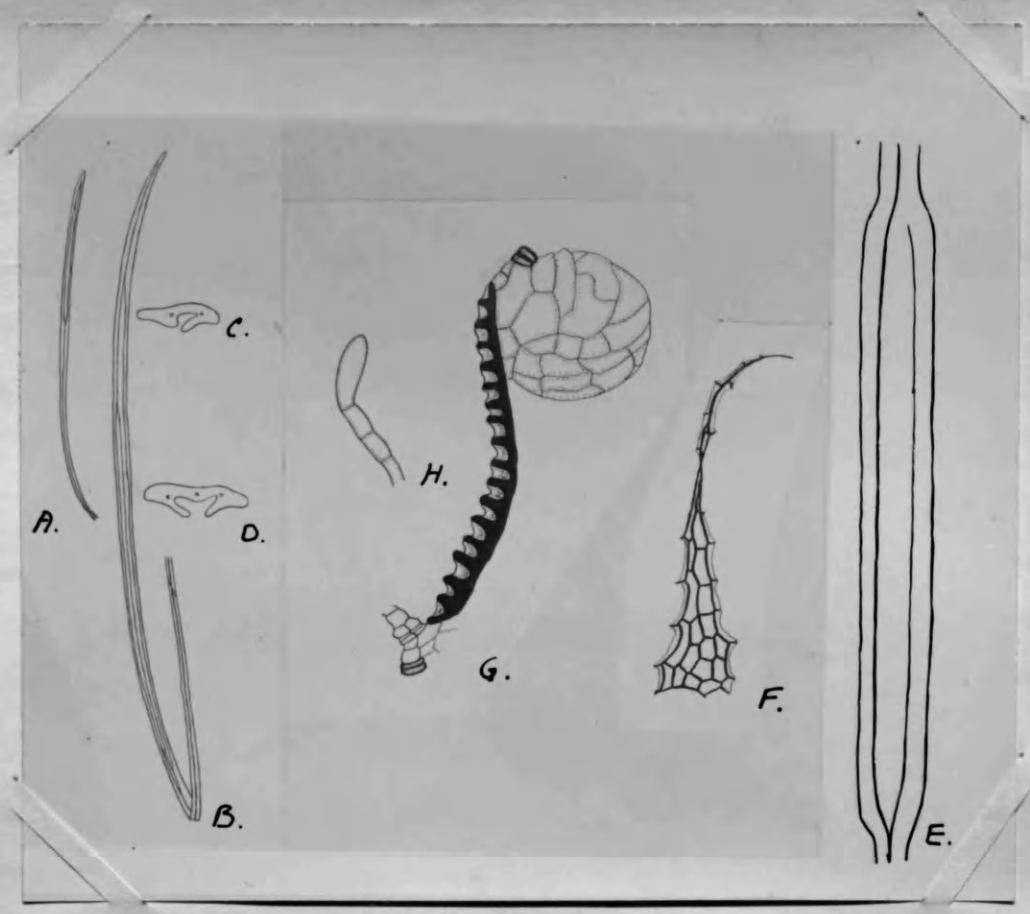

Fig.10. Monogramma paradoxa. A, small frond. B, large frond. C-D, sections of B at the levels indicated. A-D after Benedict. E, diagram of venation of fertile portion in specimens from Java. F, clathrate scale. X 45. G, sporangium. H, paraphysis. X 130.

of 25 cms. and show two areolae in the broadest portion of their laminae (Fig. 10, B). This more complex venation approximates to that characteristic of Vittaria and indeed presents an intermediate condition between the latter and the extremely simple venation of such forms as M.graminea.

Spicule cells of great length are present in abundance in the epidermis.

Dermal Appendages.

The clathrate scales (Fig. 10, F) are very similar to those of Vittaria species.

Sporangia.

In the specimens examined the sporangia are borne in a single groove which extends the whole length of the lateral vein. In the larger specimens figured by Benedict, and in specimens figured by Hooker, the sporangial groove is double in the broadest portion of the frond, becoming single in the narrower distal region. The morphology of the sporangial grooves and the ridges bounding them has been discussed at length by Goebel (l.c.1924.) but no satisfactory conclusion can be reached until the ontogenetic development of the fronds has been traced. The double groove condition appears, however, to be comparable with such a form as V.lineata and the single groove condition may possibly be regarded as a reduction from this.

The sporangia (Fig. 10, G) are of the usual Vittariaceous type with an annulus of 15-18 cells and a four celled stomium. The sporangial stalk is single celled below but immediately beneath the capsule it is several celled as in the sporangia of Vittaria species. The paraphyses which are intermingled with the sporangia are of a

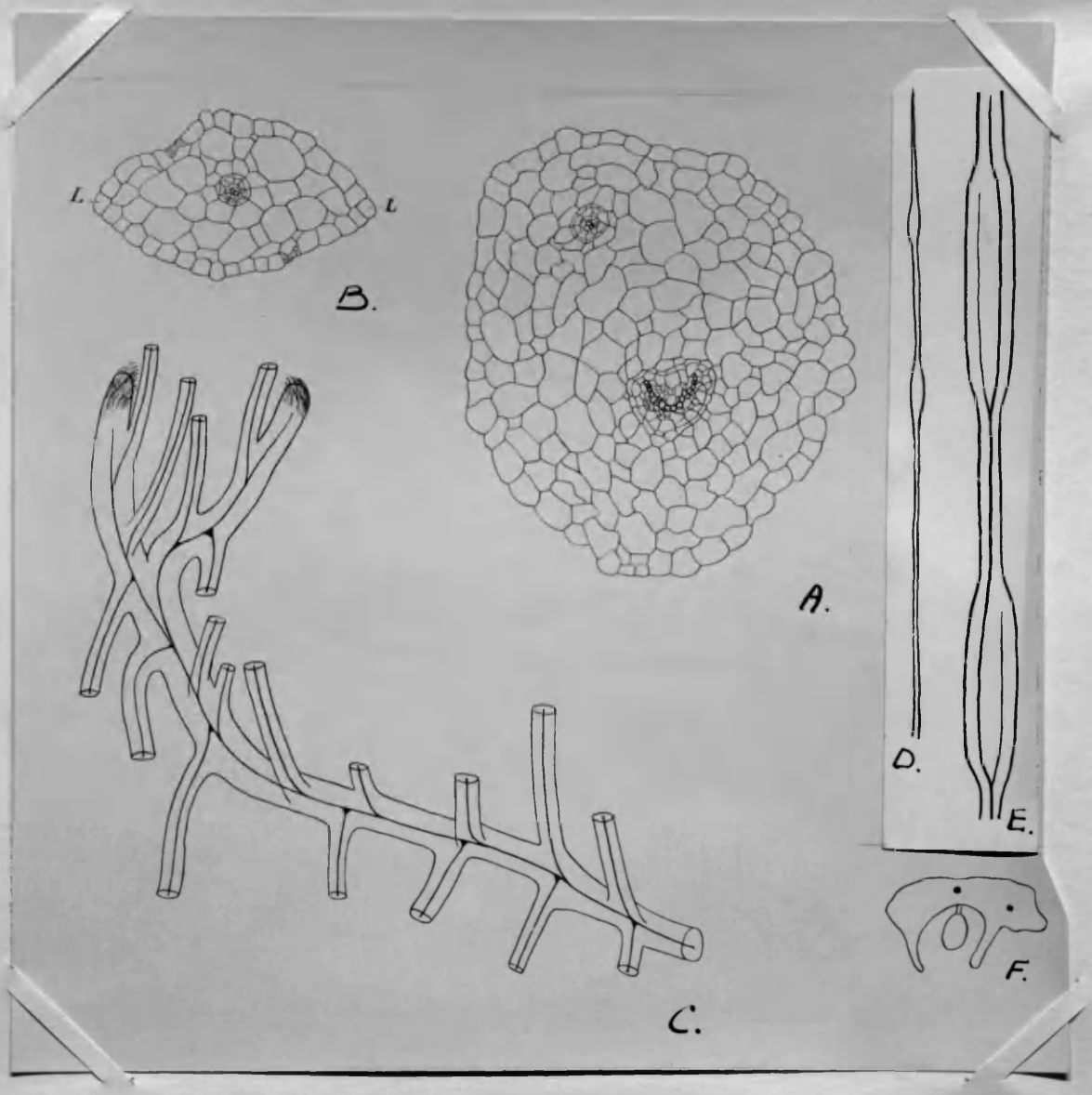

Fig.11. Monogramma trichoidea. A, T.S.of rhizome. B, T.S. frond. A and B after Goebel. C, drawing showing the general course of the vascular strands. X . D, frond showing two fertile zones (Nat. Size). E, diagram showing venation in fertile zones. F, section across fertile zone. X 55.

very simple type and which differ from those of most other Vittarieae in not having club-shaped end cells. (Fig. 10, 11.)

Monogramma trichoidea, J.Sm.

This species from the Philippines and Borneo is a very small one with an extremely slender rhizome and thread like fronds 3-4 ins. long. On account of the presence of lateral veins the species is another of those included by Goebel in the genus Vaginularia. The following account is based on herbarium specimens collected by Cuming in Luzon, the largest of the Philippine Islands.

Anatomy.

The anatomy has been very briefly described by Goebel (Organographie, p.911.) and I have been able to verify this description. The stele is protostelic and is surrounded by an endodermis in the primary condition. The xylem consists of a horse-shoe curve one or at most two tracheids in thickness. Phloem is present on both the dorsal and ventral sides of this and there is a well marked pericycle. The leaf traces depart alternately from the right and left of the stele as very small and simple strands. Fig. 11, C is a slightly diagrammatised drawing of a dichotomously branched rhizome cleared in Eau-de-Javelle and stained with Ammoniacal Fuchsin. An interesting point is that in the older portion of the rhizome there is a definite relationship between the insertion of the roots and leaves, there being one root at each leaf insertion.

The Frond.

The sterile fronds have a very simple structure showing an indistinct mid-rib and no lateral veins. The fertile fronds show two or three sporangiferous regions, each about ¼ in.long), and

in these regions the frond is somewhat dilated (Fig. 11, D, E). As in the fronds of M.paradoxa the venation is obscure but after treatment with Eau-de-Javelle and Ammoniacal Fuchsin it is possible to make out that in each sporangiferous region there is a lateral vein which runs parallel to the mid-rib (Fig. 11, E). Goebel states that occasionally the lateral vein joins up with the mid-rib to form a single areola.

Numerous long spicule cells are present in the epidermis.

Dermal Appendages.

The clathrate scales are of XXXXXXXX exactly the same type as those of M.paradoxa. In each sporangiferous area the sporangia are situated at the base of a broad and deep groove, bounded by two flanges, the morphology of which is obscure in the absence of any data concerning the ontogenetic development. The sorus is seated over the single lateral vein. (Fig. 11, F.).

The sporangia, which are mixed with branched paraphyses, are almost identical with those of M.paradoxa.

Monogramma graminea, Schkuhr.

M.graminea (Plate II, B) is another small form with fronds about two inches long which is found in Cape Colony, Mauritius and the Reunion Is. The following account is based on herbarium specimens collected in the last named habitat.

Anatomy.

The stelar construction of the small, fleshy rhizome is very simple. In the internode the stele is a small crescent shaped structure (Fig. 12, F), the xylem being in the form of a horse-shoe curve of

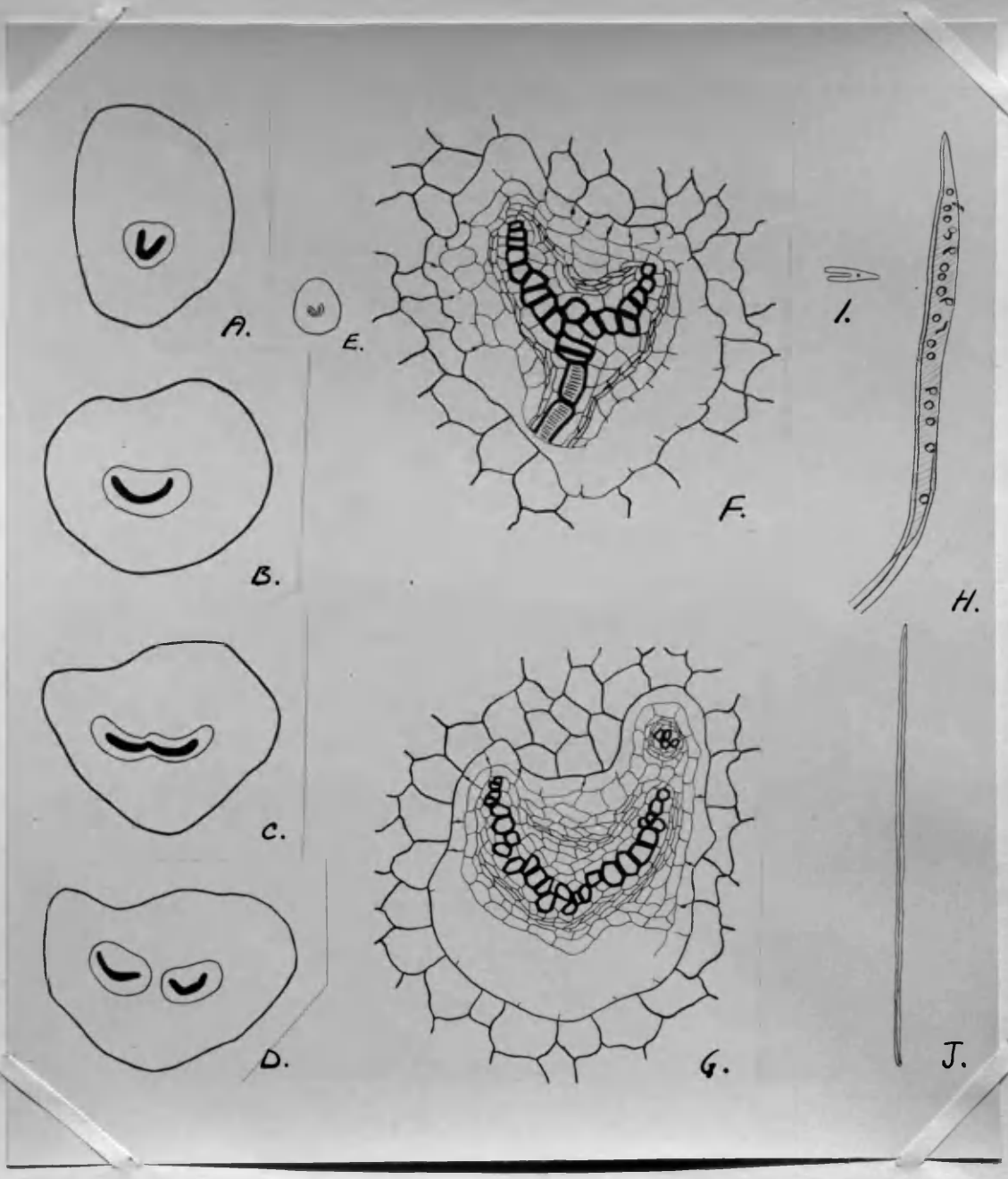

Fig.12. Monogramma graminea. A-D, series of transverse sections of the mature rhizome showing a dichotomous branching. X 55 . F, T.S. stele showing ~~leaf~~ trace departure. X 260. G, stele with departing leaf trace. X 260. H, fertile region of frond. I, transverse section of fertile region. J, sterile frond.

E, T.S. rhizome x 13 for comparison of size with ~~XXXXX~~ drawings of other genera.

twelve to fifteen tracheids. This surrounded in turn by a parenchymatous sheath, phloem, a pericycle and endodermis, this latter being in the primary condition. The phloem, as in Vittaria, is composed of small protophloem like elements. As the node is approached one arm of the xylem curve becomes elongated (Fig.\\\\\\) and finally a small group of three or four tracheids, surrouded by a small amount of phloem and an endodermis, is abstricted off from the axial stele and passes out through the cortex into the leaf base (Fig. 12, 4). At the next node this process is repeated and a similar small and simple strand is abstricted off from the other side of the axial stele.

Branching of the rhizome frequently occurs in a typically dichotomous manner. As the level of branching is approached the stele broadens out, the xylem mass becoming very broadly U-shaped. The stele then takes on the double U-shaped conformation shown in Fig. 12, C and finally each arm of the branching is supplied with a strand similar in all respects to the parent axial stele.

The root traces depart from the ventral side of the stele but their insertion appears to have no relationship with the insertion of the leaves.

The Frond.

The fronds of M.graminea are exceedingly simple. The single strand which passes off from the axial stele remains undivided throughout the length of the linear frond. Lateral veins were absent in all the specimens examined. Anatomically the frond is very simply constructed and resembles closely that figured for M.trichoidea. The vascular strand,as seen in section, consists of two or three tracheids surrounded by a small amount of phloem, a conspicuous pericycle and an endodermis.

Superficial Appendages.

The surface of the rhizome is clothed with clathrate scales very similar to those described for Vittaria species.

Sporangia.

The fertile region of the frond is distal (Fig. 12, M.) and occupies about half an inch at the apex of certain of the fronds. A section across the fertile region shows that the sporangia are seated in a deep groove formed apparently by a folding of the lamina (Fig. 12, I). A knowledge of the ontogeny of the fertile frond is required before a correct morphological interpretation of the fertile region can be advanced. The sporangia themselves are very similar to those of Vittaria species. They have a similar type of stalk dilated in the distal region. The capsule has a vertical annulus of 15-20 cells; the stomium is four celled; and there ia an epi- and hypo- stomium each consisting of two cells. The spores are tetrahedral in form and spore counts indicate that 32-48 spores are formed in each s sporangium.

Antrophyum, Kaulfuss.

Antrophyum is described by Hooker (Syn.Fil.) as " a small genus of closely allied species almost restricted to the Tropics, all with simple fronds, of firm but fleshy texture and copious uniform hexagonal areolae." Christensen (Index Fil.) gives 27 species, Diels (Pflanzenfam.) 16 species and Hooker 15 species. This discrepancy is accounted for by the fact that the limits of many of the species are not at all clear. The species are divided by both Hooker and Diels into two groups according as to whether the sori are sunk in a groove or whether they are superficial or but slightly immersed. Benedict (1) has recently removed a number of species of Antrophyum into a separate genus Polytaenium,Desv., mainly on the basis of differences of venation and geographical distribution. The genus Antrophyum is limited by Benedict to the Old World species ; these are characterised by the fact that the venation is of the "single net type",i.e. there is no distinct mid-rib and the areolae are always directed towards the base of the lamina. On the other hand, the New World species included by Benedict in the genus Polytaenium,Desv. have a"double net type" of venation with a distinct mid-rib and, as a further point of difference, they possess no paraphyses.

It appears doubtful, however, to the present writer whether these differences are sufficient to warrant a generic separation of the two types. The [illegible] anatomical construction, the structure and distribution of the sporangia and the [illegible] structure of the clathrate scales are all so similar throughout the genus as delimited by Hooker, Diels and Christensen that there seems to

1. Benedict, l.c. p.168.

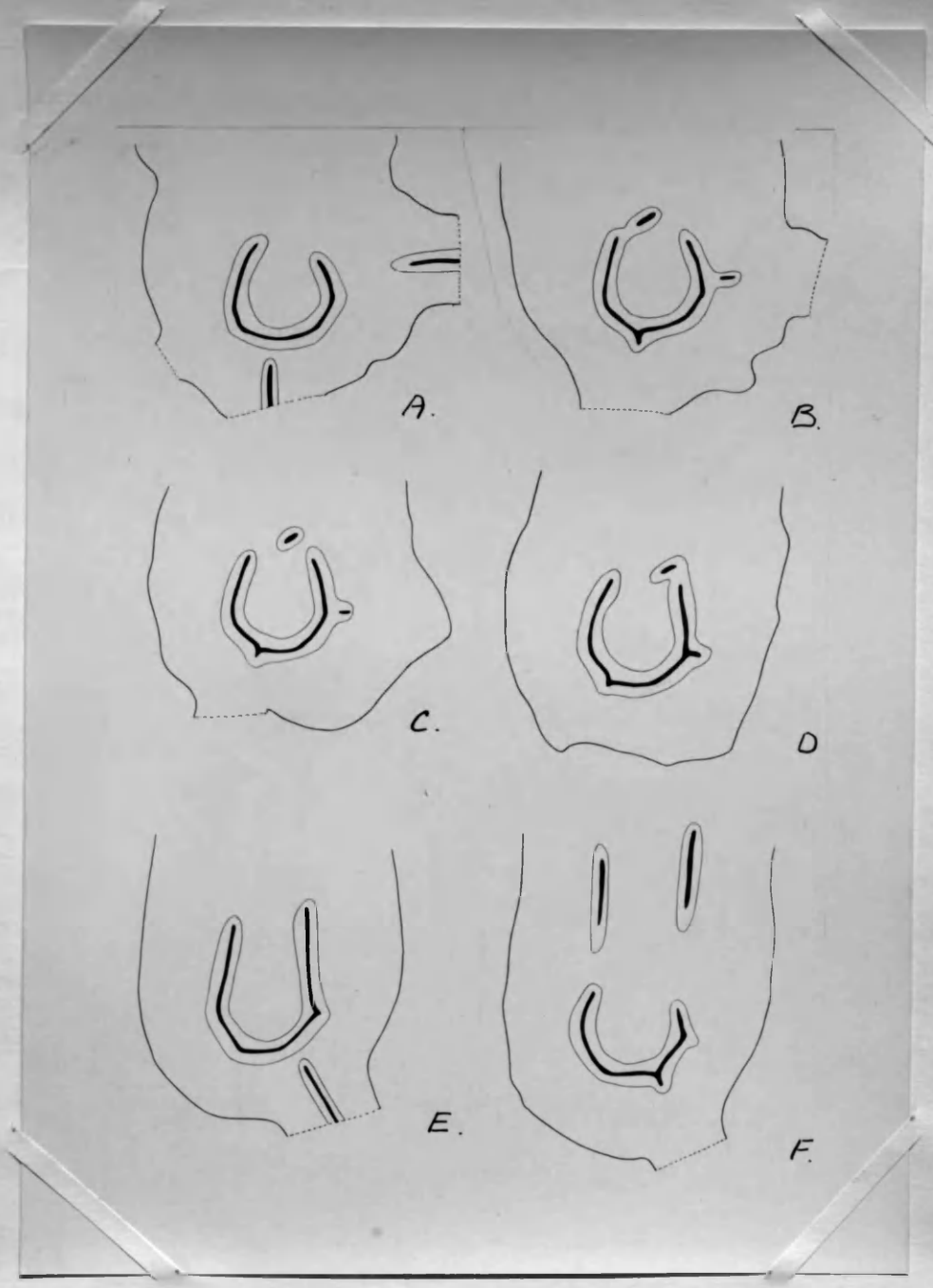

Fig.13. Antrophyum reticulatum. A-F, series of transverse sections of mature rhizome. X /3 .

be no good reason for reinstating the genus Polytaenium,Desv..

The following species have been examined : A.reticulatum,Kaulf., plantagineum,Kaulf., lineatum,Kaulf., lanceolatum,Kaulf., and brasilianum,C.Chr.. These include both forms with their sori sunk in a groove and those with superficial sporangia. They also include species placed by Benedict in the genus Polytaenium,Desv..

Antrophyum reticulatum, Kaulf..

The general appearance of A.reticulatum is shown in Plate III, B. The creeping rhizome is comparatively stout and bears in two irregular rows on its dorsal surface the fronds which attain a length of 12 ins. and a breadth of 1-3 ins.. The species appears to be confined to the Eastern Hemisphere and Hooker describes it as occurring in the "Himalayas, Ceylon, and Malaccas to Aneitium and Queensland." The material on which the following account is based was collected in Singapore by Mr.Burkhill.

Anatomy.

The mature rhizome possesses a dorsiventral dictyostele which differs only slightly from the type described for Vittaria lineata. (Fig. 13, A-F).

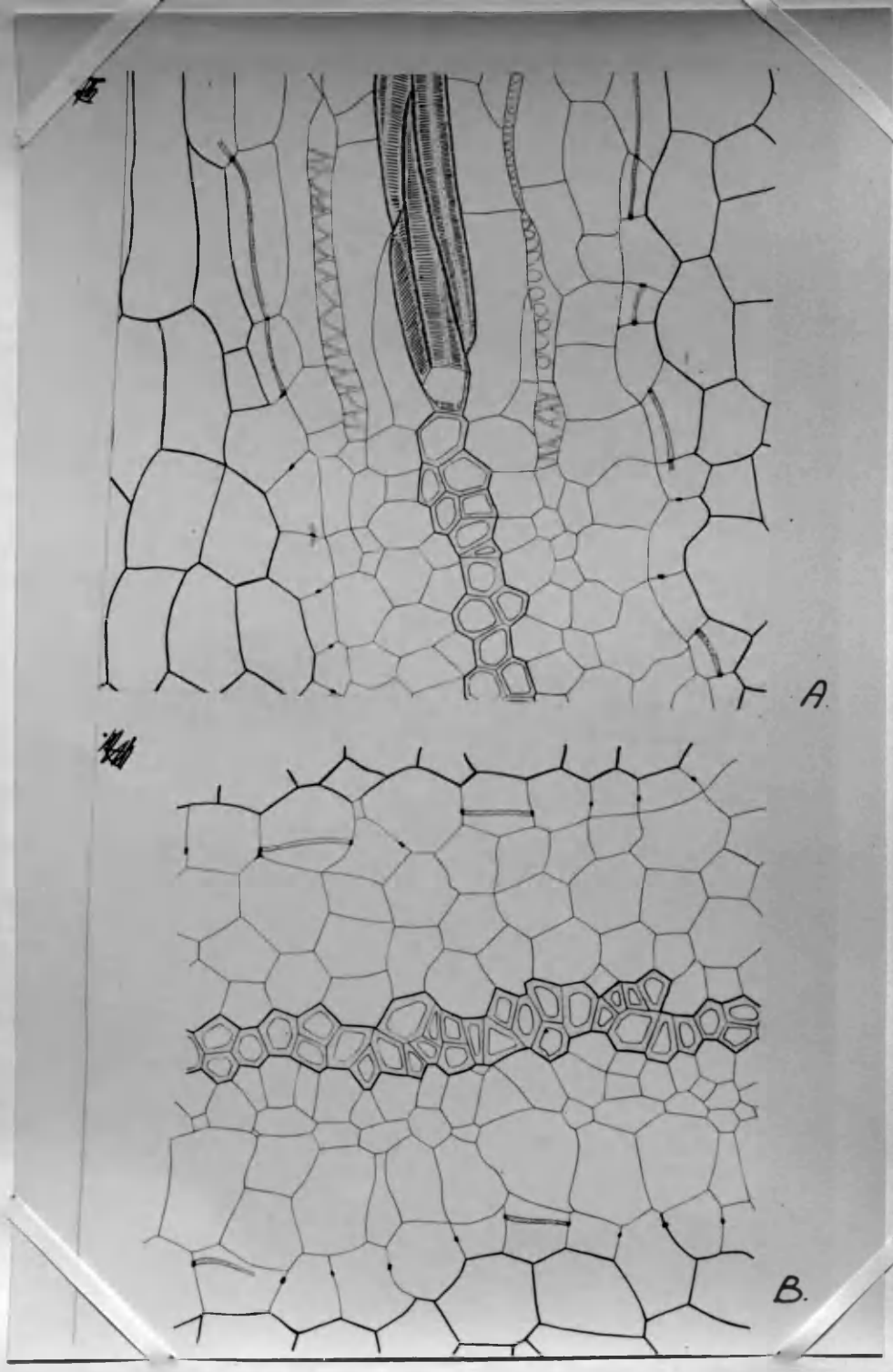

Fig.14. Antrophyum reticulatum. A, dorsal arm of meristele showing leaf trace departure. B, ventral portion of the meristele. X 260.

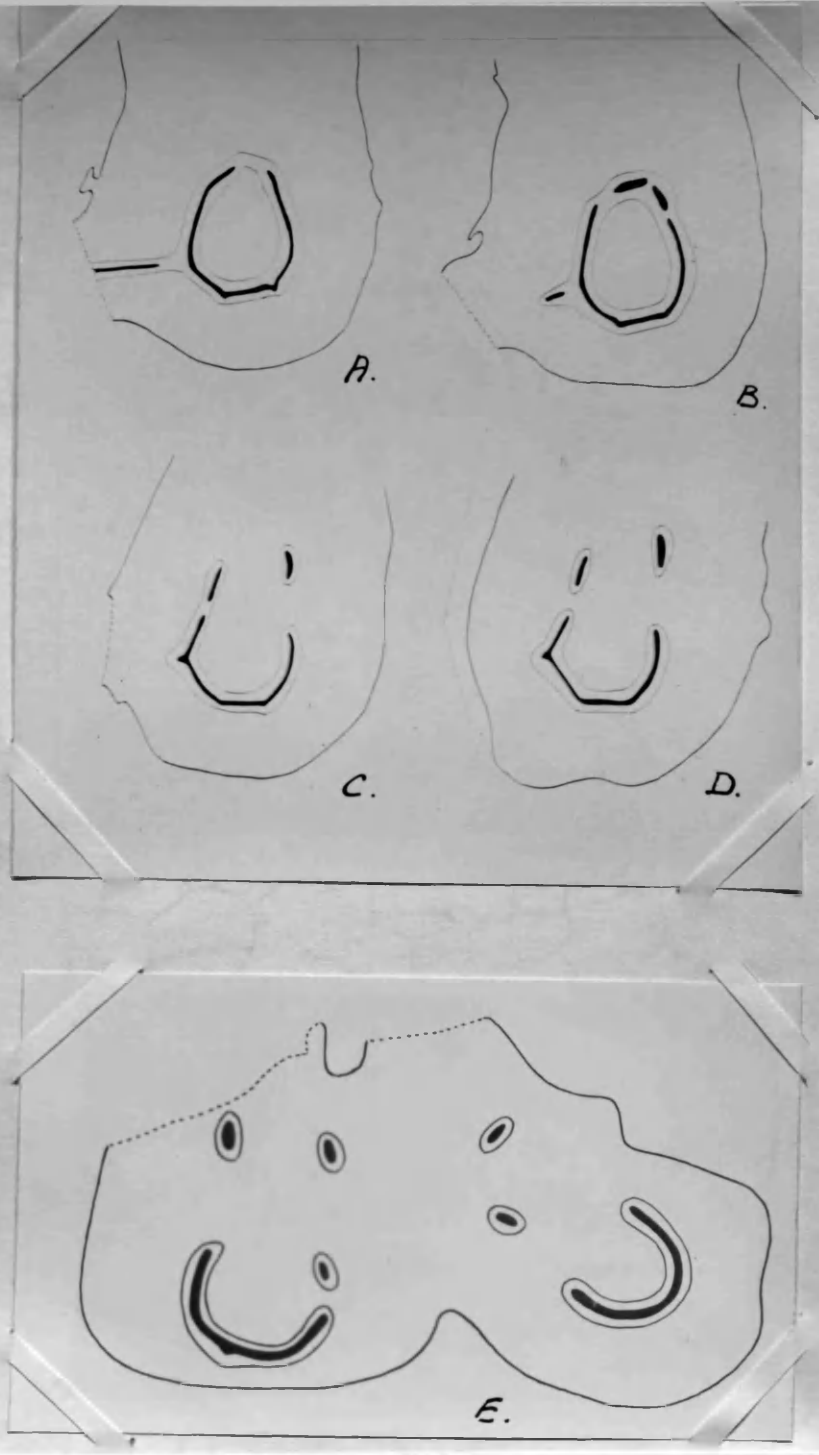

Fig.15. Antrophyum reticulatum. A-D, series of transverse sections of a rhizome showing a deviation from the normal dorsiventral dictyostelic type of structure. X 13 .

E, T.S. of rhizome at level of branching (x 13)

The distribution of the inner phloem is, however, peculiar and shows a divergence from the condition present in a typical example of this type of stelar construction. It is only present in the dorsal regions of the meristele ; it is replaced by what Gwynne-Vaughan has termed "pericyclic parenchyma" in the ventral portion of the horse-shoe curve (Fig. 14, A and B.). A slight variant of the normal dorsiventral dictyostele is present in some of the rhizomes examined. As far as the stele itself, as delimited by the endodermis, is concerned the leaf gap is closed before the succeeding leaf gap is formed but there is a slight overlapping of the xylic gaps. This results in the appearance of a small dorsal strand of xylem which moves across, within the stele, from one side of the U-shaped curve of xylem to the other at each node (Fig. 15, A-D). This type of structure is still nearer to solenostely than is the normal dorsiventral dictyostele.

It was possible to trace the ontogenetic stages in the development of the dorsiventral dictyostele above described. In the lowest internode observed (Fig. 16, A) the small cylindrical stele has the following structure as seen in transverse section. The xylem mass is in the form of a shallow horse-shoe curve, one, or, occasionally, two tracheids in thickness. On the ventral side of the xylem, and separated from it by a layer of conjunctive parenchyma, is a layer of phloem elements, distinguished by their small size and by the fact that their walls stain deeply with haematoxylin. No phloem was observed on the dorsal side of the xylem and its place is taken by large celled parenchyma. The stele is surrounded by a large celled pericycle and by an endodermis which is in the primary condition ; the Casparian strip is distinguishable but is not well developed. As the first node is approached, one arm of the curve

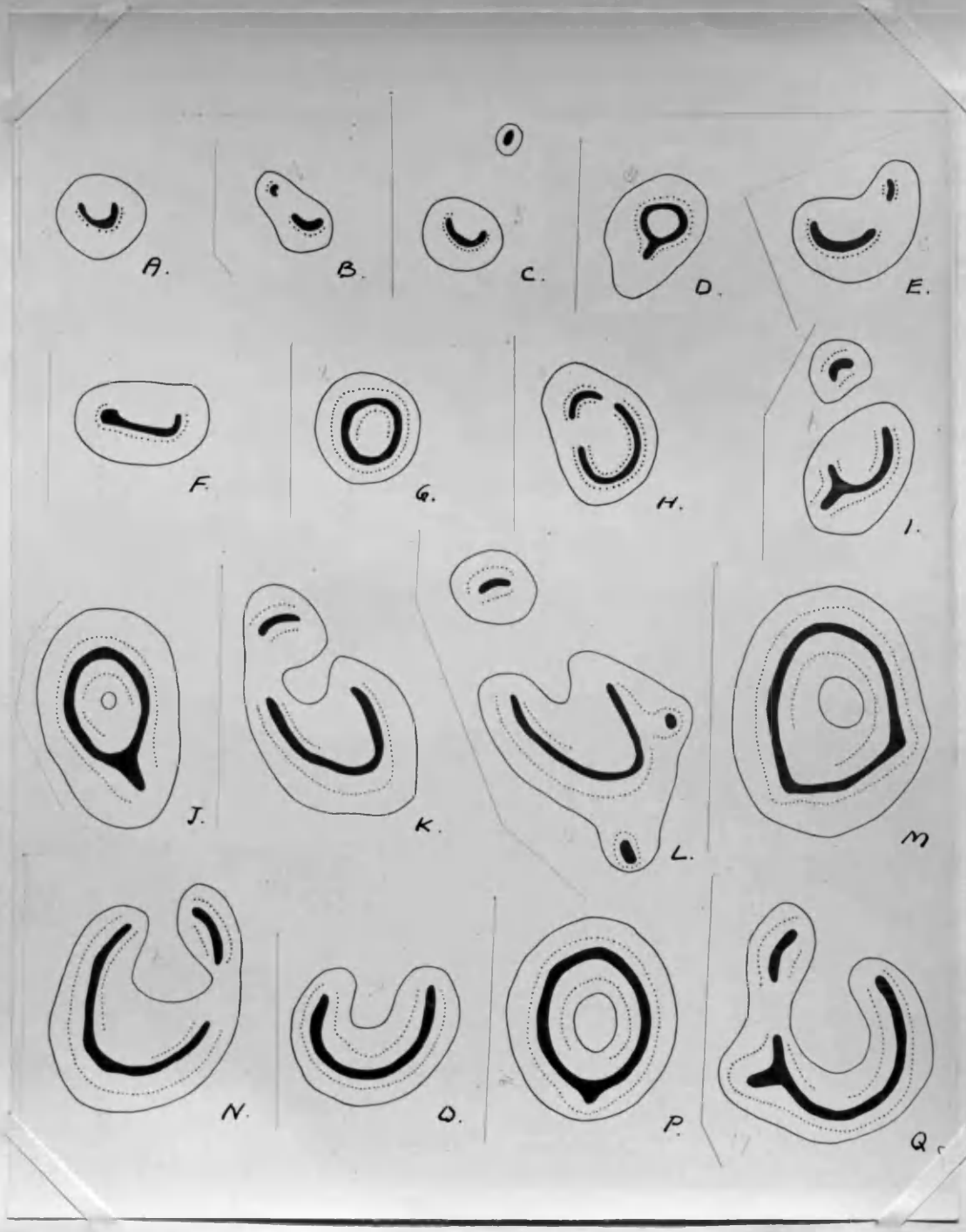

Fig. 16. Antrophyum reticulatum. A-Q, series of transverse sections of young plant ; detailed description in the text. X 40 . Xylem, black; phloem, dotted; endodermis, plain line.

of xylem becomes somewhat extended and finally the first leaf trace (Fig. 16, B) is abstricted off as a small group of two or three tracheids and a few phloem elements, surrounded by pericycle and endodermis. There is no break in the endodermis during this process nor is the axial stele disturbed in any way by the departure of the leaf trace. The second and third internodes are similar to the first one and the second and third leaf traces depart in a very similar manner to the first trace, being abstricted off from the right and left arms of the horse-shoe curve alternately. In the lower portion of the fourth internode the structure is as in the lower internodes but at higher levels (Fig. 16, D) the arms of the xylem curve close round to the dorsal side so that a practically complete ring of xylem is formed. This is surrounded by conjunctive parenchyma, phloem, pericycle and endodermis. The interior of the ring is occupied by large celled parenchyma and a few phloem elements. The fourth leaf trace departs from this stele in the manner indicated in Fig. 16, E. The fifth leaf trace departs in a similar fashion. In the basal region of the sixth internode (Fig. 16, F) the stele shows a somewhat flattened curve of xylem with phloem present round the convex side of it. As the internode is traversed the xylem curve closes round to the dorsal surface so that a complete ring is formed (Fig. 16, G). At this level there is a complete ring of external phloem ; internal phloem is present on the dorsal side of the stele only, and no internal endodermis is evident. Fig. 16, H and I indicate the way in which the sixth leaf trace departs as a crescentic strand of xylem with both internal and external phloem. The seventh trace departs in a very similar manner. As the eighth

internode is traversed the xylem again forms a ring, one or two tracheids in thickness and of considerably greater diameter than the xylic rings observed in lower internodes. It is surrounded on the outside in centrifugal order by conjunctive parenchyma, a complete ring of phloem, pericycle and endodermis. Inside the xylem ring are conjunctive parenchyma, a band of phloem in the dorsal and lateral regions, and large celled parenchyma in the centre. At higher levels, i.e. approaching the eighth node, a small circle of internal endodermis makes its appearance, indicating a slight pocketing in of the endodermis at the node (Fig. 16, J). The eighth leaf trace leaves the axial stele in the manner indicated in Fig. 16, K and L. The trace has a crescentic xylem mass which is for the most part only one tracheid in thickness ; phloem is present on both the ad- and ab-axial surfaces. The ninth, tenth, and eleventh leaf traces depart in a very similar manner to the eighth and the only point which need be noted is that the ninth and subsequent leaf traces divide into two portions during their passage through the cortex so that two strands enter the petioles of these leaves. Internal endodermis makes its appearance low down in the twelfth internode indicating a deep pocketing in of the endodermis at the twelfth node. As a result of this a solenostelic structure is seen in the upper portion of the internode (Fig. 16, M). The twelfth leaf trace leaves in the manner indicated in Fig. 16, N and from this level on to the seventeenth internode a typically solenostelic type of structure is present, the only point of interest being the deficiency of the internal phloem on the ventral side of the stele. The first divergence from normal solenostelic structure was observed in the seventeenth internode. As the node is traversed the sixteenth leaf gap becomes closed so far as the

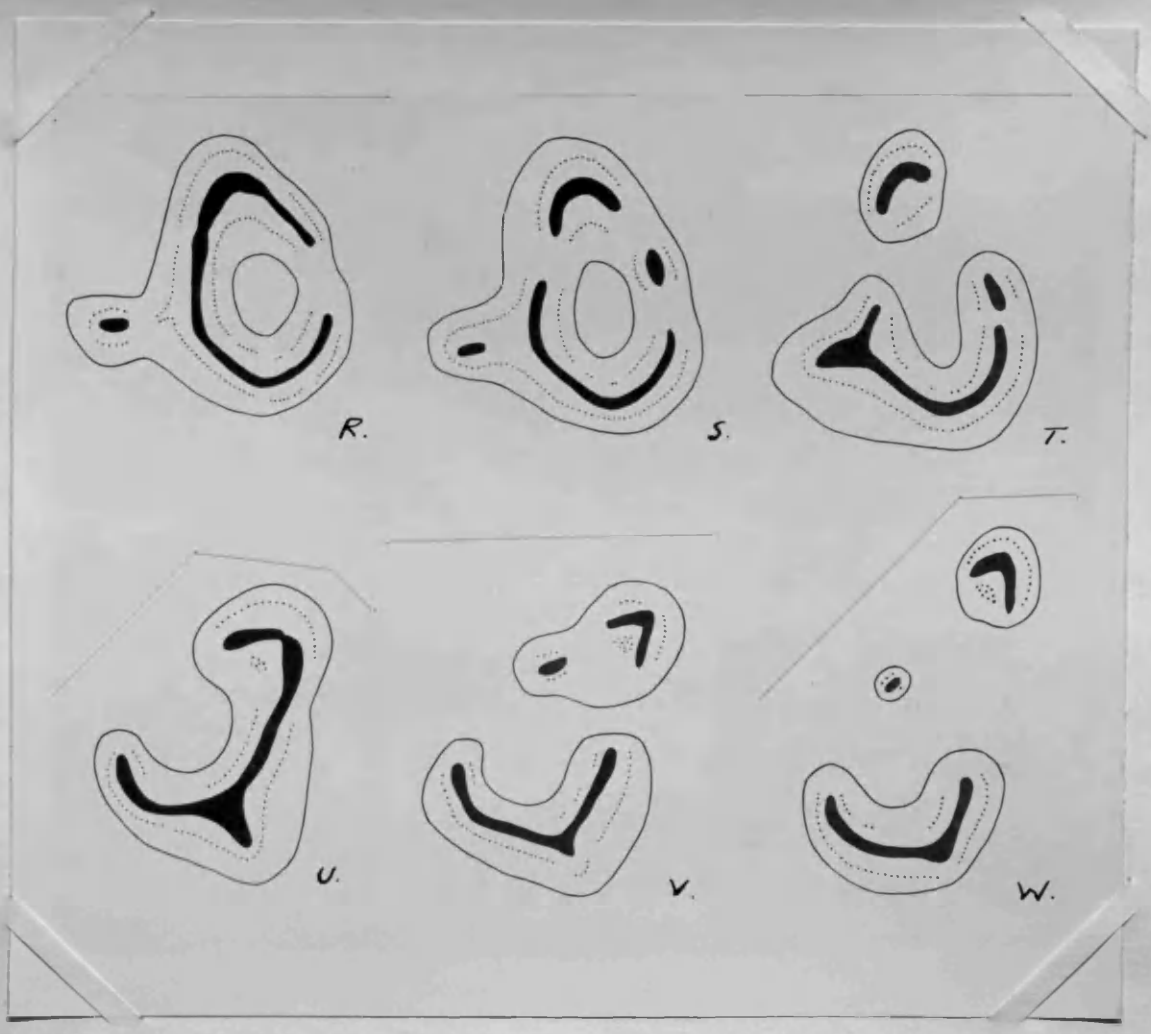

Fig.17. Antrophyum reticulatum. R-W, continuation of series in Fig.16. Description in text. ×40

endodermis is concerned (Fig. 17, R) but the xylic gap remains open. There is here then a complete ring of external and internal endodermis ; the xylem ring is still showing a gap ; and phloem is present both internally and externally with the same limits as the xylem except that it is absent on the internal ventral side. As the node is approached a small group of tracheids, with internal and external phloem, becomes separated off from the main xylem curve (Fig. 17, R,S.) The first indication of the departing seventeenth leaf trace is here seen as an arc of tissue bulging out somewhat from the circular outline of the stele. At levels approaching the node the small mass of xylem and phloem moves slowly across from one side of the xylic gap to the other (Fig. 17, S), and simultaneously the curve of xylem and phloem forming the leaf trace becomes detached from the axial stele (Fig. 17, T). It may be noted that this type of structure (1) is on the border line between solenostely and dorsiventral dictyostely. The eighteenth and nineteenth internodes revert to the normal solenostelic structure and show no points of particular interest. At the base of the twentieth internode the stele has the usual horse-shoe form. As the node is approached changes take place in the conformation of the strand as indicated in Fig. 17, U, V, and W. The important point is the appearance of a small dorsal meristele which moves across from one side of the leaf gap to the other surrounded by its own endodermis. This indicates the establishment

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1. Cf. the structure described as occurring occasionally in the mature rhizome and the account of Gwynne-Vaughan of the stele of Cheilanthes lendigera.

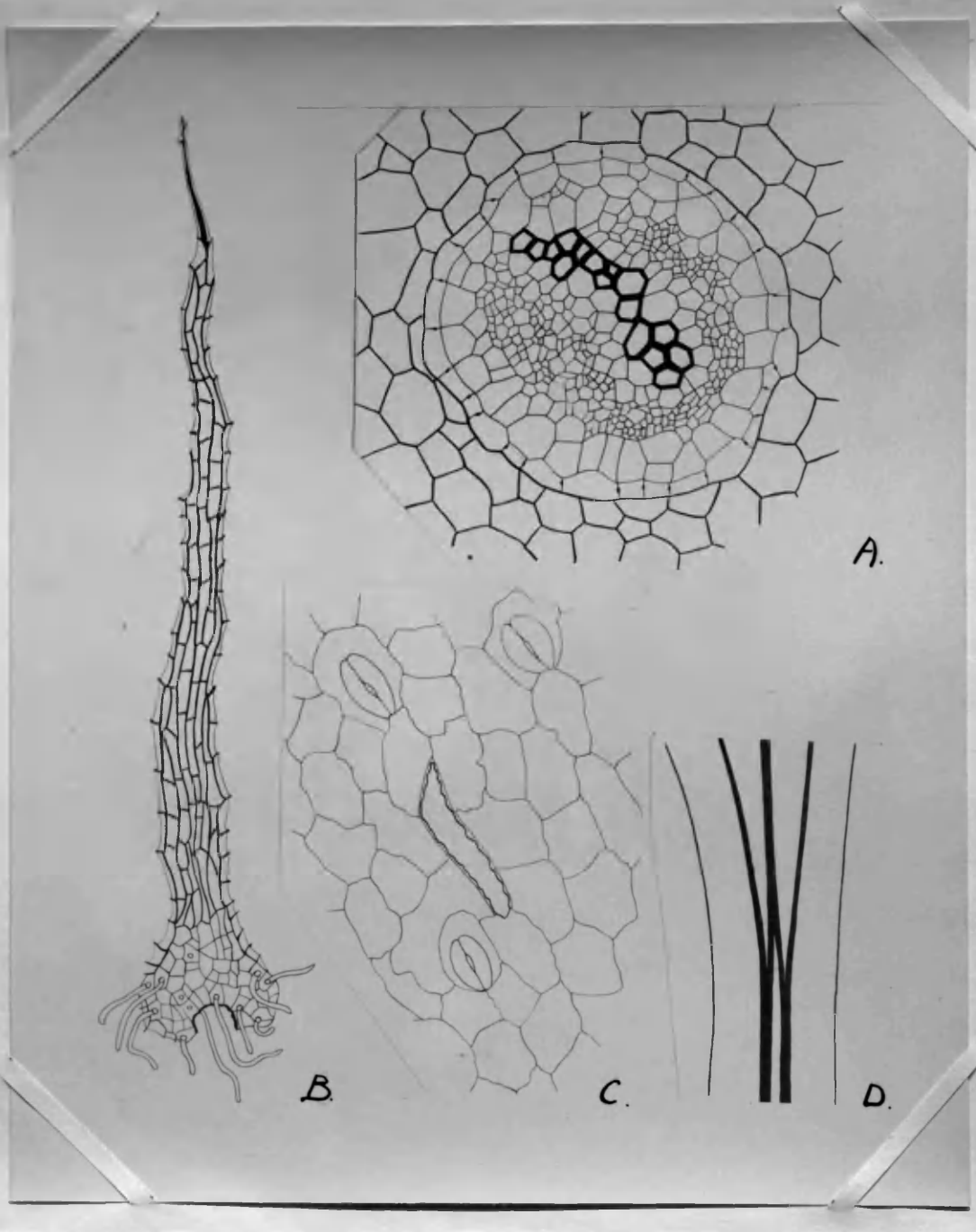

Fig.18. Antrophyum reticulatum. A, transverse section of one of the leaf traces. X 260. B, clathrate scale. X 50. C, spicule cell and stomata in surface view. X 425. D, vascular supply at junction of petiole and lamina. X 6.

of a dorsiventral dictyostelic condition similar to that described for the mature rhizome. The twentyfirst internodes and node revert to the solenostelic condition but in the twentysecond node there is an indication of dorsiventral dictyostely being again initiated. At this level the strands of the specimen examined are in the desmogen condition and any further steps leading up to the persistent dorsiventral dictyostely of the mature rhizome were not observed.

Root.

There is nothing of particular interest in the anatomy of the root, it having the diarch structure typical for the majority of Leptosporangiate Ferns. The roots, like those of all the other Vittarieae, are clothed with a dense mass of dark brown root hairs so that the whole root system forms a spongy mass, probably in relation to the epiphytic habit of the plants.

The Frond.

At the base of the petiole there are two strap shaped strands, the detailed structure of which is shown in Fig. 18, B. These strands divide as they pass up the petiole in a rather irregular, but generally dichotomous, manner. The arrangement of the strands at the base of the laminal portion is shown in Fig. 18, D, and this indicates that the mid-rib is formed by the union of the two inner shanks of a double dichotomy. The laminal portion itself shows up to eighteen almost vertical hexagonal areolae. The mid-rib which is distinguishable at the base of the lamina dies out in the more distal portion of the frond. Spicule cells are present in the epidermis.(Fig. 18, C).

Dermal Appendages.

The surface of the rhizome is densely clothed with clathrate scales of peculiar and characteristic form (Fig. 18, B) They are relatively long and narrow but are fixed to the rhizome by a

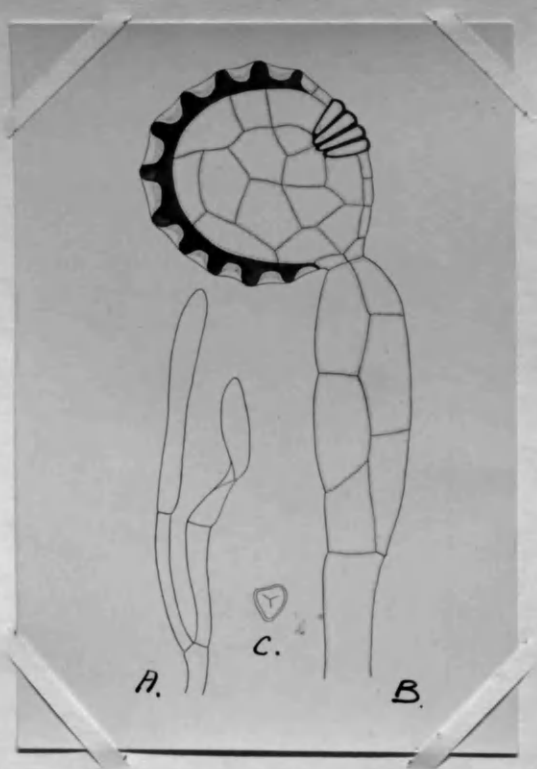

Fig.19. Antrophyum reticulatum. A, paraphysis. B, sporangium. C, spore. All X 185.

broad base of thin walled cells from which spring brown, unicellular, rhizoid like structures. These latter resemble the root hairs and may possibly perform the same function.

Sporangia.

The sporangia are arranged in grooves situated over the longitudinally running veins and are rarely found on the transverse connections of the areolae (Plate III, B). Paraphyses of the type shown in Fig. 19, A are copiously intermingled with the sporangia. The latter are very similar in construction to those described for Vittaria species. They possess a four celled stomium and an epi- and hypo-stomium each consisting of two or three cells. The stalk is similar to that described for Vittaria sporangia, being one celled at its base and dilated just below the capsule (Fig. 19, B) Spore counts yielded the numbers 58, 58, and 59 indicating that 64 is probably the typical number for each sporangium. The spores are tetrahedral in form. (Fig. 19, C).

Antrophyum plantagineum, (Cavan.) Kaulf..

This species has a wide distribution, it being described by Hooker as occurring in Ceylon, Himalayas, Malay, the Philippine and Polynesian Islands. The general form of the species is shown in Plate IV, A and it will be seen that it closely resembles A.reticulatum. The fronds are from 6 - 9 ins. long and from 1½-2 ins. broad. They are inserted in a rather irregular manner on the dorsal side of the creeping rhizome, and are closely crowded together.

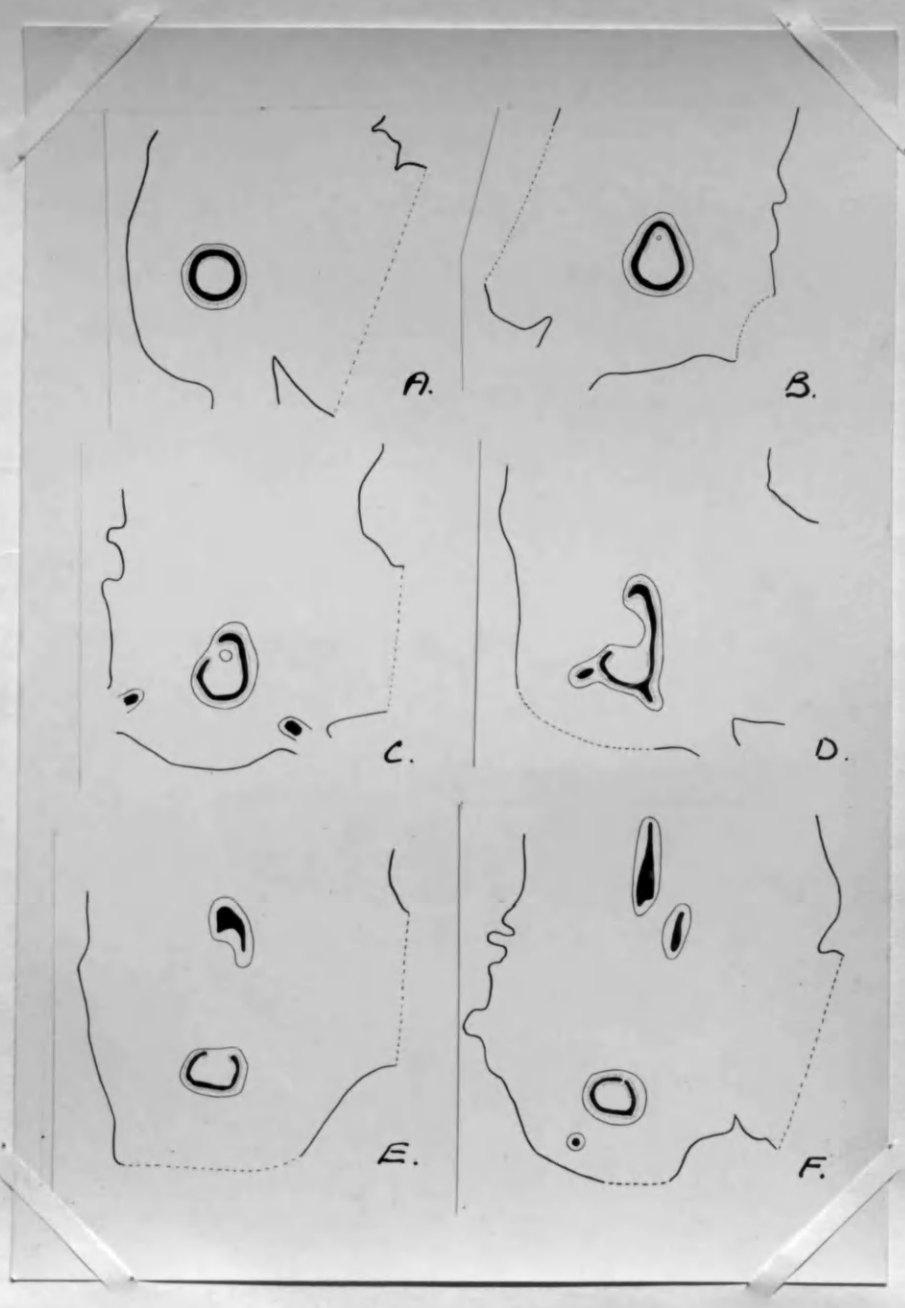

Fig.20. Antrophyum plantagineum. A-F, series of transverse sections of mature rhizome showing method of leaf trace departure. X 13.

Anatomy.

The creeping rhizome is a fleshy structure, the ground tissue being entirely parenchymatous. The anomalous stelar structure of this species has received brief mention from various writers, notably Gwynne-Vaughan(1) and Tansley(2), who both regard it as being reduced ; and by Jeffrey(3) who states that the peculiar features are to be " considered as indications of specialisation away from the usual concentric tubular type of central cylinder." The descriptions given by the above writers are very brief and omit several points of interest so that a more complete description may now be given.

In a transverse section through an internode the stele appears as a cylindrical structure which is very small compared with the diameter of the rhizome (Fig. 20, A). The xylem is in the form of a ring, one or two tracheids in thickness, and in which no definite protoxylem elements can be distinguished. Outside the xylem ring in centrifugal order are the following : a sheath of parenchyma; a more or less complete ring of phloem (composed of very small elements, very similar in appearance to the protophloem of other Ferns); a pericycle of one to three layers of large cells; and an endodermis which is in the primary condition, showing a not very clearly defined Casparian strip. The interior of the xylic ring is occupied by parenchyma though there are a few phloem elements in a dorsal position; no internal endodermis is present. (Fig. 21). The method of leaf trace departure is indicated in

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1. Gwynne-Vaughan, l.c. p.720.
2. Tansley, Lectures on the Filicinean Vascular System.
3. Jeffrey, Trans.Roy.Soc.,B,Vol.195, 1903.

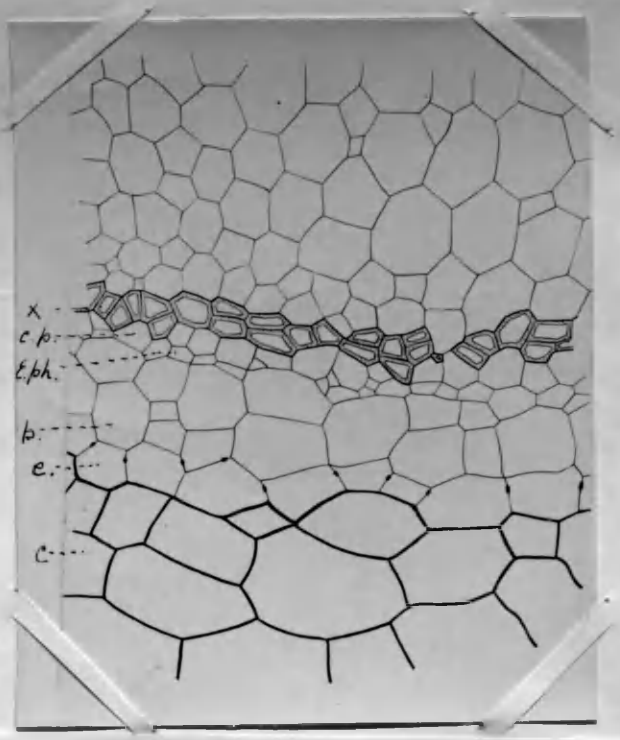


Fig.21. Antrophyum plantagineum. Ventral portion of stele. Lettering as in Fig.2. X 260.

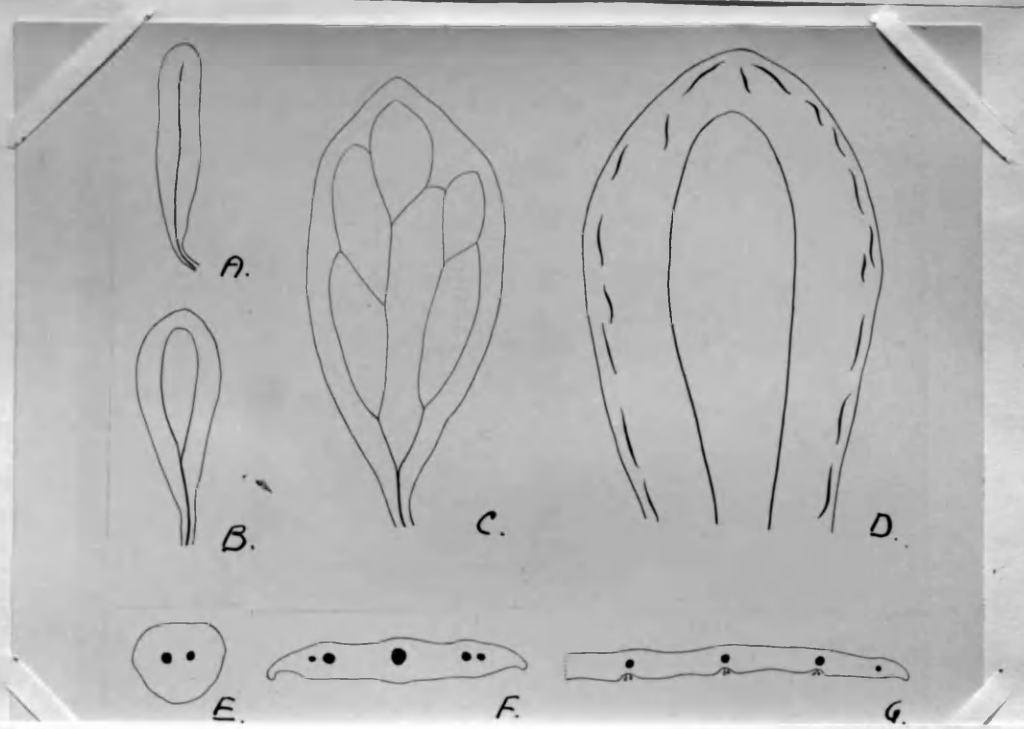


Fig.22. Antrophyum plantagineum. A-C, series of fronds from a young plant. X 4 . D, arrangement of spicule cells round the margin of a frond of a young plant. X 13 . E, transverse section of base of petiole. F, T.S.base of lamina. G, T.S. middle of laminal portion. E,F and G X 4 .

Fig. 20, B-F. There is an endodermal pocket formed at the node, and, during the departure of the leaf trace, no connection is established between the cortex and the pith. The xylem ring remains open for a short distance but it is closed again before the next leaf trace departs. The C-shaped trace consists of a crescentic band of xylem with phloem on both sides of it, the whole being surrounded by endodermis. After passing rapidly through the cortex this trace divides to give the two strands which are present at the base of the petiole.

The Frond.

The frond has a reticulate venation very similar to that of A.reticulatum. There is no definite mid-rib except in the proximal portion of the lamina. The venation of the leaves of young plants is indicated in Fig. 22, A, B, and C. The earliest formed fronds have a single vein ; a number of the next formed ones show a simple dichotomous structure, though even at this stage the two shanks of the dichotomy are united at their tips to form a single areola ; in later formed leaves the reticulate condition is well established although the underlying dichotomous plan of construction is still evident. An interesting feature in the structure of the earlier formed fronds is the way in which the spicule cells are arranged round the margin (Fig. 22, D). This suggests that the function, or, at any rate, one of the functions, of the spicule cells is the prevention of the tearing of the leaf margin.

Dermal Appendages.

The surface of the rhizome and leaf bases is covered with clathrate scales very similar to those figured for A.reticulatum.

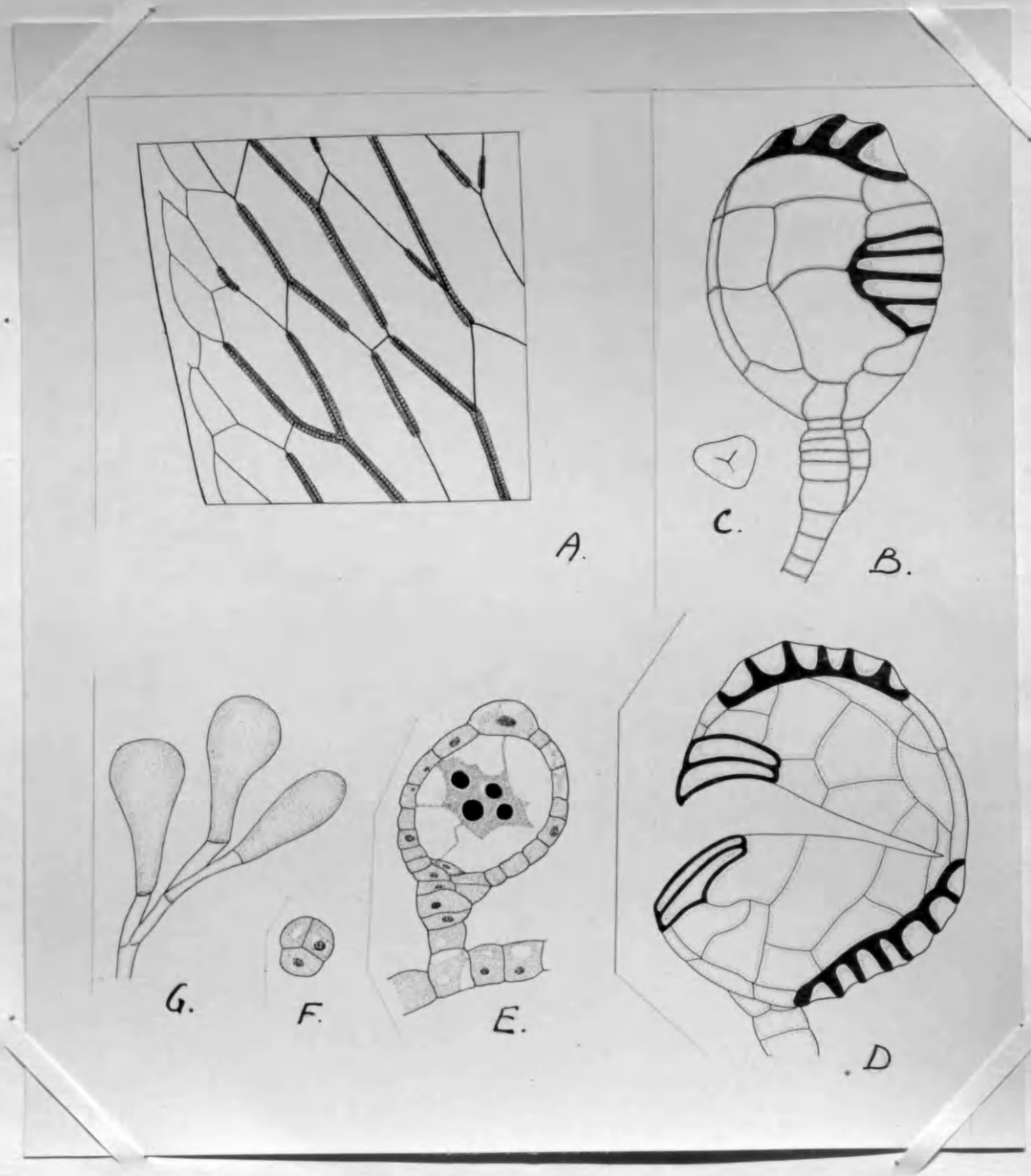


Fig.23. Antrophyum plantagineum. A, venation and sporangial distribution. X 4 . B, sporangium. C, spore. D, abnormal sporangium with interrupted annulus. E, young sporangium showing stalk characters. F, T.S.stalk of sporangium just below the capsule. G, paraphysis. B-G all X 185 .

Sporangia.

The sporangial arrangement is very similar to that described for A.reticulatum (Fig. 23, A.). The sporangia (Fig. 23, B) are large and have a spore output of 56 (as indicated by spore counts which yielded the numbers 53, 54, and 56.) The annulus is vertical and is composed of 15 - 18 cells ; the stomium is four celled and there is an epi- and hypo-stomium each consisting of two cells. The stalk shows the same general features as in the sporangia of Vittaria species and A.reticulatum. The sporangial structure is very constant but occasionally anomalous types are found such as the one delineated in Fig. 23, D where the annulus is interrupted in the middle of its length for a considerable distance.

Intermingled with the sporangia are numerous branched paraphyses, the branches terminating in large club-shaped cells which are dark in colour.(Fig. 23, G.)

Antrophyum lineatum, Kaulf..

A.lineatum is somewhat divergent from the rest of the Antrophyum species and it has accordingly had a very varied systematic history. It was first described by O.Swartz (1788) as Hemionitis lineata and the same writer later (1799) renamed it Vittaria lanceolata. Kaulfuss (1824) described it as Antrophyum lineatum while Desvaux (1827) placed it in the genus Polytaenium and Presl (1836) in Loxogramme. Most later systematists, including Hooker, Diels and Christ, have placed it under Antrophyum but Benedict has recently described it under the genus Polytaenium, Desv.. The present writer, however, regards it as sufficiently similar to other Antrophyum species to justify its retention in that genus.

The material available for examination was collected by Prof.Bower at Holly Mount, Jamaica. According to Hooker, the range of the species is from "Cuba and Mexico to Ecuador and Brazil."

Anatomy. (Plate VIII)

The stele of the mature rhizome is a typical dorsiventral dictyostele with both internal and external phloem. It is very similar in all essential points to that described for A.reticulatum and therefore need not be described in detail. In the youngest rhizomes examined there is a very simple little protostele with at most four or five tracheids. Small single strands pass out from this into the fronds. In older rhizomes examined the dorsiventral dictyostelic condition had already been established. No solenostelic stage was observed in any of the material available for examination.

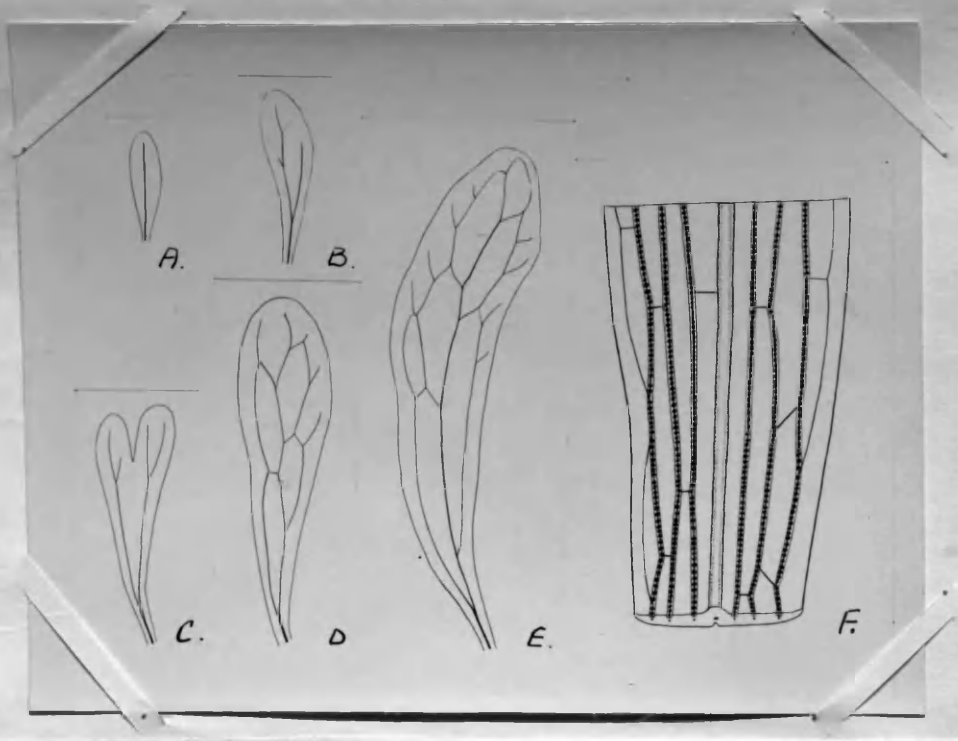


Fig.24. Antrophyum lineatum. A-E, series of fronds of a young plant. X 4 . F, venation and sporangial distribution of portion of mature frond. X 4 .

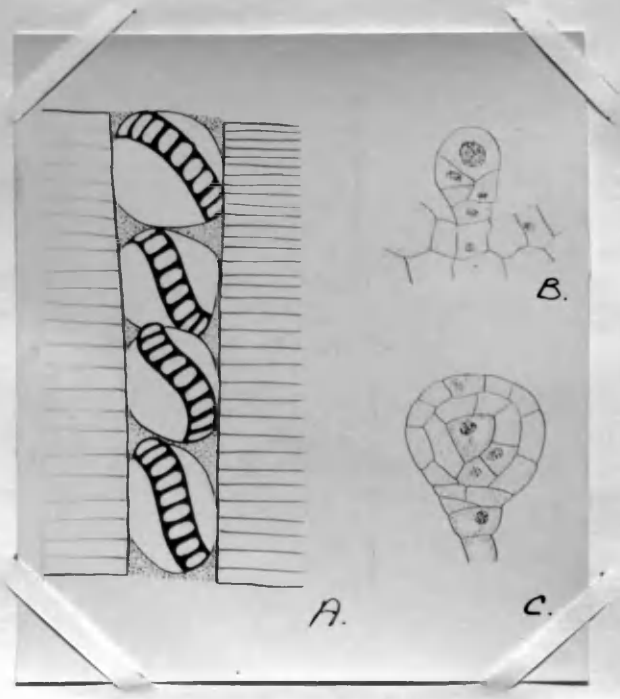


Fig.25. Antrophyum lineatum. A, sporangial groove. X 55 . B and C, developmental stages of sporangia. X260.

The Frond.

The long narrow leaf has a distinct mid-rib and two or three rows of very long meshes on either side of it. These meshes are almost rectangular in shape, differing in that particular from other species of Antrophyum. A series of fronds from a young plant is shown in Fig. 24, A-E. The youngest leaf has a single vein; the succeeding two stages have an open venation of a clearly dichotomous type, though in a few examples a certain degree of sympodial development is found. Older fronds show the reticulate venation established.

Spicule cells are present in the epidermis.

Dermal Appendages.

The dermal appendages are clathrate scales very similar in form and construction to those described for A.reticulatum.

Sporangia.

The sporangia are borne in two or three distinct and almost continuous lines on either side of the mid-rib (Fig. 24, F). The arrangement of the sporangia in well defined lines is different from the condition found in the other species of Antrophyum. The difference is due to the fact that the areolae are almost rectangular in A.lineatum whereas they are hexagonal in the species previously described. In all of them, however, the sporangia are inserted on the longitudinally running veins of the meshes. The sporangia are immersed in deep grooves with raised edges and are unmixed with paraphyses, which latter is another point of difference from the species previously described. The arrangement of the sporangia in the grooves is very regular and their orientation is such that the annulus of each is able to function efficiently

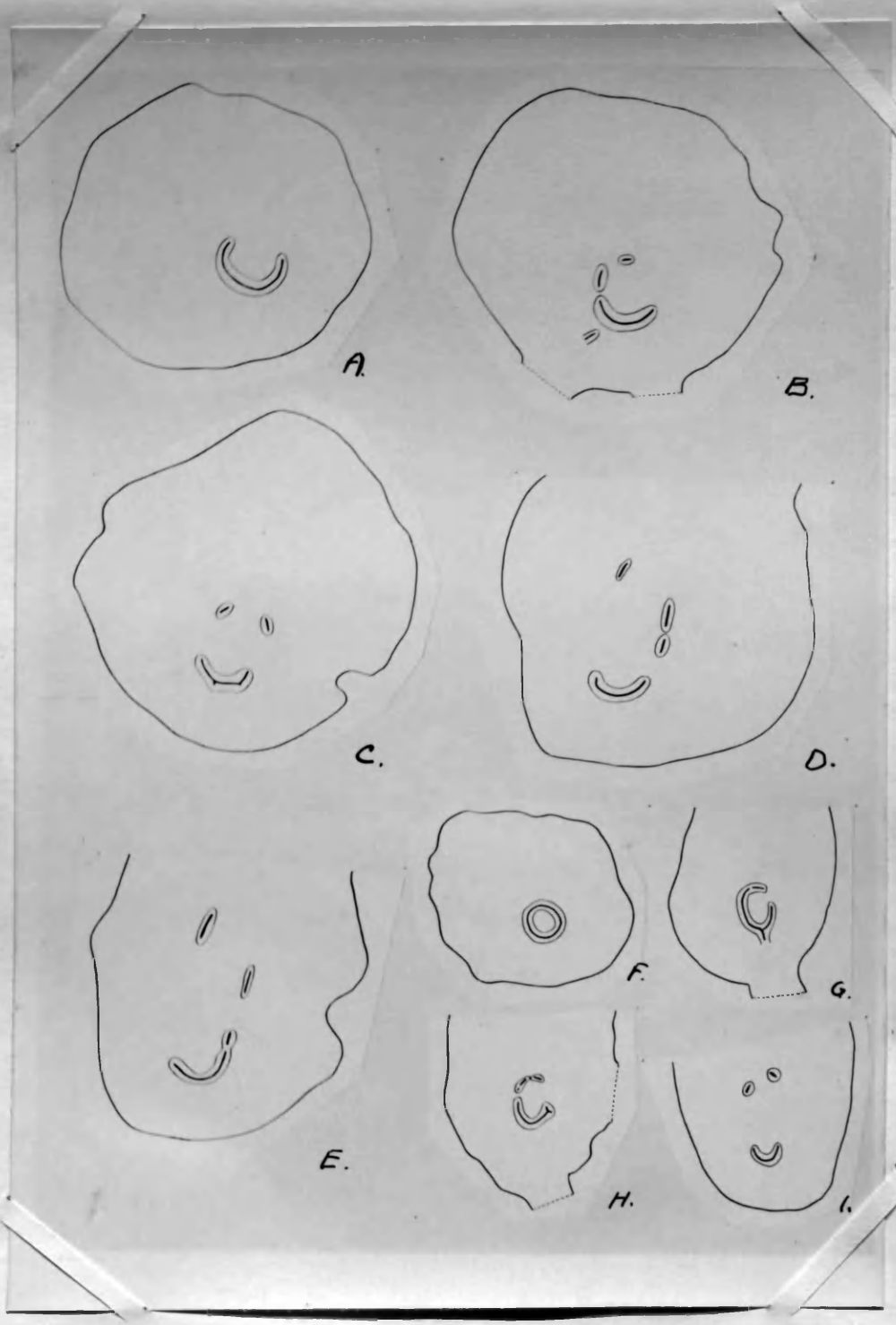


Fig.26. Antrophyum lanceolatum. A-E, series of transverse sections of mature rhizome. F-I, series of transverse sections of young rhizome. All X 13 .

in spite of their closely crowded insertion (Fig. 25, A).

The sporangia themselves are very similar to those of A.plantagineum, showing a similarly constructed stalk, annulus and stomium. Spore counts yielded the numbers 57 and 59, indicating that the typical spore output for each sporangium is probably 64. The ontogenetic development of the sporangia follows very closely that of other advanced Leptosporangiate types, a three sided archesporial cell being formed.(Fig. 25, B,C.).

Antrophyum lanceolatum, Kaulf..

This species differs from the species previously described in the fact that the sporangia are borne superficially on the surface of the frond. The fronds, which are a foot or more in length and about half an inch broad, have a distinct mid-rib and on this account the species is placed in the genus Polytaenium by Benedict. Hooker describes its distribution as being from the West Indies and Mexico to New Granada. The material used in this investigation was collected by Prof.Bower in Jamaica.

Anatomy.

The mature rhizome possesses a dorsiventral dictyostele which is of very small size in proportion to the diameter of the rhizome (Fig. 26, A - E.) In detailed construction the stele is very similar to that of A.reticulatum except that the internal phloem forms a complete band, not being absent on the ventral side as in the latter. The vascular supply of the youngest rhizomes

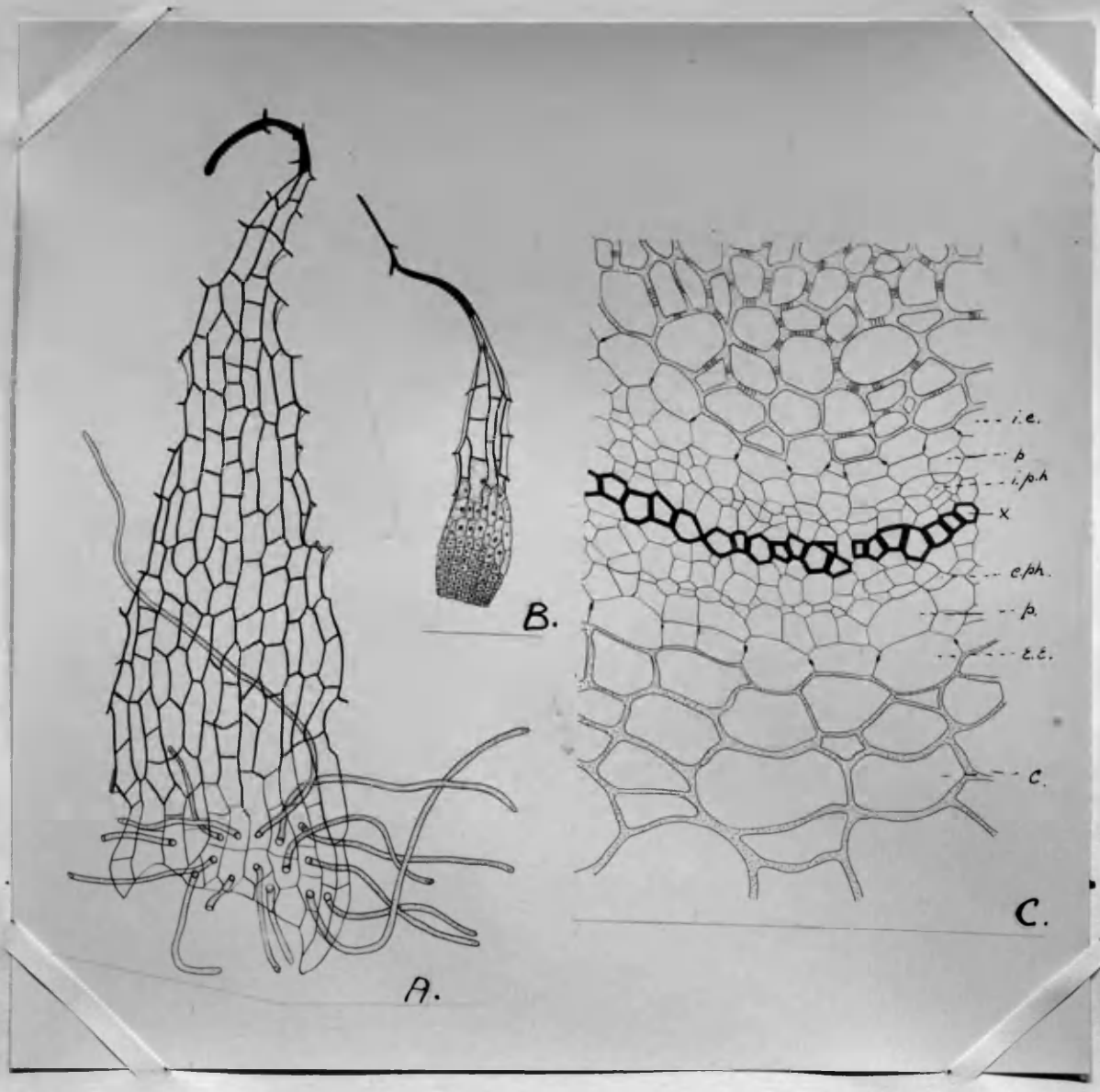


Fig.27. Antrophyum lanceolatum. A, clathrate scale. B, young clathrate scale. A and B X 50 . C, portion of solenostele of young plant X260.

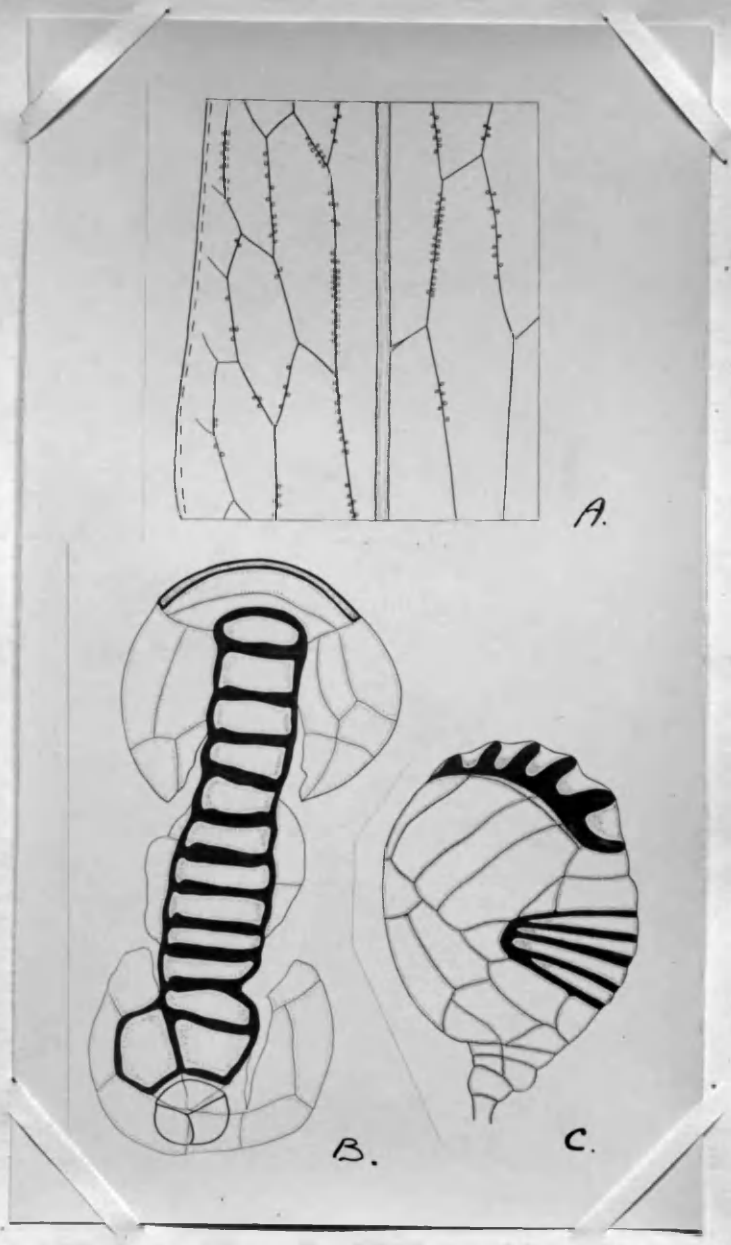


Fig.28. Antrophyum lanceolatum. A, venation and sporangial distribution. X 4 . B and C, sporangia. X 185.

available for examination is solenostelic (Fig. 26, F-I), each leaf gap being closed, though only for a short distance, before the next gap opens out. The first indication of the departure of a leaf trace is the breaking of the stelar ring and the outward arching of a band of xylem and phloem. This band divides into two before the basiscopic margin of the leaf trace is freed from the axial strand so that the trace actually departs as two separate strands. The detailed structure of the solenostele need not be described since there are no divergences from typical solenostelic structure. Both internal and external phloem are present. (Fig. 27, C)

The Frond.

The lanceolate fronds have a very distinct mid-rib and three or four rows of hexagonal meshes on either side of it. The marginal meshes are often incomplete showing free vein endings. Spicule cells are present only in the upper epidermis of the specimens examined and they are mainly disposed around the margin of the frond.

Dermal Appendages.

The clathrate scales (Fig. 27, A) which cover the surface of the rhizome are of the usual Antrophyum type but they are mixed with simple hairs which are not present in any of the other species examined.

Sporangia.

The sporangia, which are borne superficially on the longitudinally running veins, are of the same type as described for other species (Fig. 28, B,C.). Paraphyses are absent. Spore counts yielded the numbers 43 and 45 indicating that the typical number of spores produced in each sporangium is 48.

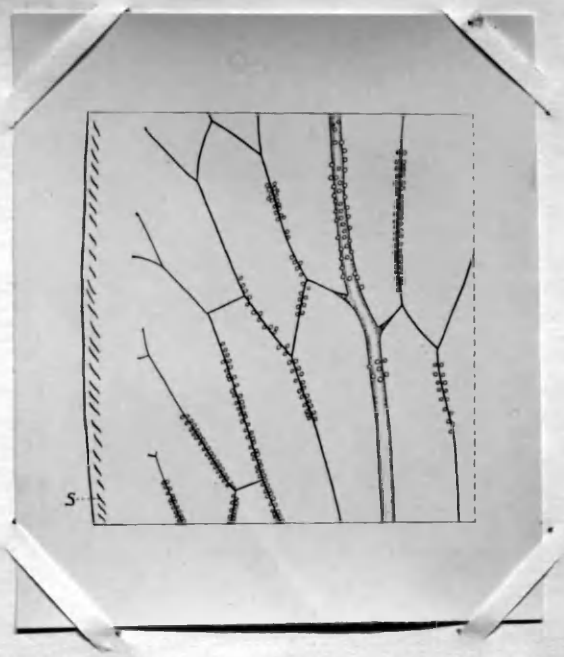


Fig.29. Antrophyum brasilianum. Venation and sporangial distribution. s = spicule cells. X 4 .

Antrophyum brasilianum, C.Chr..
(= A.subsessile,Kunze.)

A.brasilianum may be taken as an example of a broad leaved form with its sporangia borne superficially. The fronds are from 6-12 ins. long and from 1-1½ ins. broad. They possess a distinct mid-rib and on that account the species is included in the genus Polytaenium by Benedict. Its distribution is described as being from Cuba and Guatemala to Peru.

Anatomy.

The mature rhizome shows a dorsiventral dictyostele, though occasionally a more advanced type of dictyostely is met with owing to the overlapping of more than two leaf gaps at any one level. The detailed structure presents no features of special interest.

The Frond.

A distinct mid-rib is present and on either side of it are two or three rows of meshes. As in A.lanceolatum the outer meshes are incomplete and free vein endings are visible at the margin of the frond. The spicule cells of the epidermis are mainly distributed round the periphery of the frond.

Dermal Appendages.

The clathrate scales are similar in every respect to those figured for A.reticulatum.

Sporangia.

The sporangia, which are unmixed with paraphyses, are situated superficially on the longitudinally running veins. They are of the usual Antrophyum type with a four celled stomium and two epi- and hypo- stomial cells. The stalk is similar to that figured for A.lanceolatum. Spore counts yielded the numbers

, 45, 46 and 49 indicating that 48 is probably the typical
ber of sporangia produced in each sporangium.

THE VITTARIEAE. (Continued)

5. Hecistopteris.
6. Anetium.
7. The Gametophyte.
8. Stelar Problems.
9. The Operation of the Size Factor.
10. The Endodermis.
11. Taxonomy and Affinities.

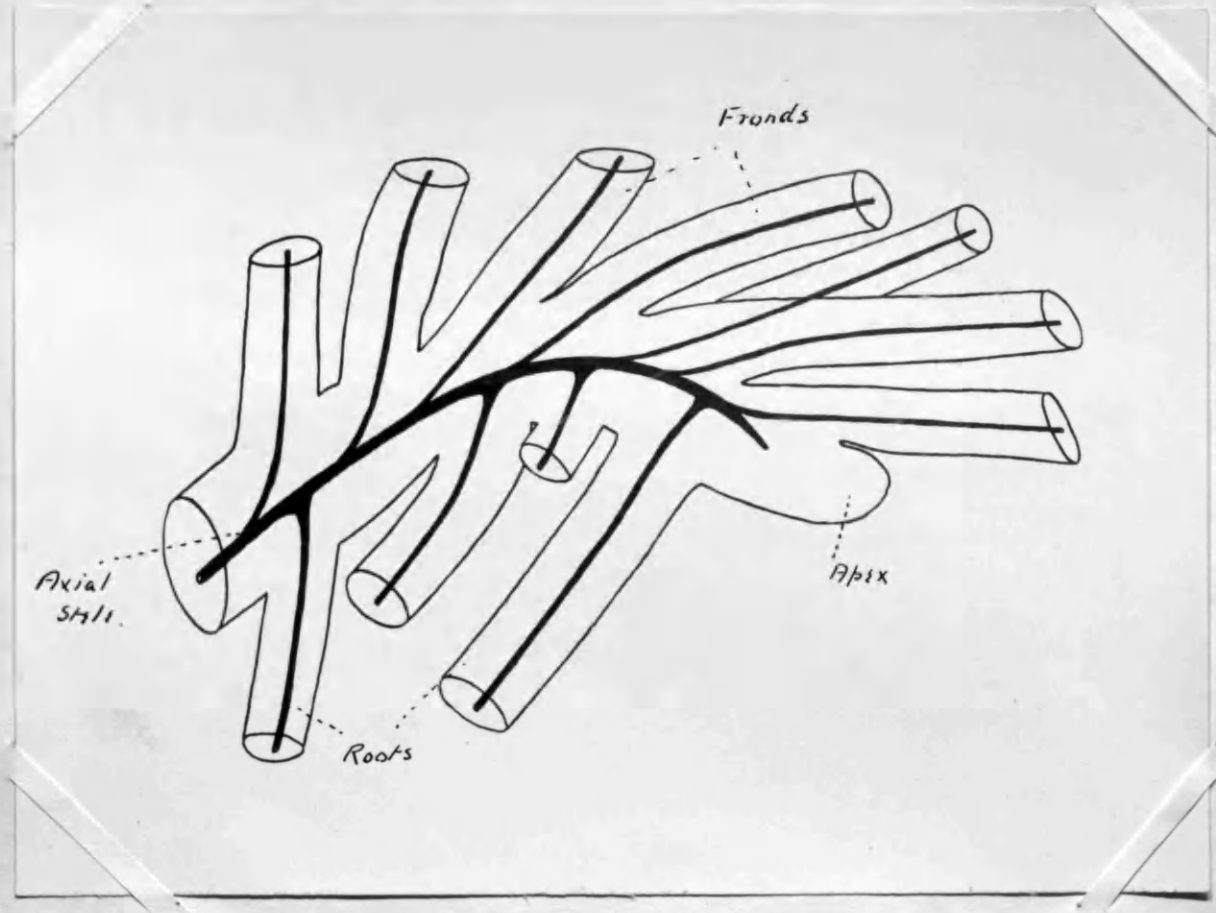


Fig.30. Hecistopteris pumila. Distal portion of a rhizome cleared in Eau-de-Javelle and stained with ammoniacal fuchsin, showing arrangement of vascular strands.

Hecistopteris pumila, J.Smith.

(Plate IV, B)

Hecistopteris pumila is an extremely small form having a slender creeping rhizome and reproducing frequently by root buds. The leaves may, according to Hooker, reach a length of 1½-2 ins. but the specimens available for examination were much smaller. The leaves are characterised by the fact that they possess an open dichotomous venation, the outline of the frond also being branched in a dichotomous manner. These leaf characters are distinctly anomalous in the Vittarieae. Sprengel (1828) and Hooker (Syn.Fil.) included this form in §§§§ Eugymnogramme of the genus Gymnogramme but J.Smith had already in 1842 instituted the new genus Hecistopteris for its reception since, as he states in the Historia Filicum (1877), "it did not appear to me to form any natural alliance with any of the groups of species of that genus (i.e.Gymnogramme)". The same writer points out that certain structural features "indicate its relationship with Monogramma and Pleurogramma." It remained for Goebel (l.c. 1896) to demonstrate clearly the soundness of separating Hecistopteris from Gymnogramme and also the affinity of this form with the other genera of the Vittarieae on the basis of the anomalous structure of the gametophyte, the presence of spicule cells and the absence of sclerenchyma from the shoot axis.

The following account is based on specimens from the Herbarium of the Royal Botanic Gardens of Edinburgh. The label accompanying the specimens is as follows "Plants of Trinidad. No.132. Gymnogramme pumila, Anton Sprengel. Legit A.Fendler, 1877-80."

Anatomy.

The material did not soak out sufficiently well to allow of

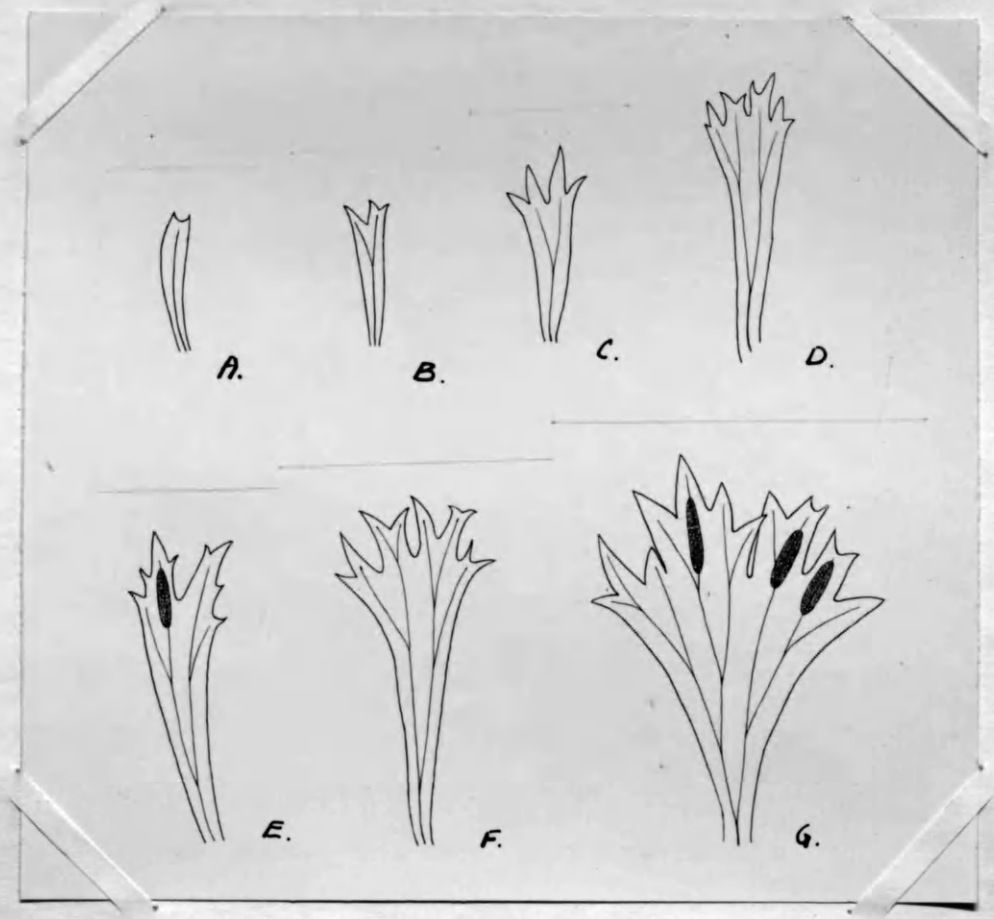


Fig.31. Hecistopteris pumila. A-G, fronds from plants of different ages showing venation and, in E and G, the sporangial distribution. X 4 .

any detailed anatomical study. It was possible, however, to verify Goebel's statement that the stelar structure of the rhizome is very similar to that of Monogramma species. Indeed, in the small specimens available for examination, the stele is even simpler than that of the Monogramma species examined. It consists of a small protostele, oval in outline, and possessing a short bar of xylem. The leaf traces depart from this as very small and simple strands. The general course of the vascular strand in the rhizome is shown in Fig. 30 , which is a slightly diagrammatised drawing of a length of rhizome cleared in Eau de Javelle and stained with ammoniacal fuchsin.

The frond.

The first formed fronds of young plants are single veined but even at this stage the outline of the frond shows a distal dichotomy (Fig. 31, A). Later formed fronds show a single dichotomy (Fig. 31, B, C), while the fronds of older plants exhibit a repeated dichotomy of the veins, the latter remaining free and ending in little bunches of tracheids. The outline of the frond itself follows the plan of the venation although the distal dichotomies of the frond are often in excess of the number of vein endings.

Numerous long spicule cells (Fig. 32, F) are present in the epidermis and, apart from giving mechanical rigidity to the frond as a whole, their arrangement suggests that they also prevent tearing of the leaf margin.

Dermal Appendages.

The surface of the rhizomes and leaf bases is clothed with small clathrate scales (Fig. 32, E). They have very thick walls and are inserted on the rhizome by a broadened base.

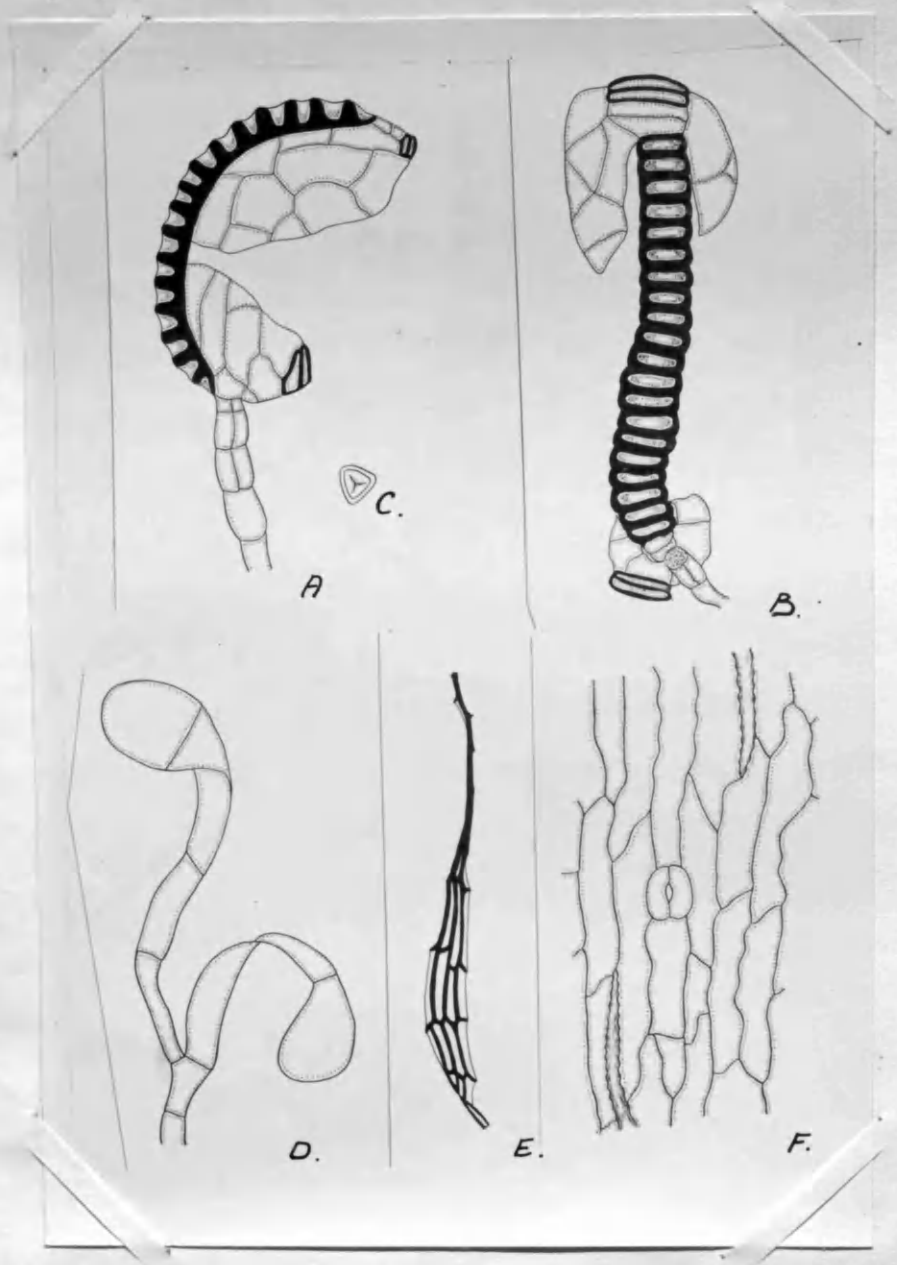


Fig.32. Hecistopteris pumila. A and B, sporangia. C, spore. D, paraphysis. All X185. E, clathrate scale. F, portion of epidermis with stoma and the end portions of two spicule cells. X185 .

Sporangia.

The fronds reach a fertile condition at a very early stage, as is shown by Fig. 31, E which is a drawing of the frond of a young plant with only a double dichotomy but which already possesses a sorus along one of its veins.

The sporangia themselves are very similar to those of other genera of the Vittarieae. The annulus is vertical and consists of 16-20 cells. The stomium is usually four celled but in some of the specimens examined it was five celled. The stalk is single celled below but is dilated just below the capsule. It was impossible to determine the exact constitution of the stalk owing to the poor preservation of the material. The spores are tetrahedral in form (Fig. 32, C) but no spore counts were possible. The sporangia are mixed with branched paraphyses of the usual Vittariaceous type, the branches ending in swollen, club shaped cells. (Fig. 32, D)

Anetium citrifolium,(L) Splitgb..

(Plate V)

Anetium is a curious and anomalous monotypic genus which has undergone various vicissitudes of classification. Originally named Acrostichum citrifolium by Linnaeus, it has since been described under various generic names. Presl placed it under §2 Antrophyum of the genus Hemionitis as H.spatulata. Fee placed it in the genus Antrophyum, while Hooker placed it again under Hemionitis as §§ Anetium, remarking that it is "an anomalous species, with the habit of Antrophyum." John Smith and most later systematists have described it under Anetium,Splitgb.. Goebel and, more recently, Frau Schumann,have emphasized its relationship with the other genera of the Vittarieae, mainly on the basis of its general form and the fact that spicule cells are present in the frond. It is an epiphytic form of the West Indies, usually growing in very moist situations. It has a slender creeping rhizome on which simple pendent leaves are inserted in two rows at rather distant intervals. Branching of the rhizome appears to be infrequent but does occur occasionally. The material upon which the following description is based was collected by Prof. Bower in Jamaica.

Anatomy.

Anetium citrifolium is more advanced in its anatomical construction than any other genus of the Vittarieae. It is very different from the other genera both in its gross stelar morphology and in anatomical detail. The mature rhizome is fleshy and about a quarter of an inch in diameter ; the amount of vascular tissue present is relatively very small,

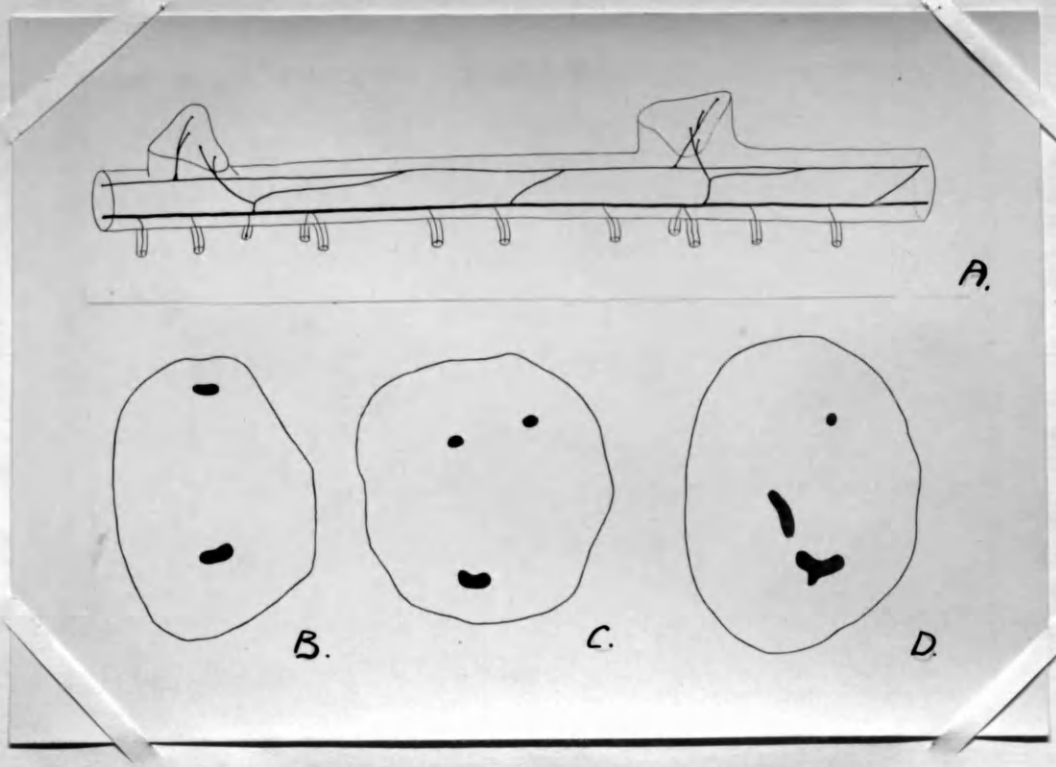


Fig.33. Anetium citrifolium. A, drawing of a model of the mature rhizome showing the general arrangement of the vascular strands. B-D, transverse sections of the rhizome at different levels. X /3 .

In any internode two or sometimes three meristeles are present. Of these, one is considerably larger in size and this is situated in a ventral position while the other one or two meristeles are smaller and dorsally situated. The structure of the large ventral meristele, from which the root traces depart, is as follows (Fig. 34, C.). The xylem is in the form of a shallow U-shaped curve one or two tracheids in thickness and frequently not continuous. The walls of the tracheids are thin and only slightly lignified. Phloem is present on both sides of the xylem curve and consists of small elements whose walls stain deeply with haematoxylin. The meristele is surrounded by a one to several layered pericycle and an endodermis which is in the primary condition, showing an ill developed Casparian strip. The structure of the dorsal meristeles is very similar to this except that the xylem is in the form of a straight bar of tracheids.

The gross morphology of the stele is anomalous and difficult to relate to any of the types of stele usually present in the Ferns. It varies in detail in different rhizomes but in all the cases examined it is in the form of a dictyostele complicated by perforation. The general appearance of the stele in a length of rhizome is shown in Fig. 33, A, drawn from a model built up from successive hand sections and the structure of the stele at a node a little way back from the apex is represented in Fig. Plate VII. The leaf trace departs as two strands, one from either side of the leaf gap, and these divide while still in the cortex into four strands which divide again in the base of the petiole. A section across the base of the petiole shows a shallow horseshoe curve of strands with the open end of the horseshoe to the adaxial surface.

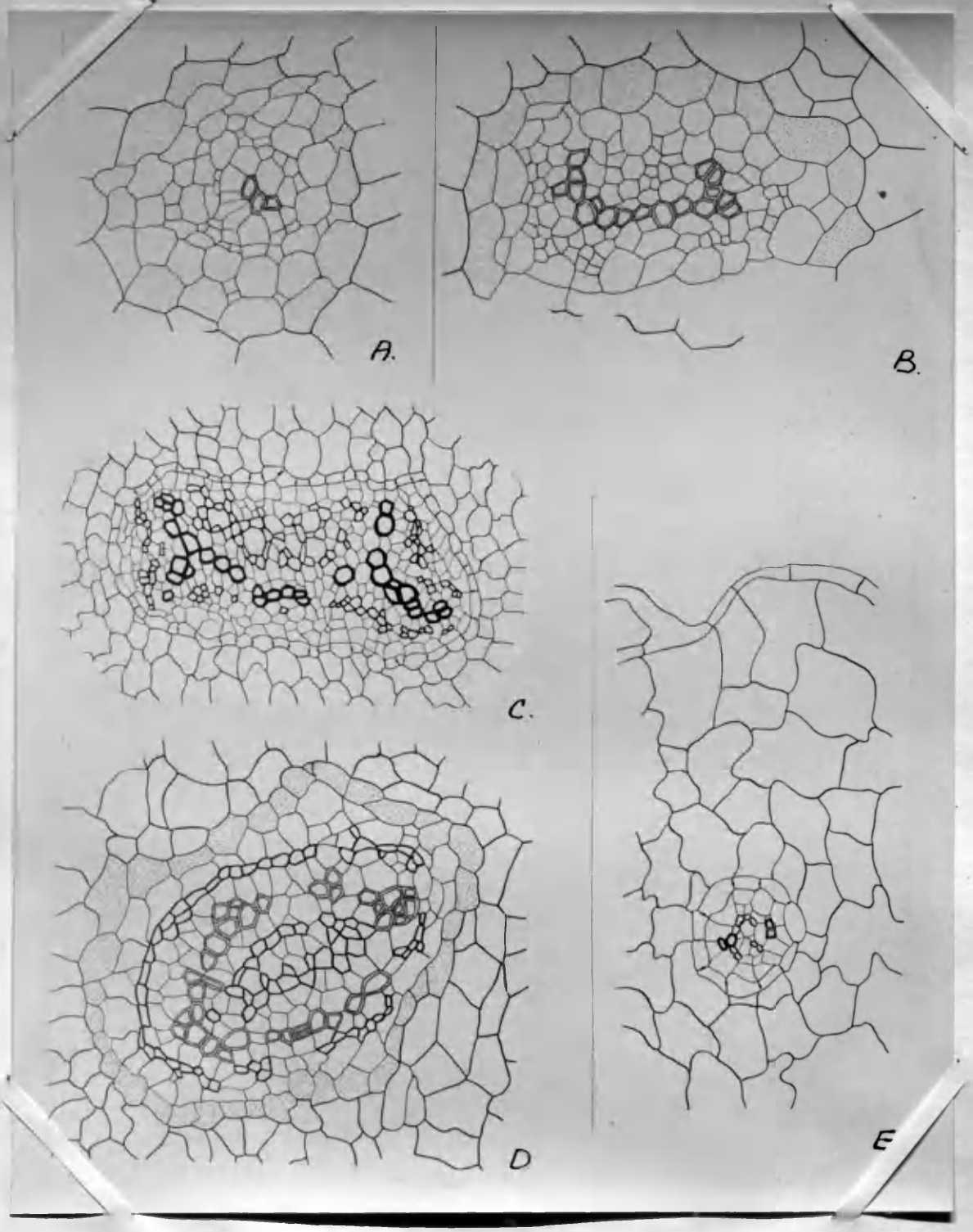


Fig.34. Anetium citrifolium. A, stele at base of young plant. B, stele at higher level in same seedling. X 425. C, ventral meristele of mature rhizome. X 155. D, stele at the base of a branch ; description in text. E, sector of root. D & E × 260

The stele of seedling plants is in the form of a simple protostele (Fig. 34, A.). The xylem consists of a very small group of tracheids around which there are in centrifugal order : a sheath of large celled parenchyma; a broken ring of small phloem elements; a one to several layered pericycle and an endodermis. The leaf traces are given off from this protostele as single small and simple strands without disturbing the xylem. The protostelic condition persists through a considerable length of rhizome. The xylem extends somewhat and takes the form of a shallow U-shaped curve, resembling in miniature that of the ventral meristele of the mature rhizome.(Fig. 34, B.) Even at this stage the leaf traces depart alternately from the right and left hand side of the stele as single strands whose departure does not disturb the xylem of the axial stele. The material available did not allow of the observation of the transition from the protostelic condition to the more complex structure of the mature rhizome. In rhizomes of slightly larger diameter than those just described, however, the dictyostelic condition is already established and it seems highly probable that the protostele passes directly to the dictyostelic condition. A sufficient number of young rhizomes were examined to render it extremely unlikely that any intermediate conditions occur.

Branching has been observed in a number of rhizomes of different ages, though in all the examples which were sectioned the stele had already attained the dictyostelic condition. These branchings are not, as far as could be determined, related in any way to the insertion of the leaves and must be regarded

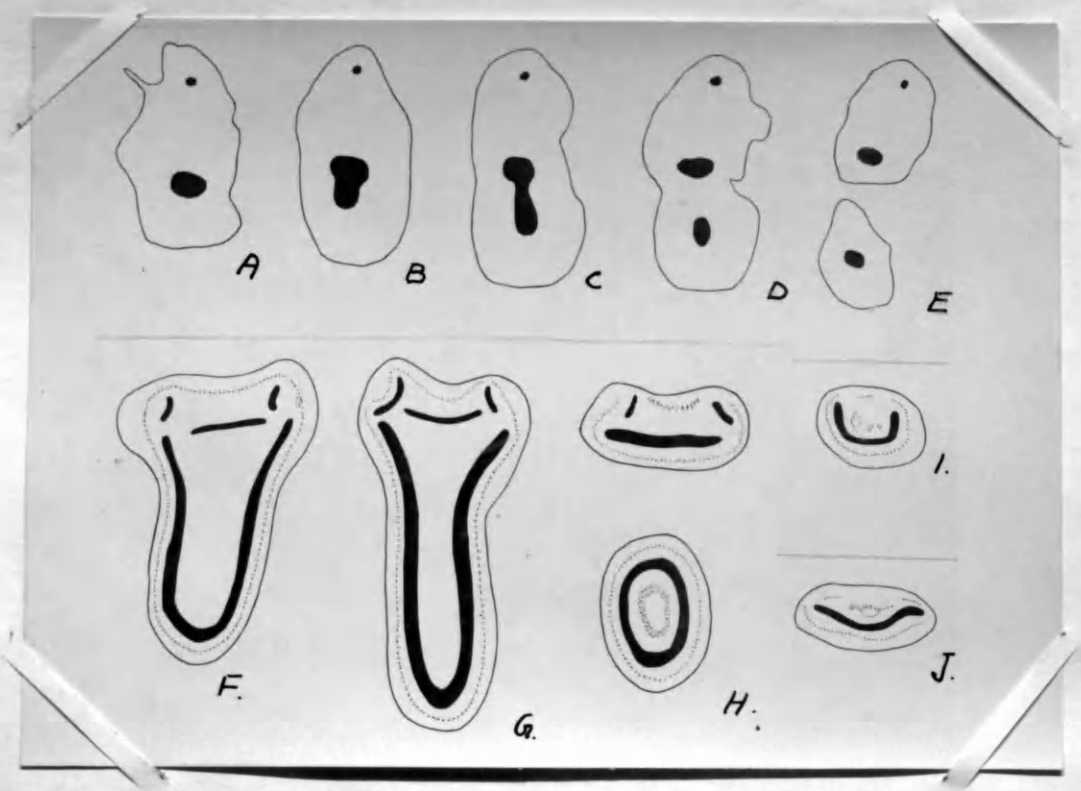
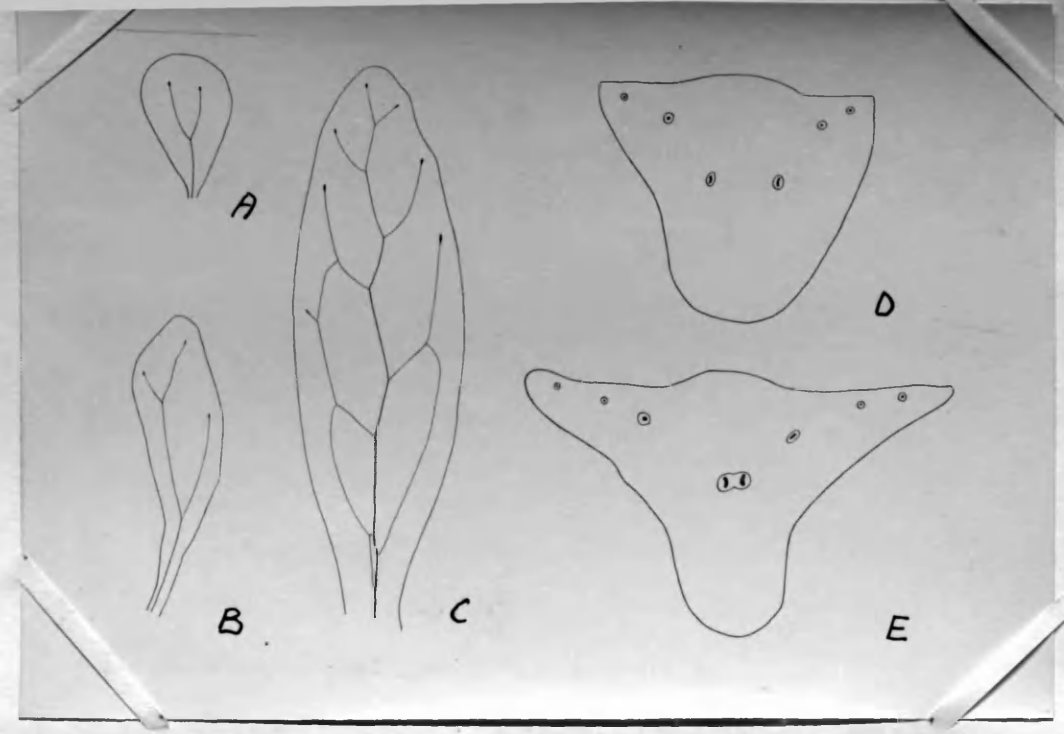


Fig.35. Anetium citrifolium. A-E, series of transverse sections of a young rhizome in the region of branching. X 13 . F-H, transverse sections of the stele at levels of B,C and D. I-J, branch stele. F-J X 60.

as essentially dichotomous though showing an unequal development of the two shanks. Fig. 35, A-E represents a series of sections taken in the region of branching and indicates the unequal nature of the division of the vascular supply. As the level of branching is approached changes take place in the conformation of the large ventral meristele with the result that it assumes the curious conformations shown in Fig. 35, F and G, and finally the smaller branch trace is abstricted off (Fig. 35, H.). One arm of the branching continues with its vascular supply still dictyostelic and closely resembling that of an unbranched rhizome. The stele of the other branch (Fig. 34, D) is unlike anything observed in the structure of unbranched rhizomes, either in the mature condition or in the ontogenetic stages. The xylem is in the form of a broken ring of relatively large tracheids. The centre of the stele is occupied by parenchyma mixed with tissue the walls of which stain deeply with haematoxylin and which is probably internal phloem. No internal endodermis is present. Outside the xylem is a practically complete band of phloem and the whole stele is surrounded by a somewhat irregular endodermis in the primary condition. In the material available for examination it was unfortunately not possible to observe the departure of any leaf traces from this branch stele. Further along the branch changes take place in the conformation of the vascular strand. The xylem ring becomes broken on the dorsal side and appears first as a U-shaped curve and later as an almost flat plate (Fig. 35, I and J). It was impossible to determine whether the branch stele ever becomes dictyostelic.



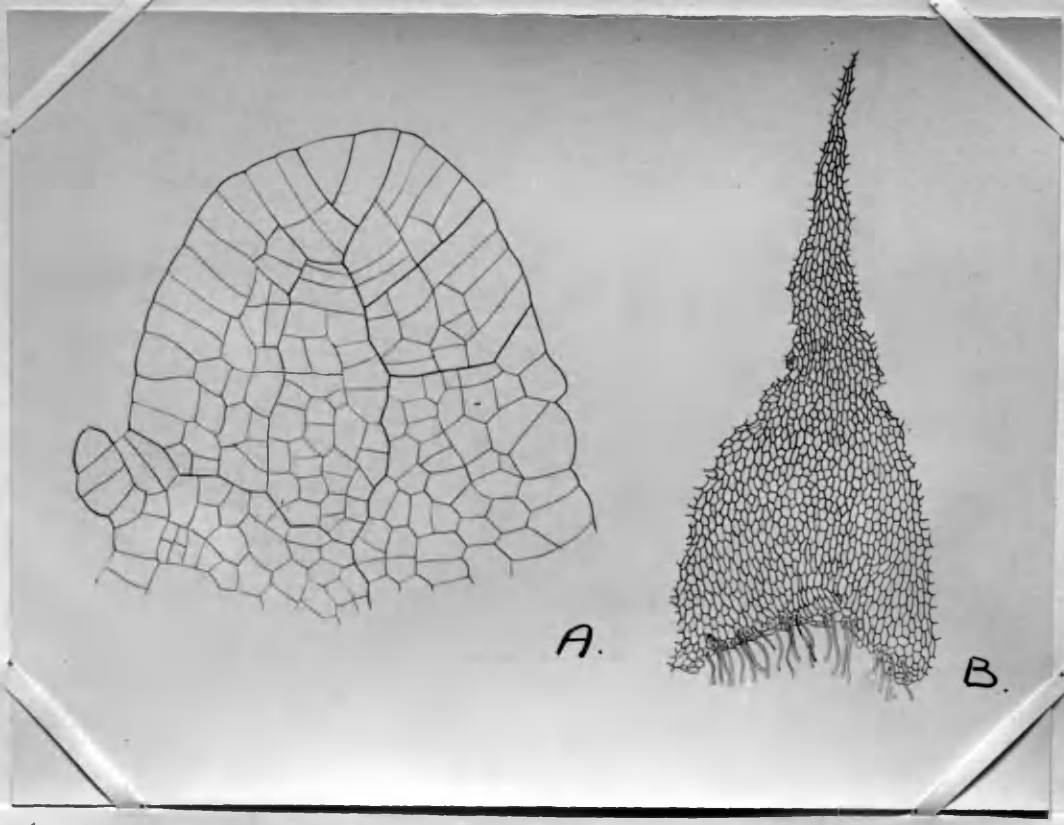


Fig.36. Anetium citrifolium. A-C, series of fronds of a young plant. X 4 . D and E, transverse sections at the base of the petiole and the base of the lamina respectively. X 13 .

Fig.37. Anetium citrifolium. A, apex in longitudinal section. X 260. B, clathrate scale. X 16 .

Apex of rhizome.

The apex of the rhizome is conical with a single three sided apical cell from which the segments are cut off in regular sequence (Fig. 37, A.). The apex is clothed and protected by a covering of clathrate scales.

The Frond.

The fronds measure up to 9 ins. long and 2 ins. broad and are shortly petiolate. At the base of the petiole a shallow horse-shoe curve of strands is present (Fig. 36, D), the two central ones moving together at a higher level (Fig. 36, E) to give a mid-rib which remains distinct except in the distal portions of the frond. Eight or nine hexagonal meshes are present on either side of the mid-rib, the marginal ones being incomplete and showing free vein endings. (Fig. 38, A). Spicule cells are scattered throughout the upper epidermis and a number of very large ones are arranged round the periphery, presumably for the purpose of preventing tearing of the leaf margin(Fig. 38, A and B).

The venation of the fronds of young plants is indicated in Fig. 36, A-C. No stage was observed in which only a single vein is present as in the fronds of seedling plants of Antrophyum and Vittaria. The first frond shows a simple dichotomy (Fig. 36, A), while subsequent fronds show a sympodial development and finally the establishment of the reticulate venation characteristic of the fronds of mature plants.(Fig. 36, B,C.). The surface of the fronds of young plants bears what are presumably glandular hairs. These are small club-shaped structures consisting of about three cells with dense granular contents.(Fig. 38, B). Similar hairs have been described as occurring on the fronds of Vittaria lineata.

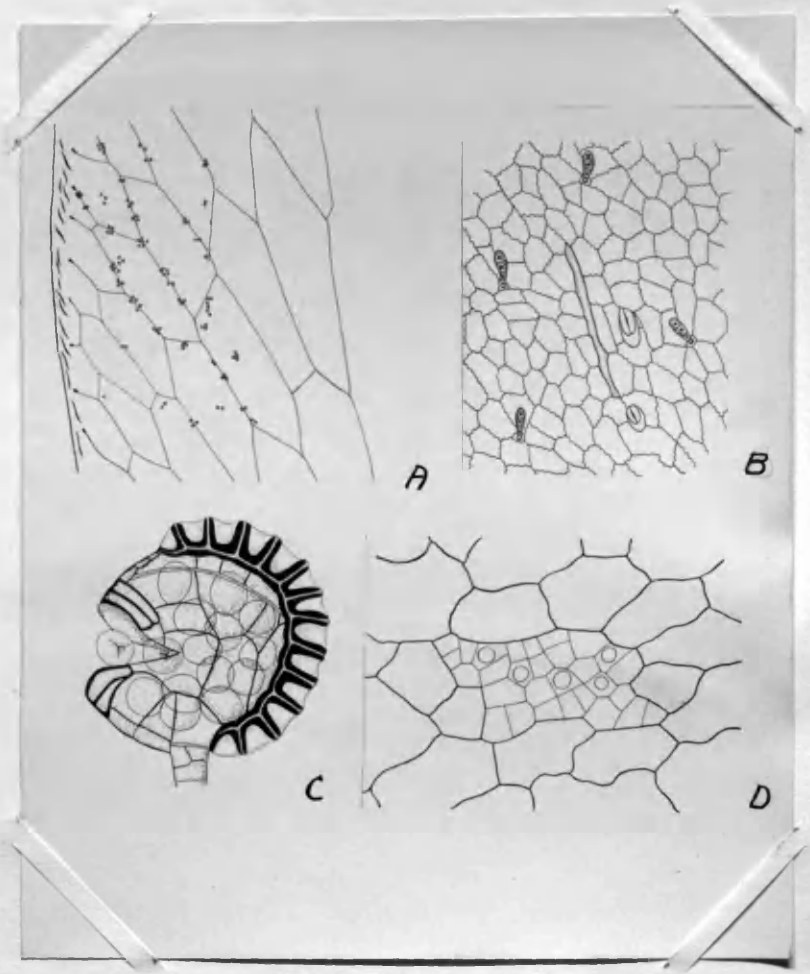


Fig.38. Anetium citrifolium. A, venation and sporangial distribution. X 4 . B, epidermis with stomata and a spicule cell. X 40 . C, sporangium. X 185. D, group of small cells from which the sporangia arise. X 185

Root Structure.

The roots arise in an irregular manner all round the ventral side of the rhizome. They resemble those of other Vittarieae in that they are densely clothed with brown root hairs. The structure of the root stele is exceedingly simple (Fig. 34, E). There are two groups of lignified elements each consisting of one or two tracheids and two small groups of phloem alternate with these. The stele is surrounded by a large celled pericycle and endodermis. The cortex is entirely parenchymatous.

Superficial Appendages.

The superficial appendages are very broad clathrate scales, (Fig. 37, B) very similar to those described for Antrophyum species but distinct from the latter in that they are much broader at the base and in that their walls are much less strongly thickened. As in the scales of Antrophyum species the cells at the base remain thin walled and give rise to rhizoid like structures.

Sporangia.

The arrangement of the sporangia is peculiar and anomalous and has attracted attention for a considerable time. The sporangia are inserted in small groups superficially both over the veins and on the intervening parenchyma of the areolae (Fig. 38, A). This arrangement led Fée and Mettenius to regard this form as a transition between Elaphoglossum and Polypodium punctatum in spite of its similarity in general appearance to Antrophyum. Each group of sporangia is situated on an area of very small cells, which arise, according to Frau Schumann(1), in the following manner. A group of three or four epidermal cells divide by walls parallel to the surface. In the outer cells cut off in this way anticlinal walls are formed so that a group of very small cells is produced.

1. Schumann, "Die Acrostichen und ihre Stellung im System der Farne" Flora N.F.8

It is from these cells, which possess densely granular contents, that the sporangia arise.

The individual sporangia are very small compared with those of Antrophyum (Fig. 38, C). They are short stalked, the stalk being three celled just below the capsule but tapering down to a single cell at the base. The annulus is vertical and consists of from twelve to fourteen cells. As in other Vittarieae the stomium consists of four cells and the epi- and hypo-stomium of two cells. The spores are tetrahedral in form. Spore counts yielded the numbers 29, 32, 30, and 46, indicating that there are typically 32 or 48 spores produced in each sporangium.

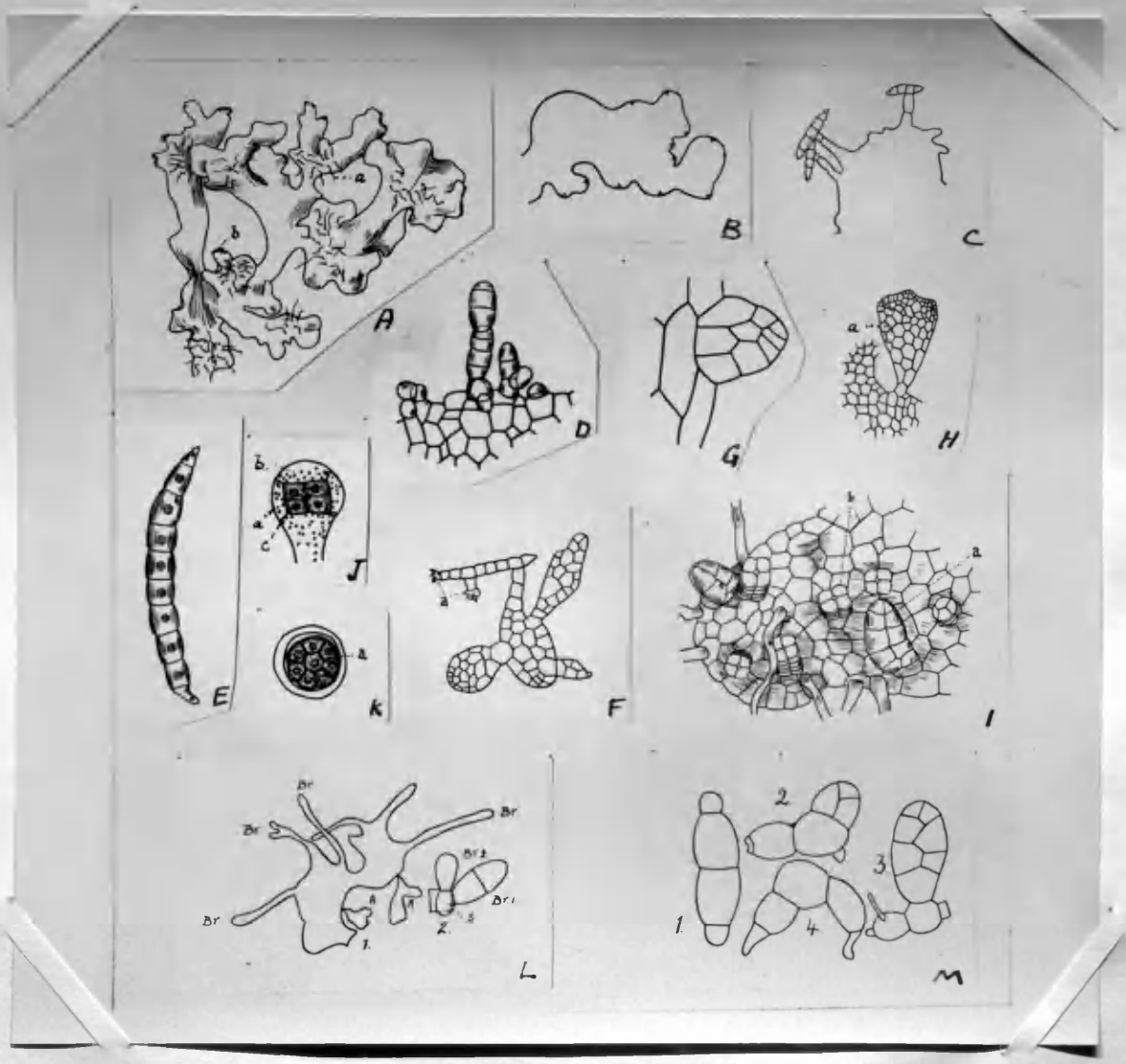


Fig.39. The gametophyte of the Vittarieae. A-K, Vittaria lineata z(after Britton and Taylor.) A, under side of a prothallium showing its irregular branching. a,rhizoids; b,sterigmata. B, a prothallium showing eleven growing points. C, prothallus showing gemmae. D,margin of prothallus with sterigmata. E,gemma. F, a gemma with two withered antheridia (a,a.) and a young prothallium, from the margin of which have arisen three prothallia. G, young prothallus starting from margin of old one. H, a young prothallium,a, with three growing points, starting from a single cell of an old prothallium. I, under side of wing of prothallium showing archegonia,a,b, the four stigmatic cells. J,antheridium; a,peripheral cell; b,cap cell; c,central cell dividing into the mother cells of the antherozoids. K, antheridium; a,mother cells. L and M, Hecistopteris pumila (after Goebel.) L, 1,prothallus; Br,gemma bearing lobes, A,adventitious prothalli. 2, sterigma (s) and young gemmae (Br.1 and Br.2.). M, 1,mature gemma; 2 and 3, gemmae which have formed young prothalli; 4, gemma, the end cells of which have grown out into short rhizoids.

THE GAMETOPHYTE.

The structure of the gametophyte of Ferns is so simple and shows so little differentiation in its tissues that it does not usually provide many characters of importance for systematic comparison. This is particularly the case in the more specialised groups of Ferns where the prothallus is almost always of the heart-shaped type, though liable to modification under the action of various environmental conditions. Prof.Bower (1) has already pointed out that " the form and physiology of the prothallus may provide material for comparison, though this is not very reliable since it varies readily and often directly with the external conditions."

The prothalli of the Vittarieae, in the three genera where they are definitely known, are epiphytic, and it is not surprising, in view of the plasticity already mentioned, that they all show characters divergent from the common cordate type. The prothalli of Vittaria, Monogramma, and Hecistopteris have been accurately investigated, chiefly by Goebel (2) and, in the case of V.lineata, by Britton and Taylor (3). In all of them the prothallus is a very irregularly lobed structure (Fig. 39,A,B,L.) consisting of a single layer of cells. The prothallus of Antrophyum is not yet definitely known. Goebel first described it as being heart-shaped but he was unable to be sure that the spores he had sown had not become mixed.

1.Bower,F.O.,Filicales,Vol.1,p.62.

2.Goebel, Ann.Jard.Buit.7,pp.78-87.

3.Britton and Taylor, Mems.Torrey Bot.Club,Vol.8.

In his latest publication (Flora,1924.) he states that he desires to leave the question open, but thinks it possible, in view of his belief that Antrophyum is relatively more primitive than the other Vittarieae, that the prothalli are heart-shaped as originally described. It appears safer, however, to await further information. The prothallus of Anetium citrifolium does not appear to have been described.

The following is a brief resume of the facts relating to the prothalli of Vittaria, Hecistopteris, and Monogramma.

The young prothallus is club-shaped in outline and its growth is entirely marginal. As development proceeds certain portions of the marginal meristem pass into a permanent condition and further growth takes place by a number of growing points separated from one another by the areas of permanent tissue.(Fig. 39, B.) This results in the formation of the markedly lobed outline of the mature prothallus.

The prothalli of Vittaria, Hecistopteris, and Monogramma all multiply rapidly by vegetative means, a feature which, as it is suggested by Britton and Taylor, may be useful in the case of epiphytic prothalli which are much subject to the attacks of small animals. In all three genera abundant and very characteristic gemmae are produced (Fig. 39, C,D,E.) Spherical or barrel shaped sterigmata, each usually consisting of two cells, arise at the margin and near the apices of the prothalli. At the tips of these sterigmata spindle shaped gemmae arise, each being composed of a varying number of moniliform cells. The gemmae become detached to give rise to new prothalli, the terminal cells often giving rise to rhizoids. The gemmae of V.lineata often bear antheridia before giving rise to the new prothallus.(Fig.39, F.)

In addition to the formation of gemmae the prothalli of Hecistopteris and Vittaxia readily proliferate and new prothalli grow out from marginal cells or from two or more lamellar cells of the parent prothallus.(Fig. 39, G.H.L.)

The archegonia appear to be of the usual Leptosporangiate type. In V.lineata they occur"on the under surface of the prothallus and also on the small lobes among the rhizoids"(Fig. 39, I.) In the Vittaria spp. described by Goebel the archegonia occur mainly between the lobes of the prothallus on the portions which have passed over into the permanent condition.

The antheridia are of the type usual for the more highly advanced Leptosporangiate Ferns and their development, in V.lineata at any rate, shows no features of particular interest. The prothallus of V.lineata is often pseudo-dioecious the archegonia being borne on the parent prothallus while the antheridia are produced on the gemmae formed from the same prothallus(Fig. 39, F.) In addition to the antheridia formed on the gemmae, others are produced on the lower surface, the margins, and occasionally on the upper surface of the prothallus. The only record of the number of spermatozoids produced in each antheridium is that of Britton and Taylor for V.lineata. In this species 12-24 spermatozoids are formed in each antheridium, this small number running parallel with the small number of spores produced in each sporangium.(1)

1. Cf. table on page 292 of Prof.Bower's Filicales,Vol.1.

STELAR PROBLEMS.

The steles of the Vittarieae have attracted attention for a considerable time on account of the fact that they frequently exhibit divergences from the more common types of Fern steles. Poirault, Jeffrey, Gwynne-Vaughan and Tansley have all given brief descriptions of the steles of various species of the Vittarieae and in all cases they regard the divergences from typical solenostelic or dictyostelic structure as being due to reduction. The occurrence of such anomalous steles has a direct bearing on certain questions of stelar morphology but before proceeding to discuss the problems involved it is necessary to define exactly what is meant by the term "reduction". The term, as usually used, implies the loss of tissues originally present, due, presumably, to a change in the physiology of the plant consequent upon a change of habitat. In the questions under consideration it is necessary to distinguish between :-

(a) Reduction which results in the diminution of the amount of xylem and phloem present in the stele, without, however, the general type of the stele being altered.

(b) Reduction which results in the disappearance of either the internal or external endodermis, thereby leading to an alteration of the type of stele.

Reduction appears to have affected the xylem of all the Vittarieae examined to the extent of reducing it to a ring of tracheids only one or two layers in thickness. The amount of phloem present is also small and consists entirely, so far as I have been able to distinguish, of small protophloem like elements, which, however,

have the typical structure of Filicinean sieve tubes. Here again it is probable that reduction has lead to a diminution in the amount of the tissue present. With reference to the absence of internal phloem on the ventral side of the stele in such forms as Antrophyum reticulatum and a number of Vittaria species, it is difficult to decide whether this is the result of reduction or whether it is due to the fact that the pocketing in of the phloem at the nodes has never extended to the ventral side of the stele. It is in any case a small point of no particular importance. The reduction in the amount of xylem and phloem may possibly be correlated with the epiphytic habit, but, so far as I am aware, the physiology of such forms with large fleshy leaves and relatively small axes has never been examined.

The main interest raised in this question of reduction centres round the curious forms of stele found in Antrophyum plantagineum and Vittaria elongata. The absence of internal endodermis in these steles is the critical point and the question raised is as to whether or not reduction is responsible for this absence with the consequent change in the type of stele. Poirault states in his description of the stele of Vittaria elongata "j'ai vu de même l'endodermis très distinct à la face externe de la stèle, tout à fait indistinctive à la face interne", and he states elsewhere that the internal endodermis has lost its distinctive characters. It is not altogether clear whether Poirault regarded the internal endodermis as having been present originally and lost by reduction or not, and apart from mentioning his statements they will not be brought further into the discussion. Jeffrey, however, definitely regarded the peculiar structure of the steles as "indications of

specialisation away from the usual tubular type of central cylinder" and it is clear that an actual loss of the internal endodermis by reduction was contemplated. Gwynne-Vaughan, as has been previously mentioned, has given brief descriptions of a number of Vittaria and Antrophyum species and he clearly regarded their steles as showing reduction, though he makes no definite statement as to its extent. This writer points out in his discussion of the primitiveness or otherwise of the Lindsaya type of stele that there are certain differences between the latter and the anomalous steles of the Vittarieae. These differences he regarded as important in the arguments advanced in support of the thesis that the Lindsaya type is primitive and that it has not arisen as a result of the reduction of a more complex type. It appears from the general trend of this argument that Gwynne-Vaughan actually regarded the anomalous steles of the Vittarieae as having resulted from the reduction of typical solenosteles and dictyosteles, the reduction involving the loss of the internal endodermis. Tansley has also stated that the anomalous steles under consideration are reduced structures.(The Filicinean Vascular System,p.65.)

There appears then to be a concensus of opinion that the steles of Antrophyum plantagineum and Vittaria elongata are modifications of more complex types of stele by reduction. Opinions have varied however, and, indeed, have never been really definitely stated, as to what weight can be given to this evidence in a consideration of the question of medullation and the related question as to the primitiveness or otherwise of the medullated protostele. The general question of the origin of the pith need not be entered into in this memoir ; the question and the solution have already received adequate attention elsewhere (1). The related question

1. Bower, F.O., Filicales, Vol. 1, p. 124 et seqq.

as to the primitiveness of the medullated protostele has also been satisfactorily settled on the basis of evidence derived from a study of the ontogeny of a number of different Ferns and from a study of the fossil record of the Osmundaceae. It is true, nevertheless, that while the belief is held that the stelar structure of forms such as Antrophyum plantagineum and Vittaria elongata has resulted from the operation of reduction processes leading to the loss of the internal endodermis, then these structures must be accepted as evidence as to the possibility of the medullated protostele being, in some cases at any rate, the product of reduction. The view that the medullated stele is the product of reduction is not now generally accepted but it is still upheld by Jeffrey. The latter writer states that " The simplest view, and that most in harmony with all the facts, seems to be that the medullated monostelic central cylinder, so strikingly characteristic of the more modern vascular plants, has been derived from an ancestral siphonostelic condition with internal phloem by reduction."(2) Elsewhere the same writer speaks of the origin of the medullated protostele from the siphonostelic condition " through the loss of internal phloem and endodermis."(2) It seems worth while therefore to discuss briefly the question as to whether in the steles of the Vittarieae reduction has lead to the loss of internal endodermis with the consequence that a medullated type of stele has arisen from a solenostelic or dictyostelic type.

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1. Jeffrey, l.c. p.143
2. Jeffrey, "The Anatomy of the Woody Plant", p.291.

If the endodermis has merely lost its distinctive characters, such as the Casparian strip, by reduction, then it might be expected that its position could still be detected by reason of the shape and definite arrangement of the line of cells, and, further, by the presence immediately inside it of a layer of pericycle, which latter layer is strongly developed in other Vittarieae. In neither Antrophyum plantagineum nor Vittaria elongata can any such indication of a degenerate endodermis be found. On the basis of this negative evidence one may conclude, though without certainty, that the internal endodermis has never been present in these steles and that consequently the similarity to a medullated protostele is not due to a process of reduction. It must be admitted, however, that this evidence is by no means conclusive for the endodermis in other species of the Vittarieae is very irregular and it is also possible that the internal pericycle has lost its distinctive characters.

More satisfactory evidence as to the real nature of the anomalous steles under consideration is provided by the facts relating to the ontogeny of Antrophyum reticulatum which have been described above. It is necessary to consider here the steles of Antrophyum plantagineum and Vittaria elongata separately. If we take A.plantagineum first and consider it in the light of the ontogeny of A.reticulatum a very important fact emerges. The solenoxylic condition of the stele of A.plantagineum is identical with the structure of the stele in some of the lower internodes of the young plant of A.reticulatum. This at once brings to mind similar examples, as for instance in the Schizaeaceae where the adult structure of the stele of Schizaea rupestris is very similar to

an ontogenetic stage in the development of the dictyostelic condition of Anemia phyllitidis. In this example it is now generally accepted that the stele of Schizaea rupestris is not a reduced structure but a primitive one. In A.plantagineum also it appears probable that the stele is either truly primitive or else it is simple as a result of "arrested development". It is probably impossible to decide with certainty which of these two alternatives is correct. Evidence from other criteria points to the conclusion that A.plantagineum cannot be regarded as a primitive type and it therefore seems probable that the stele of this form is simple by an arrest of the normal ontogeny which leads in other species to the establishment of the dorsiventral dictyostele.

The type of stele present in Vittaria elongata offers rather more difficulty. The structure of the stele of this species has not been observed in the ontogeny of related forms so that it cannot be explained as a simple arrested development. The dorsiventral dictyoxylic condition is, however, probably to be regarded as a further modification of the solenoxylic condition of A.plantagineum although it is off the usual track of ontogenetic development as described for other Ferns. The change from the solenoxylic to the dictyoxylic condition is probably consequent upon either an increase in the size of the leaf gaps, or else a shortening of the internodes. The size of the respective steles may also be one of the factors concerned ; this point will be mentioned again below.

The conclusion of the present writer is therefore that the somewhat anomalous steles of the two species just considered are not to be explained as having been derived from more complex steles by a process of reduction. The solenoxylic stele of

A.plantagineum is really an arrested development ; that of V.elongata is a further development of the A.plantagineum type along an unusual line, not progressing to typical solenostely or dictyostely but to a dictyoxylic condition. This conclusion, if it be correct, destroys evidence which has hitherto pointed to the possibility of explaining the medullated protostele as a reduced structure, derived from the solenostelic type of stele by the loss of internal phloem and endodermis.

There remain to be considered the steles of Monogramma and Hecistopteris. A comparison of these with the early stages of the development of the stele of A.reticulatum suggests at once that they are not reduced structures but that they may be reasonably regarded as arrested developments, the arrest having come into operation at an early stage.

The Operation of the Size Factor.

The Vittarieae present a series of forms which show in their mature rhizomes stelar structures ranging from protosteles in Monogramma and Hecistopteris to a perforated dorsiventral dictyostele in Anetium. It has been pointed out in the discussion of the stelar problems that some of the "simpler" types of stele may best be regarded as arrested developments of the normal ontogeny which leads in other forms to the dorsiventral dictyostele. This explanation is a purely morphological one and it raises at once the question as to possible causes of the arrested development in such examples. It seems worth while, therefore, to consider whether the Size Factor (1) is not one of the underlying causal factors leading to the variations in stelar structure observed in the Vittarieae. For this purpose measurements of the steles of the various forms examined were made and these are given in the table below. The diameter of the steles is given in cms., the measurements having been made under a magnification of 28.

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(1) For full discussions of the Size Factor the following literature should be consulted :-
Bower,F.O., "Size, a neglected Factor in Stelar Morphology." Proc.Roy.Soc.Edin.,Vol.XLI ; "The Relation of Size to the Elaboration of Form and Structure of the Vascular Tracts in Primitive Plants.", Proc.Roy.Soc.Edin.,Vol.XLIII.
Wardlaw,C.W., "Size in Relation to Internal Morphology." No.1, Trans.Roy.Soc.Edin.,Vol.LIII ; No.2, Trans.Roy.Soc. Edin.,Vol.LIV.

NAME	Diameter of stele in cms.	REMARKS.
Hecistopteris pumila	.15	Protostele with simple oval xylem mass.
Monogramma graminea	.4	Protostele, curved xylem mass.
Monogramma trichoidea	.4	do.
Monogramma paradoxa	.4	do.
Antrophyum plantagineum	2.0	Medullated protostele, solenoxylic.
Vittaria elongata	2.2	Medullated protostele, dictyoxylic.
Antrophyum lanceolatum	2.5	Dorsiventral dictyostele.
Antrophyum lineatum	2.5	do.
Vittaria lineata	3.0	do.
Antrophyum brasilianum	3.0	do.
Antrophyum reticulatum	4.0	do.
Anetium citrifolium	5.6	Perforated dorsiventral dictyostele.

The measurements given in the table indicate clearly that there is a correlation between the size and the complexity of the stele. The physiological significance of this correlation has already been fully discussed by the writers mentioned and therefore need not be entered into in this place. It has already been pointed out that the dorsiventral dictyostele is probably the central type of stele in the Vittarieae and that the anomalous steles of Monogramma, Hecistopteris, Antrophyum plantagineum and Vittaria elongata are arrested developments. The interesting point is that all the anomalous steles mentioned are smaller than any of the dorsiventral dictyosteles. It may be concluded then that the arrest of the ontogenetic development at various stages, viz. the protostelic stage in Monogramma and Hecistopteris and the medullated condition in A.plantagineum and V.elongata(1) is due to, or at any rate is correlated with, a decrease in the size of the stele. On the other hand, the most complex type of stele found in the Vittarieae, namely that of Anetium citrifolium, may reasonably be regarded as due to an increase in the size of the stele, although it must be pointed out that the dictyostelic condition is already evident in quite young rhizomes with relatively small steles.

The tracheids of the xylem in all the forms examined are disposed in narrow bands one, or at most two, tracheids in thickness. This arrangement ensures an adequate surface of contact between

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(1) The dictyoxylic stele of V.elongata is slightly larger than the solenoxylic one of A.plantagineum but it seems possible that the difference between these two is due to either an increase in the length of the leaf gaps or the closer insertion of the leaves on the rhizome rather than to the operation of the Size Factor, for there is practically no difference between the ratios of surface to bulk in these two steles.

the tracheids and living parenchymatous cells, a fact which appears to be of considerable physiological importance.(1) The small protosteles of Monogramma and Hecistopteris are of interest in this respect. That of Hecistopteris has very few tracheids and these are arranged in the form of an oval mass. In the rather larger steles of Monogramma where the number of tracheids is greater these latter are disposed in a narrow curved band, so that all the tracheids are still in contact with living cells. The form of the xylem mass in Monogramma differs from that in the protosteles of other Ferns where the tracheids usually form a cylindrical core and the necessity for maintaining the xylem in contact with living cells is met by intermingling parenchyma with the tracheids.

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1. See works already cited and "Some Points in the Anatomy of Dicksonia." (S.Williams, Proc.Roy.Soc.Edin.,Vol. XLV .

The Endodermis.

The endodermis in all members of the Vittarieae examined is in the primary condition (1), a condition which is unusual in the Filicales. Apart from the Vittarieae it is only found in the Ophioglossaceae, Marattiaceae, in Trichomanes and in certain "storage rhizomes" such as that of Dryopteris Filix-mas ; elsewhere the endodermis is in a secondary condition. Priestley and Radcliffe (l.c.) have suggested that the primary condition of the endodermis in the forms they examined is to be correlated with the entirely parenchymatous nature of the cortex and medulla.which is characteristic of these forms. They state in their conclusion that they are unable to suggest any reason for the failure of the endodermis to reach the secondary stage, but elsewhere they make the statement that " it seems more correct at present to consider the absence of the suberin lamella as responsible for the bulky, food packed rhizome than the presence of these food supplies as responsible for the absence of the lamella."

In the Vittarieae, as in the forms examined by Priestley and Radcliffe, the primary condition of the endodermis appears to be correlated with the entirely parenchymatous nature of the ground tissue. It is interesting to note that in the genus Pleuro Monogramma, a genus similar in habit and habitat to Monogramma though not related to it, the endodermis is secondary and the ground tissue

1. Priestley and Radcliffe, "A Study of the Endodermis in the Filicineae.", New Phyt., Vol.XXIII. These writers distinguish between :- (a) Primary Endodermis, with Casparian strip and (b) Secondary Endodermis, with a suberin lamella.

practically entirely sclerenchymatous. It seems probable then that the nature of the endodermis and the histological nature of the ground tissue are bound together by some physiological tie although the nature of this latter is entirely unknown.

The failure of the endodermis to reach the secondary stage may be bound up in some way with the reduction phenomena which have lead to a decrease in the amount of phloem and xylem present in the Vittarieae. The lack of data with regard to the physiology of such forms as the Vittarieae precludes, however, any attempt to suggest any of the causal factors leading to this reduction.

Taxonomy and Affinities of the Vittarieae.

The first question for consideration is as to whether the Vittarieae is a homogeneous group or not. The work of Goebel and Benedict and the facts detailed in this memoir indicate that the grouping together of the genera Vittaria, Monogramma (limited to the Eumonogramme section), Antrophyum, Hecistopteris and Anetium is a very natural one. Evidence that this is so is afforded by a number of criteria :-

(a) The anatomy of the five genera is based on a common plan. In all the species examined the endodermis is in the primary condition and possibly correlated with this is the fact that sclerenchyma is entirely absent. The most common type of stelar structure is the dorsiventral dictyostele ; modifications of this type, which have already been discussed, are found in some of the genera.

(b) The sporangia in the five genera are all very similar, possessing, as they do, a four celled stomium, an epi- and hypostomium each of two cells , and stalks which are always one celled below but several celled just below the capsule.

(c) They all possess clathrate scales. These are characteristic for each genus but underlying common features are present in all.

(d) They all possess spicule cells.

(e) All the fronds, except those of Hecistopteris and Monogramma, show a reticulate venation.

(f) The roots bear numerous brown root hairs, although this character is probably to be correlated with the epiphytic habit of the plants.

(g) The gametophyte generation, in such forms as have been examined, is divergent from the normal type, being deeply lobed and

characterised by the occurrence of vegetative budding and the formation of gemmae.

Although at the present time attempts to place even genera in phylogenetic relation with one another is viewed with suspicion yet the present writer feels that it is worth while to endeavour to indicate the possible lines of development of the structural features characterising the group of genera under consideration. Goebel holds the view that Antrophyum represents the most primitive condition within the group and that the other genera are derivative from this along a number of lines. The evidence advanced in support of this view does not appear to the present writer to be conclusive and it seems unlikely that Antrophyum, with its sporangia distributed over the whole leaf surface, is a primitive form. It seems, indeed, far more probable that the structural features of Vittaria are the most primitive within the group. The anatomy, the character of the dermal appendages, the construction of the sporangia are all so constant in Antrophyum and Vittaria that they do not give much help in deciding which of these two genera is the more primitive. The arrangement of the sporangia in slightly intramarginal lines in Vittaria is, however, certainly more primitive than the sporangial arrangement of Antrophyum. Spore counts, while of proved value in the treatment of more primitive groups, are not so valuable in the consideration of such an advanced group as the Vittarieae. It is, however, the case that Vittaria has the largest number of spores per sporangium, viz.64, and this fact supports the view that Vittaria is relatively primitive. Moreover, Vittaria appears to offer a more favourable opportunity of linking the Vittarieae with other groups of genera.

Monogramma appears to be closely related to Vittaria and it is probable that Goebel's view that the structure of Monogramma has been arrived at by an arrest of the development of Vittaria characters is correct. M.paradoxa appears to offer the closest link, particularly if the drawings of Benedict of the venation of large fronds be correct. In these latter there is practically a typical Vittaria-like venation and sorus arrangement. In smaller fronds there has been an arrest of the ontogeny and the venation is simpler, showing a sympodial dichotomous scheme similar in essentials to that present in the fronds of young plants of Vittaria. M.graminea appears to offer the last stage of arrested development and the frond has only the mid-rib present, i.e. the same structure as the first formed fronds of the seedlings of Vittaria species. It has also been pointed out in the discussion of stelar problems that the steles of Monogramma species may be regarded as arrested developments of the dorsiventral dictyostelic type of structure which is characteristic of Vittaria species.

An advance upon the condition of such forms as V.lineata and V.elongata in the direction of a more complex venation is offered by V.(=Pteropsis) angustifolia, where, although the sporangia are still arranged in slightly intramarginal lines, there are several rows of meshes on each side of the mid-rib and, where the marginal areolae are small the sporangial groove may extend over the whole of the mesh. This condition leads on very naturally to the structure of Antrophyum with its characteristic reticulate venation of several rows of areolae and the distribution of the sporangia along the vertical veins of the meshes. Several points indicate that the characters of the section of Antrophyum with the sporangia immersed

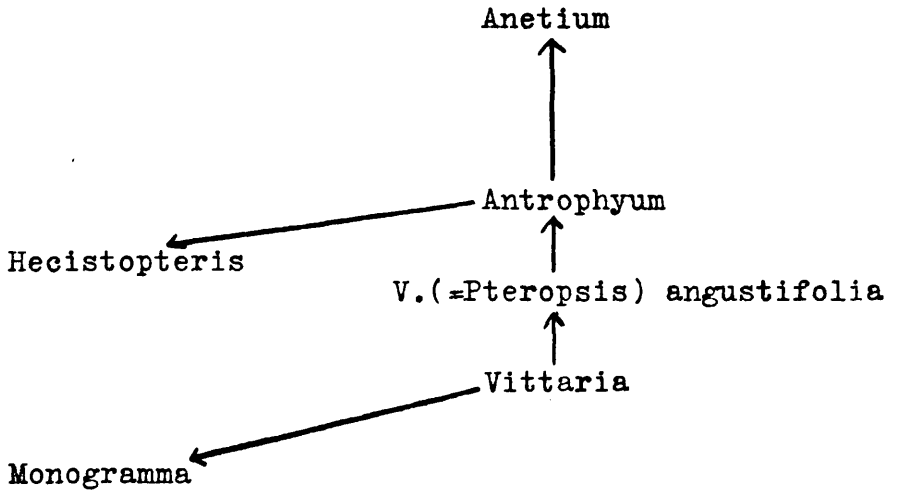
in grooves are more primitive than those of the section with the sporangia borne superficially on the surface of the frond. For instance spore counts obtained from species in the latter section indicate that the typical spore output per sporangium is smaller than counts obtained from species in the former section. Another point is that the stelar construction of such a form as A. subsessile grasilianum is more complicated than any seen in species of the first section. Finally the condition of having the sporangia naked on the surface of the frond may on general grounds be regarded as derivative from the protected condition.

The sporangial distribution characteristic of A. subsessile grasilianum and other species in the same section leads on naturally to the acrostichoid condition of Anetium citrifolium. This latter stands considerably apart from the rest of the Vittarieae and is certainly a very advanced form. The nature of the dermal appendages, the structure of the sporangia and the presence of spicule cells are all points of resemblance to the other genera of the Vittarieae. It is in the sporangial distribution and in its stelar morphology that the genus shows a considerable divergence from the other forms. The presence of sporangia not only on the veins but also on the parenchyma of the areolae is a marked advance on the condition say of A. subsessile grasilianum. The stele of Anetium is also much more complex than that of any other genus. Finally, its advanced condition is indicated by the small spore output per sporangium.(32 or 48).

There remains only to be considered the position of Hecistopteris. Goebel has put forward the view that the curious features of this genus are the result of an arrest of the development of the structures characteristic for Antrophyum, and the facts seem to

justify this view. The open dichotomous venation may reasonably be held to be due to the arrest of the development of the reticulate venation of other genera since the fronds of young plants of Antrophyum, Vittaria and Anetium show a similar type of venation. The forked outline of the leaf itself offers more difficulty but this is at least partially removed by a consideration of the fact that seedling leaves of Antrophyum are sometimes not simple in outline but dichotomously branched following the outline of the venation. One point against the view that Hecistopteris is allied to Antrophyum is that the clathrate scales of the former more nearly resemble those of Vittaria than they do those of Antrophyum for they have no unicellular outgrowths from the basal cells such as the scales of the latter genus exhibit.

The suggested relationships between the five genera of the Vittarieae may be expressed diagrammatically as follows :-



The conclusions reached above with regard to the relationships of the genera of the Vittarieae confirm Diel's arrangement of this group in the Pflanzen-familien. That writer divides the group into the Vittariinae including Monogramma and Vittaria and

the Antrophyinae including Hecistopteris, Antrophyum and Anetium. The only criticism of this arrangement is as to whether it would not be better to remove Anetium from the Antrophyinae and place it in a separate section on account of its anomalous and advanced structural features. The present arrangement is, however, sound in that it indicates the affinity of Anetium with Antrophyum.

The relation of the genera to one another above outlined seems fairly clear and justified by the facts. It is, however, a matter of considerable difficulty to make any definite statement about the phyletic relation of the Vittarieae as a whole with other and more primitive forms, and any such statement would certainly be open to the criticisms which have been levelled against phyletic morphology in general during recent years. Nevertheless, the data now available concerning the Vittarieae seem to justify at any rate tentative suggestions being made as to the affinities of this group with other forms. Such suggestions must, however, be regarded as a contribution to a natural classification of the Ferns under consideration and not as an attempt to link phyletically any forms now living.

Benedict has suggested that the Vittarieae are related to the Pterideae and Asplenieae, basing his conclusions on the nature of the scales and the sporangial arrangement. This view does not seem to be based on a sufficiently broad consideration of the criteria which have been proved to be useful in endeavours to build up a natural classification and the present writer finds himself unable to support this view. Such a consideration of a number of criteria may now be made.

A. Arrangement of vascular tissue.

The very frequent occurrence of dorsiventral dictyosteles and steles related to this type in the Vittarieae leads to an inquiry as to the prevalence of this type of stelar structure in other genera. A consideration of this point shows that such steles are most common in such genera as Adiantum, Gymnogramme, Cheilanthes and Pellaea (See Gwynne-Vaughan, l.c. and Marsh, Ann.Bot.1914.), a group of genera which Prof.Bower has already shown to form a natural and homogeneous group. It is also noteworthy that the anomalous type of dorsiventral dictyostele found in some mature rhizomes of Antrophyum reticulatum finds a very close parallel in the stelar structure of Cheilanthes lendigera. Two other points in the anatomical construction of Pellaea and Cheilanthes may be mentioned. In neither Pellaea nor Cheilanthes is any protoxylem distinguishable ; this also holds for all the Vittarieae examined. Secondly, in the species examined by Marsh, the phloem always consists of small elements corresponding to the protophloem of other Ferns; the nature of the phloem in all the Vittarieae examined is comparable to this.

B. Spicule cells.

The presence of spicule cells has proved to be a very constant feature of the Vittarieae. The only other genus in which such structures have been recorded is Adiantum. Poirault (l.c. p.208) gives a detailed account of their occurrence in a large number of species of this genus. The appearance of the spicule cells in such species of Adiantum as I have examined is very similar to that of the spicule cells of the Vittarieae.

C. Clathrate scales.

Scales of very similar appearance to those of Vittaria

are present in Adiantum macrophyllum but the data with respect to this character are very scanty. It must be noted, however, that Benedict found clathrate scales present in the Pterideae and Aspleneae though he does not state in which genera they occur.

(d) Venation.

Reticulate venation is a character which has developed in a number of circles of affinity and it is therefore a character which is not of much value for tracing relationships. The venation of the fronds of young Fern plants is always based on a dichotomous plan so that it also is not usually a very good guide to affinity. The Vittarieae, however, are almost unique in so far as the first formed frond is single veined in all the genera with the possible exception of Anetium. So far as I am aware the only other genus which possesses a single veined cotyledon is Ceratopteris. Indeed, the whole ontogeny of the frond of the latter genus resembles very closely that of some of the Vittarieae.

(e) Sporangia.

The structure of the sporangium of advanced Ferns is relatively constant and accordingly is not a very good character for comparative purposes when dealing with such advanced types as the Vittarieae. It may be noted, however, that the sporangia of Adiantum species, e.g. A.polyphyllum, and of species of Pellaea, e.g. P.cordata, are similar to those of the Vittarieae in having a four celled stomium. The marked and apparently characteristic instability of the characters of the annulus and stomium of Cheilanthes, Gymnogramme, Pellaea and Ceratopteris does not, however, find any parallel in the Vittarieae. The sporangia of the latter are very constant in their characters.

The structure of the stalk of the sporangia of the Vittarieae seems constant, with small variations, within the group. The curious dilation of the stalk immediately below the capsule may, however, be directly correlated with the protection of the sporangia in deep grooves and the consequent necessity for a special mechanism to ensure the successful scattering of the spores. That this is so is indicated by the fact that the dilation is greatest in those species with deep sporangial grooves and least marked in those where the sporangia are superficial. If this direct correlation exists, it is unlikely that the stalk characters will be of much use in tracing affinities in the group under consideration.

(f) Arrangement of sporangia.

The examination of the ontogenetic development of the sorus of V.lineata above described indicates that the origin of the sorus is slightly intramarginal. In this respect it resembles Cheilanthes and Ceratopteris and differs from the Pteroid series.

Taken in conjunction, the above points of contact between the Vittarieae and the group of genera including Adiantum, Cheilanthes, Pellaea and Ceratopteris may be held to point to an affinity between the former and the latter. Some of the points such as the presence of spicule cells and clathrate scales are admittedly small but when they run parallel with more important points such as the stelar construction and the origin of the sorus, they may reasonably be regarded as being of some value for comparative purposes. It seems probable that the condition of Adiantum presents the nearest point of contact with Vittaria but, on the facts available, there seems no good ground for assuming that there is any direct phyletic connection between them. The soundest conclusion appears to be

that the Vittarieae must be placed in any natural classification along with the complex of genera containing Adiantum, Gymnogramme, Cheilanthes, Pellaea and possibly Ceratopteris. It does not fall to the present writer to discuss the origin of this complex since this has already been dealt with by Prof. Bower.

A. Vittaria lineata.

B. Vittaria elongata.

A. Monogramma paradoxa.

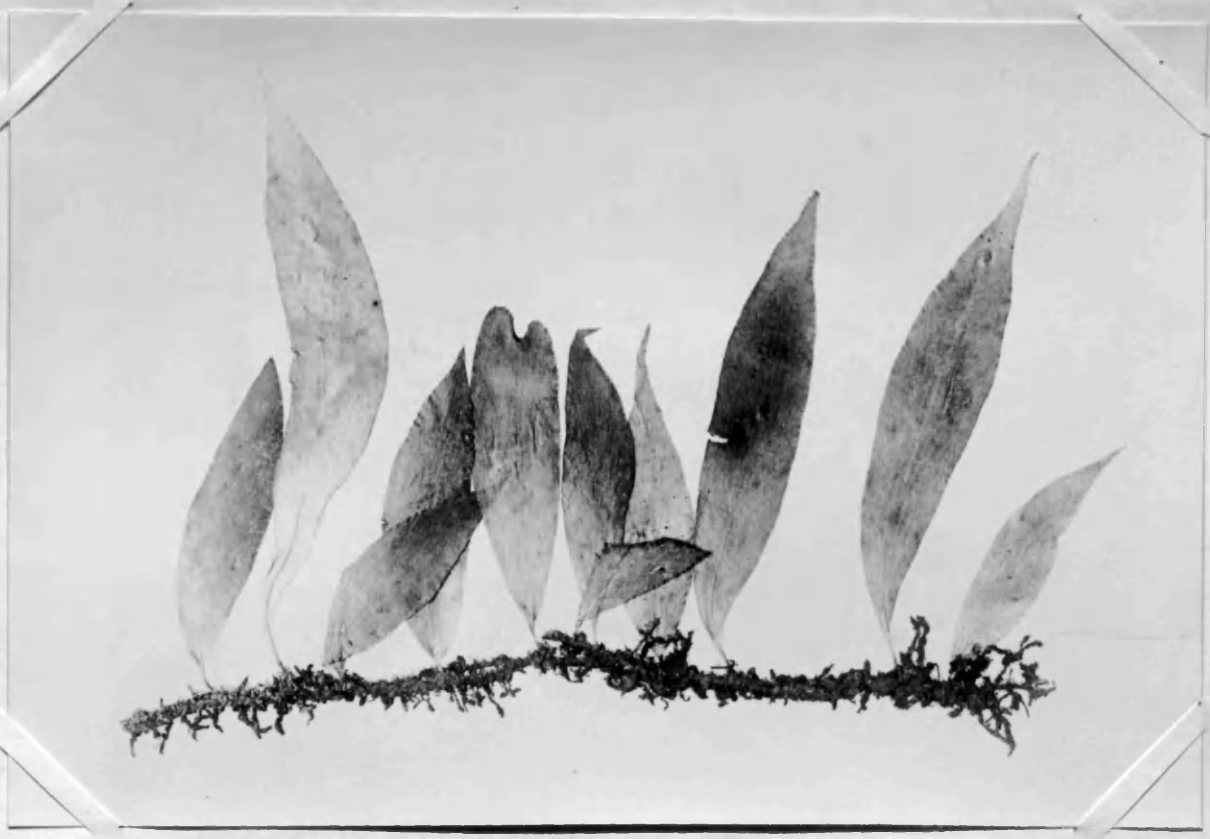
B. Monogramma graminea.

A. Antrophyum lineatum.

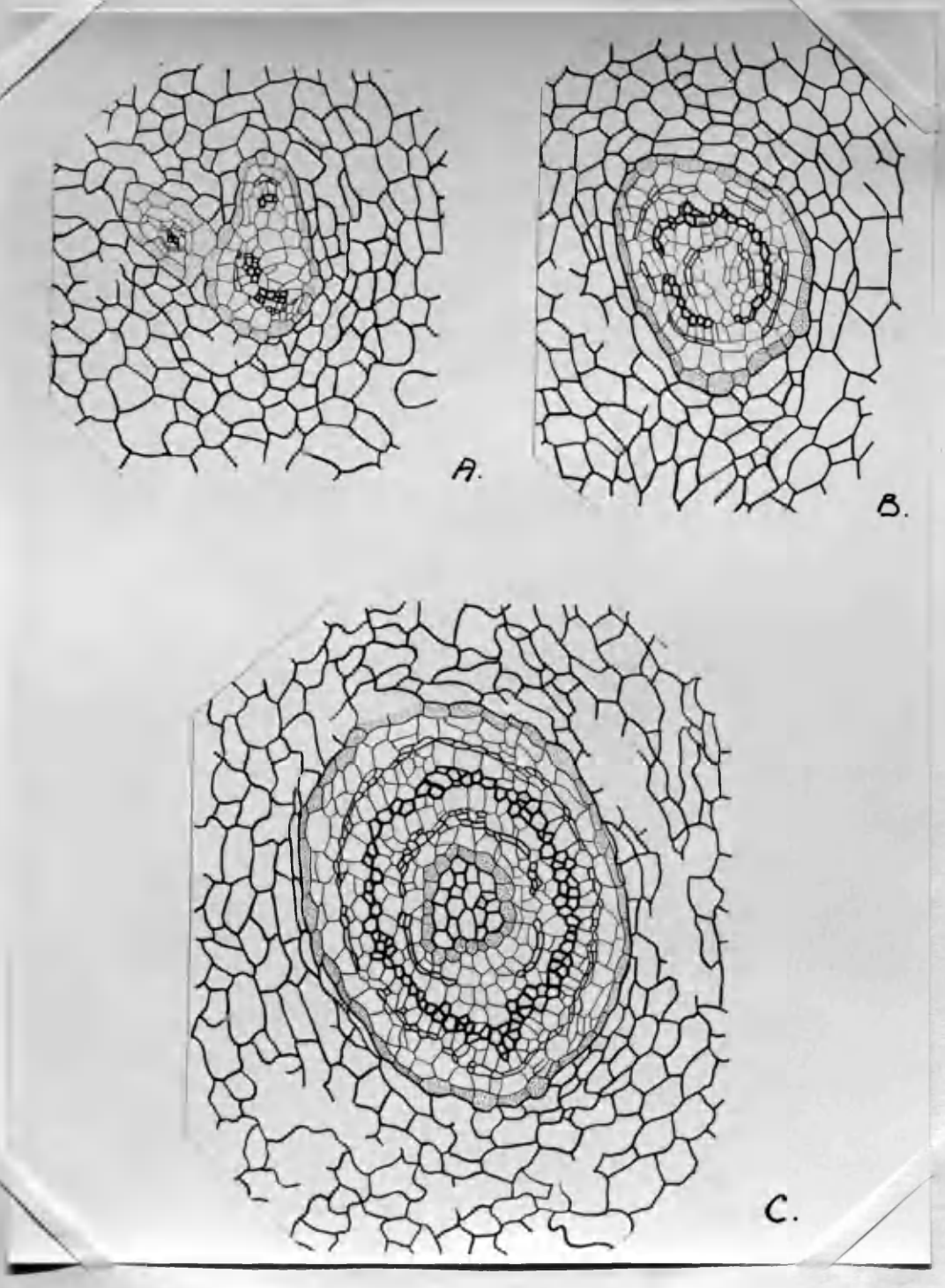
B. Antrophyum reticulatum.

A. Antrophyum plantagineum.

B. Hecistopteris pumila.



Anetium citrifolium.



Antrophyum reticulatum. Steles of young plant at different levels. For description see text.

Anetium citrifolium. Arrangement of vascular strands in the first internode and node behind an apex.(Apex to the right.)

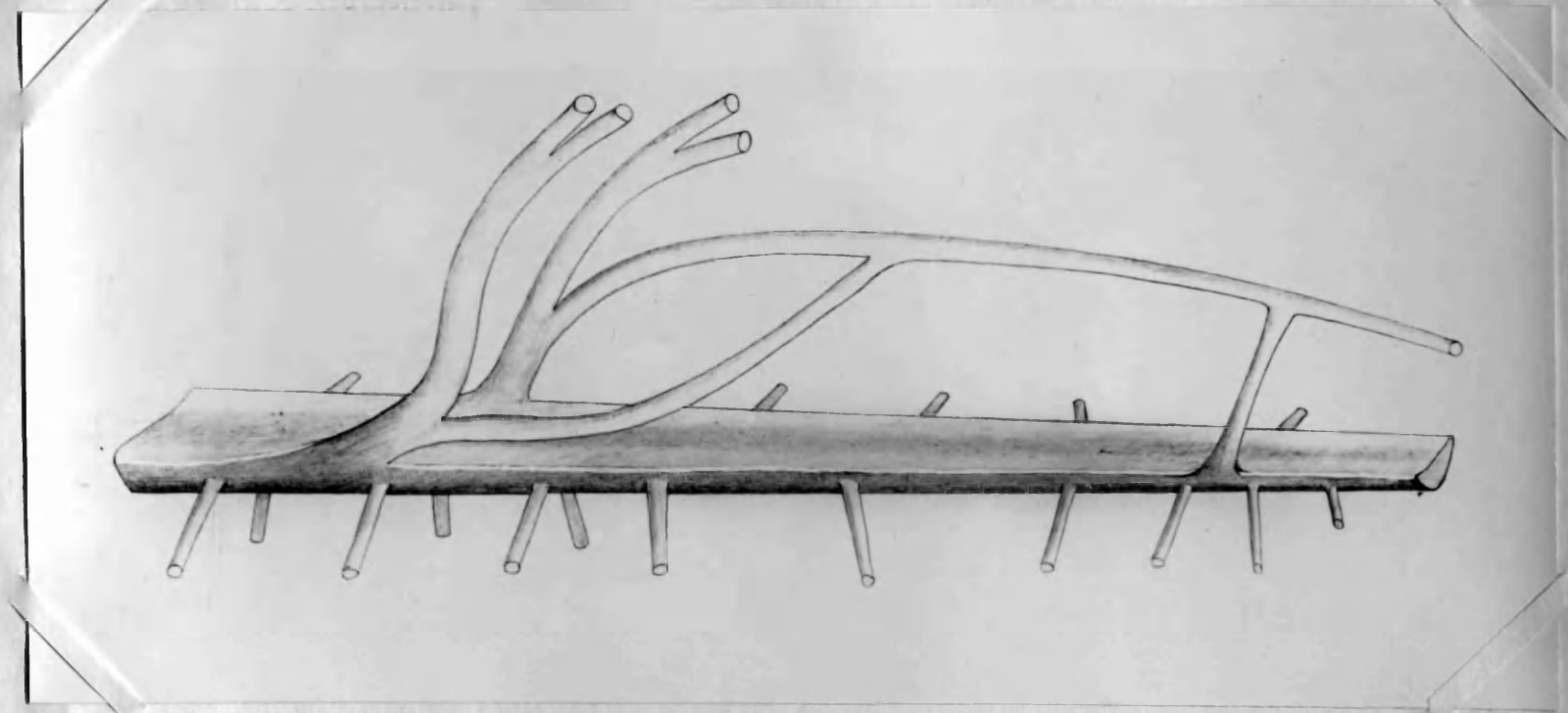


PLATE VII

Antrophyum lineatum. Portion of dorsiventral dictyostele showing two closely placed nodes.

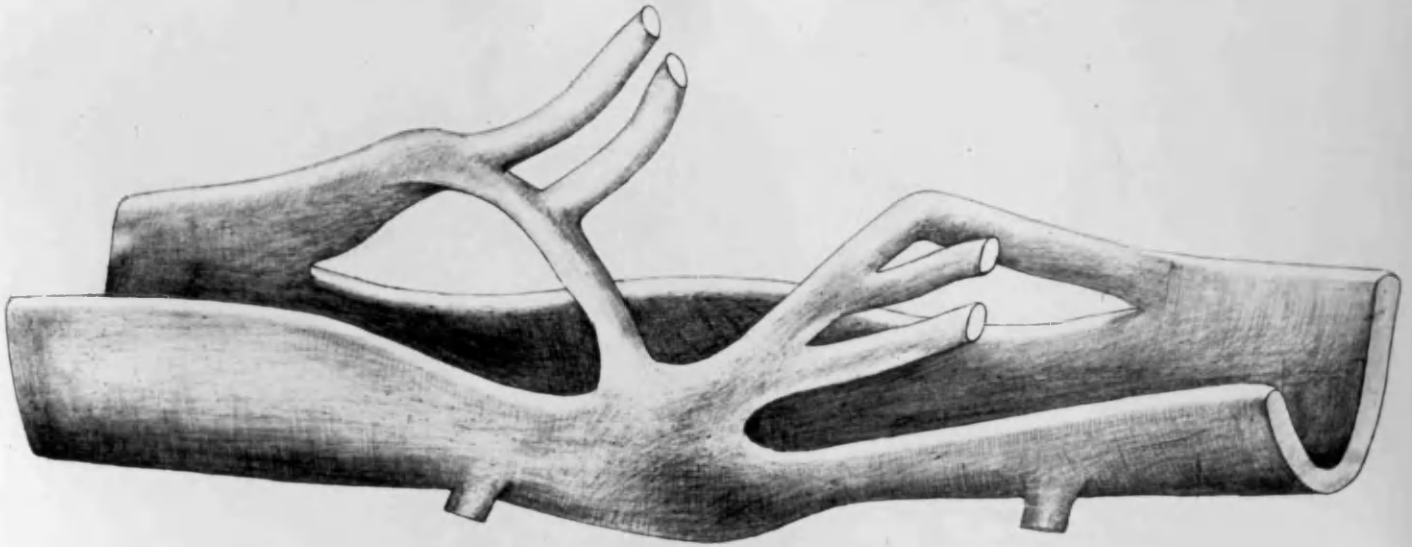


PLATE VIII