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IV. *The Structure and Development of the Stem in the Pteridophyta and Gymnosperms.*

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Communicated by Dr. D. H. Scott, *F.R.S.*

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[Plates 1–6.]

A comparison of the taxonomic criteria employed for the higher animals and the higher plants respectively results in a striking contrast. Abundant use is made of skeletal characteristics in the classification of the Vertebrata, while such features are employed to a comparatively insignificant extent in the systematic grouping of the Vasculares. The value of the osseous skeleton of the higher animals in determining their affinities has been recognised since the beginning of the last century. It is only comparatively recently, on the other hand, that the fibro-vascular skeleton of the Vasculares has been discriminatingly used for phylogenetic purposes. The Brongniartian school of palæobotanists considered the possession of secondary woody growth to be an important indication of phænogamous relationship, and on this ground grouped the Calamites and Sigillarians with the Gymnosperms. A study of the very characteristic primary wood, as well as other less-important features in these two orders, led Williamson and his successors to put the Calamites with the Equisetales and the Sigillarians with the Lycopodiales. These conclusions have been fully confirmed by the subsequent discovery of typical heterospory in the two groups. The above examples will serve to illustrate the value of the *primary* fibro-vascular skeleton from the phylogenetic standpoint.

Palæobotanists have thus led the way in the proper taxonomic use of the fibro-vascular skeleton; but from the very nature of their material they have not been able to any extent to use development as a phylogenetic key. Developmental studies which have been so fruitful in zoology have been almost entirely neglected by the Botanist in the case of the sporophyte of the various groups of the Vasculares. Here, again, we owe to a Palæobotanist the suggestion of the necessity of cultivating this field (D. H. Scott, 'Presidential Address, Section K, Brit. Assoc.,' 1896). A

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preliminary account of the writer's investigations on the development of the sporophyte was read by Professor Ramsay Wright at the May meeting of the Royal Society of Canada, 1896 ("A Theory of the Morphology of Stelar Structures," 'Proceedings of the Royal Society of Canada,' p. 106). A further abstract was published in 1897 ('Report Brit. Assoc., Toronto,' 1897). On account of the extent of the subject and the difficulty of securing material of fossilized and tropical forms, it has been necessary to publish the work in parts. The first of these appeared in 1899, and was devoted to the Equisetaceæ ('Boston Nat. Hist. Memoirs,' vol. 5, No. 5). The second, published in 1900, dealt with the Angiosperms ("Morphology of Central Cylinder in the Angiosperms," 'Canadian Inst. Trans.,' vol. 6).

It is proposed to deal in the present memoir with the remaining Vasculares, and to draw such theoretical conclusions concerning vascular plants in general as seem justified by the facts described in the present and former articles. It will be convenient to consider first the Filicales, and subsequently the Lycopodiales and Gymnosperms.

The investigations recorded here have been rendered possible by the kindness of many botanists in supplying material otherwise inaccessible to the writer, and acknowledgment is made of these favours in connection with the various groups.

I. Filicales.

Marattiaceæ.—The fibro-vascular system of the Marattiaceæ is very complex in the adult. By study of the young plant, however, it becomes easily intelligible. Photograph 1, Plate 1, reproduces a cross-section of a young stem of *Danæa alata*. Two roots are to be seen embedded in the parenchyma of the stem, and as well the crescentic central cylinder of the stem itself. The centre of the parenchyma in the midst of the crescentic central cylinder is occupied by two confluent mucilage ducts; the aperture of the crescent is a foliar gap and, opposite it, is to be seen the root corresponding to its leaf. The other root visible in the section is related to another leaf. Photograph 2, Plate 1, represents a transverse section of the same stem at a higher point. The tubular central cylinder is interrupted at two opposite points. On the right is present the lower end of a foliar gap which is subtended by the root corresponding to its leaf. On the left are to be seen two foliar traces passing off and subtending a foliar gap in the tubular central cylinder. A mucilage duct is present opposite and between the two traces. Mucilage ducts passing out of the pith to accompany the leaf-traces are a constant feature of the Marattiaceæ. Photograph 3, Plate 1, shows a still higher plane of section. On the right hand are two foliar traces subtending a gap in the tubular central cylinder of the stem. Between the leaf-traces lies the root corresponding to the leaf in question. On the left may be seen two other leaf-traces together with their accompanying mucilage duct.

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The foliar gap has not yet opened on this side. A vascular strand is fused with the inner wall of the stelar tube just above the region where the foliar gap is about to appear. A single medullary strand makes its appearance at this stage, which fuses with the wall of the tubular stele immediately above the foliar gap. Photograph 4 shows the stem at a higher plane of section. The general topography is much the same as in the last. On the right is the foliar gap with two leaf-traces, and a root subtending it. On the left the medullary strand is fusing with the wall of the stelar tube above the foliar gap of the next lower leaf, and a root is being given off corresponding to this leaf. Above the root in the photograph appear the upper ends of the two traces of the leaf in question accompanied by their mucilage duct. The root corresponding to a leaf sometimes passes out to one side of the foliar traces and sometimes between them. Both these conditions are exemplified in the case of the traces of the two leaves indicated in this section. Photograph 5, Plate 1, represents another plane of section. The medullary strand is running free in the medulla of the tubular central cylinder. A little lower down it will become fused with the wall of the tube again above the next lower leaf gap. Photograph 6, Plate 1, illustrates the condition of the stelar system in a much older stem. There are now three series of fibro-vascular strands. The outermost series consists of separate bundles. In the middle series the fibro-vascular tissues are confluent. The innermost series is formed of three strands which in other planes of section often form a tube. The innermost system of strands becomes fused with the middle one just above the point of exit of a root. From the middle series of strands, two roots are passing off. It will be seen from the above photographs that the young stelar system of *Danæa alata* is primitively a fibro-vascular tube interrupted by foliar gaps. At a later stage a medullary strand appears which joins with the wall of the stelar tube above the foliar gaps. Later the medullary strand becomes a tube or a series of strands. Subsequently the arrangement of the stelar system is further complicated by the appearance of another zone or series of strands. The stelar development described here, closely resembles that of *Pteris aquilina* as described by the writer ("Morph. Central Cylinder of Angiosperms"). Mr. Seward considers that the concentric series of strands which are characteristic of Matonia are formed in a similar way. ('Phil. Trans.,' B, Vol. 191. Also a letter to the writer March 13, 1901.)

I wish here to express my great obligations to Dr. C. C. Bell and to Mr. Fawcett, Director of the Jamaica Gardens, for very kindly supplying the material of the species here described.

Through the kindness of Dr. D. H. Scott and Professor George Brebner, I have had the opportunity of investigating some young plants of *Danæa simplicifolia*. Photograph 7, Plate 1, shows the tubular central cylinder of the young stem in this species interrupted by a foliar gap subtending a leaf-trace and its corresponding mucilage duct. Photograph 8, Plate 1, is of a section through an older region of

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the same stem. The foliar trace is now double and instead of originating from the bottom of the foliar gap as is the case with the single trace of the younger stem, its halves arise from the sides of the gap. Photograph 9, Plate 2, shows a later phase where a medullary strand has made its appearance. This strand fuses with the wall of the stelar tube in the same way as that described in the case of *D. alata*. The young stems in my possession do not show a greater complexity of stelar arrangement than that described above.

Through the kindness of Professor D. H. Campbell I have been able to examine young stems of *D. elliptica*. The youngest region of the stem had already disappeared, but the arrangement of the fibro-vascular tissues appears to be substantially the same as that described in *D. alata* and *D. simplicifolia*.

In the young stems of the species of Danæa described, the internal phloem is as well developed as that on the outside of the central cylinder. The phlœoterma is characteristically present in the younger region of the stem, both internally and externally. Higher up the *internal* portion tends to degenerate, but the outer part is still clearly distinguishable. The primitive medullary strand is generally surrounded by a well marked phlœoterma.

I have not been able to secure any young plants of *Marattia* grown from spores. Photograph 10, Plate 2, reproduces a cross-section through the base of an adventitious plant growing out of the swollen base of the petiole of a large plant. On the right is a foliar gap subtended by a single leaf-trace. Higher up this splits into two. On the left is another foliar gap, and opposite it may be seen the base of its corresponding leaf. Still higher up in the young plant medullary strands pass inward from the walls of the primitively tubular central cylinder, and the final arrangement of the fibro-vascular strands is extremely complex. Kühn has given an account of some rather advanced young plants of *Marattia fraxinea*. In these the earliest formed region of the stem had probably disappeared, for the stelar tube is ('Inaug. Dissertation,' Marburg, 1899, p. 23 and p. 50) represented as formed of a number of separate strands. In his youngest specimens a medullary strand was already present, having practically the same relation to the tubular central cylinder as described above for the genus Danæa. Kühn's figures of transverse sections of the old stem of *Marattia fraxinea* closely resemble in the arrangement of the strands that of *Danæa alata* shown in Photograph 6, Plate 1.

I owe to Professor J. Bretland Farmer the opportunity of investigating some young plants of *Angiopteris evecta* from Ceylon. Unfortunately these proved rather too young for the present purpose, since the central cylinder had as yet hardly passed into the tubular condition. Photograph 11, Plate 2, represents a section through the upper part of the oldest of these stems. There is a leaf-trace present on the left, while in the centre of the section is to be seen the tubular central cylinder. The vascular tissues are arranged in a tubular fashion with a gap corresponding to the leaf-trace. No medulla of fundamental tissue has yet made its appearance. The

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centre of the stele is occupied by phloem, as is commonly the case in young stems of ferns with the so-called polystelic type of fibro-vascular arrangement. While in London, I had the opportunity of examining some sections of older specimens in Professor FARMER'S possession, and was able to confirm the statement of DE BARY, that in the young plant the fibro-vascular system consists of a Bündelrohr with foliar gaps as described above for *Danæa* and *Marattia*. I have not been able to make any personal observations on the Marattiaceous genus *Kaulfussia*, but this matters the less because KÜHN has given a full account of it. (*Op. cit.*, p. 2.) Its creeping rhizomes appear to retain permanently the condition found in the younger stems only of *Danæa* and *Marattia*, for its stelar system remains throughout a tube with a medullary strand, such as has been described above for young specimens of those genera.

It will be apparent from the account given in the foregoing paragraphs that the complexity of arrangement which is characteristic of the fibro-vascular system of the adult Marattiaceous ferns may be traced back to a primitive condition where there is present a stelar tube interrupted by foliar lacunæ. The significance of this result will be discussed subsequently.

Osmundaceæ.—It will be convenient to consider certain anatomical features of the Osmundaceæ before referring to the development of the stem in this group. Photograph 12, Plate 2, shows the structure of the central cylinder in the stem of *Osmunda cinnamomea*. The cylinder is surrounded by a tanniniferous endodermis. The vascular bundles are separated from each other by parenchymatous medullary rays. The phloem forms a continuous sheath, as is stated by DE BARY, and is not interrupted opposite the medullary rays as has been affirmed by STRASBURGER. Inside the bundles there is present a zone of parenchymatous tissue which is continuous with the medullary rays. This zone is bounded inwardly by an internal endodermis. The pith in the present example consists entirely of parenchymatous cells, which are similar in their contents to those of the cortex outside the central cylinder. Photograph 13, Plate 2, is of another less mature specimen. The tannin containing outer endodermis is well marked. The internal endodermis is much less obvious. In this example some of the cells of the pith are brown sclerenchymatous elements identical with those of the external cortex. Photograph 14, Plate 2, shows a section through a more mature part of the same stem. The tannin has become more abundant in the internal endodermis, and a large mass of brown sclerenchyma is present in the pith.

Photograph 15, Plate 2, represents a stem of *O. cinnamomea* in the region of forking. It is obvious that the internal and external endodermal layers become continuous through the ramular gaps, and that the phloem which, as a rule, is present only on the outside of the central cylinder, here passes for a considerable distance round on the internal surfaces of the crescentic central cylinders of the branches. Between the latter the external cortex sends down a tongue of brown sclerenchy-

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matous tissue. Photograph 16, Plate 2, shows the same stem at a region a little behind the fork. The central cylinder has become elongated laterally, preparatory to bifurcation. The pith has the same configuration and its centre is occupied by an island of sclerenchyma, which is the direct continuation of the tongue of sclerenchyma, described in the above as interposed between the forks. It is important in this connection to note that the brown sclerenchyma of the cortex in this example is directly continuous with that which is present in the pith. Above and below the island of sclerenchyma there is a mass of phloem on the inside of the stelar tube. This phloem is continuous with that outside through the ramular lacunæ as is indicated in Photograph 15.

Photograph 17, Plate 3, is a cross-section of another forking cylinder. In this case each of the branches is closed, but the phloem passes inwards on the axial surface of each cylinder as far as the pith. Some brown sclerenchymatous cells are to be seen in the cortical tissue between the central cylinders of the two branches. Photograph 18, Plate 3, shows the same stem at a lower level. The interramular cortex has become an island enclosed by the central cylinders of the two branches. In the centre of this island a mass of brown sclerenchyma is present. In Photograph 19, Plate 3, the same fork appears in section at a still lower level. The cortical tongue is now seen to be continuous with the pith, and its contained mass of brown sclerenchyma now occupies the centre of the medulla. It is to be further observed that there is internal phloem for a considerable distance on the upper and lower walls of the flattened stelar tube. In these three photographs we have a type or fork in which the pith is less widely in communication with the cortex, but is nevertheless undoubtedly continuous with it.

Photograph 20, Plate 3, illustrates a phenomenon which is not uncommon in *O. cinnamomea*. The sieve-tissue is dipping down between the vascular strands, and may clearly be seen to expand at its inner end. Quite frequently the internal and external endodermal layers communicate through such a foliar gap as that shown in the photograph. Photograph 21, Plate 3, shows a vascular cylinder of *O. cinnamomea*, in which there is an internal as well as an external layer of phloem. This phenomenon is quite common in vigorous specimens of this species. Photograph 22, Plate 3, represents part of the same section more highly magnified. It is easy to make out the sieve-tubes inside as well as outside the tracheary tissue as large, apparently empty, elements. An examination of these in long section showed that they were quite typical sieve-tubes. Photograph 23, Plate 3, illustrates the structure of one of the tracheary strands of *O. cinnamomea*. It is obviously mesarch, the protoxylem being situated in the midst of the metaxylem as is the case in many cauline concentric bundles of the Filicales.

Photograph 24, Plate 3, shows a quite exceptional type of fork in *O. cinnamomea*. In this case there are no ramular gaps at all, and no communication whatever between the tissues of the cortex and those of the pith. There is not even an interruption

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of the tracheary elements permitting an inward extension of the phloem or of the stelar parenchyma. Notwithstanding the complete closure of the central cylinders in this case a well-marked internal endodermis is present, although it does not at any time communicate with a similar layer on the outside. Mr. J. H. Faull, working in the laboratory at Toronto, found that there was direct communication between the pith and the cortex in more than two-thirds of a large number of forking specimens of *O. cinnamomea* examined by him. The discussion of these interesting features of the central cylinder of *O. cinnamomea* may be deferred until the other species have been described.

Photograph 25, Plate 4, represents a central cylinder of *O. regalis*. In this species the internal endodermis, which is a constant feature of *O. cinnamomea*, is entirely absent. In the specimen here figured there is present, however, brown sclerenchyma in the pith. The occurrence of this tissue in the pith of *O. regalis* has been noted by De Bary, but has apparently escaped the attention of Zenetti and Strasburger. Photograph 26, Plate 4, shows the topography of a forking central cylinder of *O. regalis*. There is obviously no communication between the pith and the cortex. Medullary brown sclerenchyma is of comparatively rare occurrence in *O. regalis*, and no case whatever of the presence of internal phloem has been made out.

It will not be necessary to illustrate the structure of *O. claytoniana*, as it is very similar to that of *O. regalis*, except that it has not been observed to possess medullary brown sclerenchyma.

Photograph 27, Plate 4, shows the topography of a transverse section of the stem of *Todea barbara*, a forking specimen of which I owe to the kindness of Mr. Oakes Ames, Assistant Director of the Botanical Garden of Harvard University. Here, too, there is no internal endodermis, nor does the pith communicate with the cortex in the region of bifurcation of the central cylinder. An interesting feature of this species is the presence of a large amount of brown sclerenchyma in the pith which is very obvious in the specimen figured. A specimen of *Todea superba* from Kew showed neither internal endodermis nor brown sclerenchyma in the medulla.

Some observations have also been made on the young plants of the Osmundaceæ. Photograph 28, Plate 4, illustrates the structure of the stem in a young *O. claytoniana*. The wood obviously forms a tube with foliar lacunæ, one of which is well seen in the figure subtending the leaf-trace. I have not found any indication of internal phloem or an internal endodermis in the young plant of this species. Photograph 29, Plate 4, shows a section of a somewhat older specimen of *O. cinnamomea*. Several leaf-gaps may be seen in the preparation and the internal endodermis is already present in the shape of dark tannin-filled cells. In the pith are present several clusters of brown sclerenchymatous cells, similar to those found in the cortex. This section is from the older (later formed) end of a sporling of *O. cinnamomea*,

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which had not yet forked. It is of importance to note that continuous strands of brown sclerenchyma often occur in the pith of sporelings of this species, and that like the internal phlœoterma, which is equally characteristically present, they have no communication with the similar tissues of the cortex outside. In sporelings of *O. regalis* there is commonly differentiated a distinct layer of parenchyma on the inside of the stelar tube, although I have never observed it to be separated from the pith by a differentiated endodermis.

It is now in order to make suggestions as to the significance of the various anatomical facts recorded for the Osmundaceæ in the foregoing paragraphs. In this connection *O. cinnamomea* is the most interesting. According to the anatomical conceptions put forward by Van Tieghem and Strasburger, the cauline central cylinder of the Osmundaceæ is to be regarded as medullated monostelic, *i.e.*, as derived from a single concentric strand by dilatation and the formation of an intrastelar pith and medullary rays from the conjunctive parenchyma of the stele. The pith, according to this conception, has no morphological affinity with the cortical tissue outside. This idea answers quite well for *O. claytoniana*, and fairly well for *O. regalis*. The case of *O. cinnamomea*, however, appears to be quite irreconcilable with the hypothesis of medullated monostely of Van Tieghem and Strasburger.

In the first place we find in quite two-thirds of the example of this species a very obvious communication and histological identity between the pith and cortex. Secondly, we find invariably present an internal endodermis which in most cases joins with a similar external layer through the ramular lacunæ, and not unfrequently through the foliar lacunæ as well. Thirdly, internal phloem is frequently present in the region of bifurcation of the central cylinder. All these three phenomena are difficult to reconcile with the hypothesis of medullated monostely.

If in accordance with the ideas of Van Tieghem and Strasburger the condition figured in Photograph 24, Plate 3, where the pith and cortex do not become continuous in the region of forking, be regarded as primitive and resulting from the expansion of a pithless stele, there arise two serious difficulties. This hypothesis affords no explanation of the invariable presence of an internal endodermis, and the frequent occurrence of medullary brown sclerenchyma. It is possible, perhaps, to get over the first difficulty as Strasburger has done, by denying that the endodermis is necessarily always derived from fundamental tissue. The second difficulty cannot, however, be so easily set aside. I am not aware that brown sclerenchymatous tissue is ever found within the central cylinder *except in the pith*. This raises a grave doubt as to whether it can be regarded as intrastelar when it is present in the medulla. In *O. cinnamomea* the doubt becomes a certainty by the fact that the brown sclerenchyma in many cases is actually in histological continuity with the similar tissue of the outer cortex.

It is possible to take another view of the matter, viz., that the primitive condition

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is one in which the pith and cortex are the same in origin. This hypothesis has the advantage of raising no difficulties in the case of *O. cinnamomea*. Those examples in which the pith no longer communicates with the cortex are modified, but an indication of the primitive condition is even here offered by the presence of an internal endodermis and medullary brown sclerenchyma, which are still retained, although the pith has lost its continuity with the external cortex. In *Osmunda regalis* and *Todea barbara* we find that the medulla has become still further modified and only betrays its morphological nature by the occasional occurrence in it of brown sclerifications, for in these cases the medulla no longer communicates with the cortex through the ramular gaps. In *Osmunda claytoniana* and *Todea superba* all histological resemblance between the medulla and cortex has been lost. If the above conception is correct, *O. cinnamomea*, *O. regalis*, and *O. claytoniana* form a series of degeneracy in which *O. cinnamomea* is most primitive and *O. claytoniana* most specialised. It is interesting to note in this connection that Campbell, from his study of the gametophyte, has reached the conclusion that *O. cinnamomea* is more primitive than *O. claytoniana*.

But if the hypothesis presented in the last paragraph be considered to be the most reasonable explanation of the anatomical facts, it leads us somewhat further. Very striking features of the large proportion of specimens of *O. cinnamomea*, in which pith and cortex are obviously one, morphologically, are the presence of internal sieve-tissue, and the frequent communication of internal and external endodermal layers through the foliar gaps, as well as the ramular ones. In other words, there is an obvious tendency in what may be regarded as the most primitive condition of the central cylinder in the existing Osmundaceæ to approximate the polystelic type of Van Tieghem. If we admit that in *Osmunda* we have to do with a reduced and specialised polystelic central cylinder we at once have the explanation of other peculiar features. De Bary, Russow, and Zenetti have all described the continuous mantle of phloem which encircles the tracheary strands of *O. regalis*. In this, as well as the peculiarly American species, the phloem forms deep bays between the strands of xylem. This feature is so remarkable that Strasburger has been led to deny that the tissue in the bays of phloem is sieve-tissue at all ("Ueber den Bau und die Verrichtungen d. Leitungsbahnen in den Pflanzen," p. 449). There seems, however, to be no doubt that the elements in question are really sieve-tubes; for Mr. J. H. Faull, who has examined with care their structure and development, confirms the statements of De Bary and Russow. If the central cylinder of *Osmunda* be regarded as reduced polystelic with the foliar gaps very much narrowed and the internal phloem degenerate, it is possible to understand the presence of the peculiar bays of phloem between the strands of xylem. A further peculiarity of *Osmunda* and *Todea*, in addition to the one just discussed, is the concentric nature of the foliar strands. There are now recorded a number of striking examples of conservatism in the foliar strands of vascular plants, and it seems reasonable, especially in view of the facts

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described in the foregoing paragraphs, to regard the concentric structure of the leaf-traces of the Osmundaceæ as an ancestral feature which has been lost in the cauline fibro-vascular system. This view is further supported by the mesarch structure of the tracheary bundles of the stem.

If the interpretation of the facts described in the foregoing paragraphs is correct, the view of Zenetti that the type of cauline central cylinder in *O. regalis* is primitive and leads (Zenetti, 'Leitungs-System von *O. regalis*,' p. 75) on one hand to the so-called polystelic central cylinder so prevalent among the Filicales, and on the other hand to that of the Lepidodendrids and Sigillarians, cannot be entertained. That the Lycopodineous series has no near relationship to the Osmundaceæ seems apparent on various grounds, which can be more conveniently discussed at a later phase. The consideration of the anatomy of the whole group seems to establish that instead of being more primitive than, and antecedent to, the fern-type with the so-called polystelic central cylinder, they are merely a specialised condition of the latter. The resemblance to the condition which Zenetti finds in the young axis of the polystelic ferns is only an apparent one and arises from the degeneracy and specialisation of the stelar system of the Osmundaceæ.

Ophioglossaceæ.—The development of the sporophyte in *Botrychium virginianum* has already been described by the writer. The young stem is ("Gametophyte of *B. virginianum*," 'Canadian Inst. Trans.,' 1898) essentially like the adult. Poirault has called attention to the fact that in the young stem of certain species of Botrychium and Ophioglossum an internal endodermis is present, which is continuous with the external one through the foliar gaps of the central cylinder.

Farmer has more recently described a similar phenomenon in the adult plant of *Helminthostachys zeylanica*. The central cylinder of the Ophioglossaceæ closely resembles that of the Osmundaceæ. Evidences of its derivation from an originally concentric stelar tube are, however, not so abundant. The presence of concentric petiolar bundles in *Botrychium virginianum* and of mesarch wood in the stem of Helminthostachys, however, point in this direction (Farmer, 'Ann. of Bot.,' vol. 13, p. 432).

Schizæaceæ.—There is considerable variety of stelar structure in this group. Its anatomy has been studied by Prantl, and more recently by Boodle ("On the Anatomy of the Schizæaceæ," 'Ann. Bot.,' vol. 15). A number of illustrations have been prepared for this order, but the admirable recent work of Boodle cited above makes their publication unnecessary, since, in regard to the facts of structure and development, my results are in agreement with his.

In *Lygodium* the cauline central cylinder is protostelic, *i.e.*, a non-medullated concentric strand. In *Anemia phyllitidis* the adult stem is characterised by the presence of so-called polystelic structure. By studying the development of this species, however, it is possible to trace the stelar systems back to a condition where there is present a concentric tube interrupted by foliar lacunæ, a condition which is

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only less obvious in the adult on account of the overlapping of the leaf-gaps in a given plane of section. Boodle (*Op. cit.*, figs. 22–31) gives a good account of the development of the young stem in *Anemia phyllitidis*, which is quite in harmony with the writer's observations, and agrees closely with the description given above of the earlier stages of the Marattiaceous stem before the medullary strands have made their appearance. In *Mohria caffrorum* the stelar system is very similar to that of the foregoing genus, and passes through the same developmental phases.

In *Schizæa pusilla* the central cylinder of the stem belongs to the so-called medullated monostelic type, *i.e.*, is a collateral fibro-vascular tube surrounding a supposedly intrastelar pith. Boodle has decribed several species of *Schizæa* which practically differ from each other only in the more or less complete sclerification of the pith. Unfortunately the anatomy of the species of *Schizæa* at present described does not offer any series of gradations such as is presented by the American species of *Osmunda*; hence, it is impossible to discuss by reference to this genus alone the mode of origin of the medullated central cylinder, or its possible relationship to the types presented by the stem of *Lygodium* on the one hand, and those of *Anemia* and *Mohria* on the other. More facts are urgently needed which may or may not be supplied when we are thoroughly acquainted with the anatomy of all the living species of the *Schizæa*. Boodle follows Zenetti (*op. cit.*) in deriving the type of central cylinder found in *Anemia* and *Mohria* from that found in *Schizæa*, and this in turn by dilatation from the solid concentric stele of *Lygodium*. In the absence of facts bearing on the transition from one type of central cylinder to another in this group, it seems to be impossible to more than speculate. However, on the evidence afforded by the Osmundaceæ it seems probable that the type of central cylinder found in *Schizæa* is derived by reduction from that which is characteristic of *Mohria* and *Anemia*. Boodle introduces certain general theoretical considerations which may be more conveniently discussed at a later stage.

Gleicheniaceæ.—Gleichenia is monostelic. The leaf-traces of this genus are somewhat interesting. Photograph 30, Plate 4, represents the foliar bundle of *Gleichenia flabellata*. It presents no special feature except the absence of phloem on the inside of the incurved stele. Photograph 31, Plate 4, shows the structure of the foliar bundle in *Gleichenia circinata* variety microphylla. Here the concentric foliar stele has become completely closed and shuts in a mass of brown sclerenchyma. This tissue on longer communicates in any way with the similar cortical tissue outside. We have thus in the leaf-trace of the Gleicheniaceæ a phenomenon similar to that occurring in the cauline central cylinder of the Osmundaceæ, viz., the disappearance of internal phloem together with the complete shutting in of an extrastelar mass of parenchymatous tissue. In this case there can be no reasonable doubt that the condition represented by *Gleichenia flabellata* is more primitive. We owe the discovery of the facts described here to Poirault. ("Recherches sur les Cryptogames Vas-

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culaires." 'Ann. d. Sci. Nat., Bot.' 7 Ser., vol. 18.) POIRAULT has also described the central cylinder of the stem in *Platyzoma microphylla*. It closely resembles that of *Osmunda cinnamomea* since it is a collateral stelar tube with an internal endodermis. There is, however, no brown sclerenchyma present in the pith. Through the kindness of Dr. D. H. SCOTT the writer has had the opportunity of examining some sections of a dried stem of this species. The foliar gaps are nearly degenerate in this small extremely xerophytic fern. It would be interesting to investigate branching specimens of this species, if such occur, to discover whether the internal endodermis is continuous with the outer one through the ramular gaps. It seems not improbable that this may turn out to be the case.

Cyathaceæ.—Photograph 32, Plate 4, is of a section through the young stem of *Cyathea macarthuri*. The central cylinder at this stage is obviously tubular. A leaf-trace is passing off and subtends a foliar gap in the cylinder. Photograph 33, Plate 5, shows a latter phase of the same species. Internal and external bands of brown sclerenchyma have made their appearance, and three foliar gaps are present. A little higher up, the small medullary bundles which are characteristic of most of the Cyathaceæ begin to come off from the inside of the stelar tube. In *Alsophila australis* the stelar structure is the same as in *Cyathea*. The central cylinder of the young stem in *Cibotium princeps* is obviously tubular with foliar lacunæ, but higher up it becomes broken into segments by the overlapping of the foliar lacunæ. It will be apparent from these examples that the stelar system of the Cyathaceæ is essentially a concentric fibro-vascular tube with foliar lacunæ. The medullary strands are of later origin and are derived from the inner wall of the stelar tube as in the Marattiaceæ. The material for the observations described in this section was grown at the Botanic Garden of Harvard University from spores supplied by the Botanic Garden at Sydney, N.S.W., and the writer wishes to express his obligation to Professor GOODALE, Director of the Harvard Garden, and to the authorities at Sydney for their kindness in this matter.

Polypodiaceæ.—This group is important from the standpoint of stelar morphology, because, although possibly not so ancient as some of the foregoing, by its comparative luxuriance under modern conditions it affords us the best field for the study of the possibilities of modification in the so-called polystelic type of cauline axis. It is further important because most of the work on stelar development has been done in this order. VAN TIEGHEM states that the polystely which is so characteristic of these ferns, originates by the repeated bifurcation of the central cylinder. LECLERC DU SABLON ('Ann. Sci. Nat. Bot.,' 7 Ser., vol. 2. "Recherches sur la Tige des Fougères") has made a study of the development of the stem in several Polypodiaceous species. I have been able to confirm his results for the most part. Curiously enough, he does not draw attention to the fact that the data of development do not support VAN TIEGHEM'S theory of polystely resulting from repeated bifurcation of the young concentric cylinder. The figures of LECLERC DU SABLON

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show that the central cylinder of the young stem quickly becomes a concentric tube with foliar gaps. The tubular nature of the central cylinder is finally disguised by the overlapping of the foliar lacunæ.

Perhaps the most interesting of the species studied by Leclerc du Sablon is *Polypodium aureum*. He describes the young central cylinder of *P. aureum* as being composed of a ring of wood surrounded by phloem and containing an intrastelar pith. Later on the stelar tube becomes enlarged, and phloem appears on its internal surface. The pith has now disappeared, and the centre of the stelar tube is occupied by extrastelar fundamental tissue which becomes continuous with the cortex through the foliar gaps. I have looked in vain in my preparations for the pith of Leclerc du Sablon. Although my series were numerous I have never seen anything corresponding to the large-celled intrastelar parenchyma figured by Leclerc du Sablon as occupying the centre of the young cauline stele. I have secured young plants of this species from three different sources, and in each lot found the same results. I am disposed to believe that the specimens examined by Leclerc du Sablon could not have been quite normal. This belief is strengthened by the fact that young plants of *P. vulgare* gave similar negative results. In my specimens of *P. aureum* and *P. vulgare*, when the tube of xylem is first established, it has phloem on its internal surface as well as on the outside. A core of fundamental tissue is likewise enclosed almost immediately. Photograph 34, Plate 5, is of a section through the young stem of *P. aureum*.

It is a pecularity of *Polypodium* that even at a comparatively early stage in the development of the young plant the leaf-trace is double, and one-half of the trace becomes separated from the cauline central cylinder sooner than the other, as may be seen in the photograph, where the projection from the stem is a leaf-base containing two traces which are just beginning to separate from each other. The case of *P. aureum* is cited by Zenetti in favour of his hypothesis that the so-called medullated monostelic central cylinder is the primitive type of tubular stele. It seems obvious that no comparison is valid between the pith of *Osmunda* and the apparent pith which may sometimes occur in *P. aureum*, for the former is extrastelar, whereas the latter is intrastelar, and in direct continuity, according to Leclerc du Sablon's own account, with the parenchyma of the internal phloem. In any case it seems inadvisable to erect a stelar hypothesis on a peculiarity of a single species of *Polypodium* which has not yet been matched, either in additional species of the same, or any other Polypodiaceous genus, especially as this feature does not appear to be constant even in *P. aureum* itself.

I have examined young plants of the following Polypodiaceous species:—*Nephrolepis cordata*, *Microlepia hispida*, *Onychium japonicum*, *Polystichum setosum*, *Lastræa opaca*, *Davallia plumosa*, *Nephrodium hirtipes*, *Platyloma falcata*, *Blechnum occidentale*, *Lomaria ciliata*, *Gymnogramme sulphurea*, and species of *Pteris*, *Adiantum*, *Pellæa*, *Aspidium*, and *Asplenium*, without finding anything to record

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beyond the fact that the young central cylinder in these species is throughout a concentric fibro-vascular tube with foliar lacunæ.

Photograph 35, Plate 5, represents the tubular stele of *Antrophyum semicostatum*. The gap in the central cylinder is subtended by two concentric leaf-traces. Photograph 36, Plate 5, shows the central cylinder more highly magnified. By looking carefully, the sieve-tubes may be made out as small, apparently empty, elements separated from the wood by a single row of parenchymatous cells. Although the layer of phloem is continuous around the outside of the central cylinder, it quickly disappears on its inner surface. Photograph 37, Plate 5, is more highly magnified, and it shows the feature already described very clearly. The internal phloem comes to an end not far from the left-hand margin of the photograph. This peculiarity has been described by POIRAULT as of frequent occurrence in species of *Antrophyum*. (*Op. cit.*)

Photograph 38, Plate 5, shows another condition not referred to by POIRAULT. The species here is *A. plantagineum*. A stelar tube is present which possesses a pith very similar to that of Botrychium, except that on the lower side some internal phloem can be made out. The small sieve-tubes are continuous around the outside of the central cylinder, except in the middle of the upper border. Outside the external phloem is the pericycle, and external to that, a well-marked outer endodermis. There is no internal endodermis present. Photograph 39, Plate 5, is of a section through the central cylinder of *A. reticulatum* at a point where a leaf-trace is being given off. There is no phloem on the inner wall of the stelar tube, except on the internal margin of the foliar gap. A continuous zone of sieve-tubes runs around the outside of the central cylinder. Here also, there is no internal endodermis, although the outer one is well marked. The pith-like central parenchyma is very different histologically from the fundamental tissue of the cortex, and if it is to be regarded as a true pith, has very largely lost its identity. The external endodermis skirts the margin of the pith where it is exposed by the foliar gap. I owe material of these species to the kindness of Sir WILLIAM THISELTON-DYER, Director of the Royal Gardens, Kew, and Dr. M. TREUB, Director of the Botanic Garden at Buitenzorg, Java.

Vittaria elongata is a species described by POIRAULT as having lost not only its internal phloem, but also the internal endodermis. I have been able to confirm his statement in regard to the absence of internal phloem, but in my material which came from Buitenzorg, there is generally an internal endodermis. Professor THAXTER, of Havard University, was good enough to send me fresh specimens of *Vittaria lineata* from Florida. The cauline central cylinder is quite normal in this species.

The peculiar features of the above species of *Antrophyum* and *Vittaria* must be considered as indications of specialisation away from the usual concentric tubular type of central cylinder.

In *Davallia stricta* there is also present a tubular central cylinder with a paren-

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chymatous pith, but no internal phloem or endodermis. We have here another example of a reduced central cylinder, *Davallia plumosa* and *D. fijiensis* are quite normal, and show the usual tubular concentric central cylinder.

Photograph 40, Plate 5, is taken at a plane in the stem of *Adiantum pedatum*, where the foliar gap has just closed. It is easy to see that the sieve-tubes form a continuous zone on the outside on the fibro-vascular cylinder, but that they are absent along a considerable portion of its inner surface. This feature is quite commonly present in the Polypodiaceæ, but does not seem to have been previously described. It will serve as another example of the proneness of the phloem to degenerate on the inside of the typical concentric stelar tube.

Pteris aquilina is a type of Polypodiaceous fern with a very complex stelar arrangement in the adult. The writer's observations on the structure of the quite young stem in this species coincide with those of Leclerc du Sablon. The central cylinder becomes a concentric tube with foliar lacunæ. Leclerc du Sablon did not follow it beyond this stage. Van Tieghem in his 'Traité de Botanique' describes the two large central strands of the adult as the direct continuation of the stelar system of the young plant, and the outer series of bundles as cortical strands subsequently derived from these. The study of development, as described in the writer's memoir on the Angiosperms, does not bear out this suggestion.

Hofmeister long ago observed that the young stem of *P. aquilina*, after growing a while vertically, bifurcated, the two halves plunging into the soil to pursue a horizontal course. Curiously enough, Leclerc du Sablon describes the horizontal rhizome as originating adventitiously on the young vertical stem. I am able to confirm the entire accuracy of Hofmeister's description. Shortly after the young stem begins its horizontal course, the tubular central cylinder becomes involuted dorsally on its ventral surface, and gives off a medullary bundle. It is thus apparent that the external bundles of *P. aquilina* are primitive, and that the central strands are medullary bundles derived from the walls of the stelar tube in a way similar to those described above in the case of Marattiaceæ and Cyathaceæ. The second medullary strand in *P. aquilina* is sometimes derived from the wall of the stelar tube, and sometimes by splitting of the originally single strand into two. *Davallia fijiensis* has one or more medullary strands which are derived in the same way as those of *Pteris aquilina*.

In conclusion, it may be said of the Polypodiaceæ that the primitive form of tubular central cylinder is apparently that with internal phloem, but the internal sieve-tubes sometimes partially or wholly degenerate. There appears to be no evidence from the standpoint of development in favour of the view that the polystelic type of Van Tieghem is derived from the repeated bifurcation of the cauline central cylinder of the young stem. Developmental data seem further to establish the fact that the primitive condition of central cylinder in the Polypodiaceæ is a concentric fibro-vascular tube interrupted by lacunæ subtending the outgoing leaf-

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traces. The medullary strands of the Polypodiaceæ are of secondary origin, and are derived from the internal wall of the primitive stelar tube.

II. Lycopodiales.

Selaginella lævigata is a species with a tubular central cylinder. We owe a description of this form to Harvey Gibson ("Contributions towards a Knowledge of the Anatomy of the Genus Selaginella," 'Ann. Bot.,' vol. 13). Photograph 41, Plate 6, illustrates the structure of the central cylinder in this species. I am indebted for material to Dr. D. H. Scott. The fibro-vascular system is obviously tubular. Above and on the right is a gap corresponding to a branch-trace which can just be seen on the margin of the photograph. There are two partially confluent medullary strands which become fused periodically with the wall of the stelar tube at the points of origin of branch-strands. On the left in the cortex may be seen a small trace belonging to a leaf. There is a toothed projection of the xylem of the central cylinder subtending this, but no foliar gap, as in the Filicales. The writer has already drawn attention, in his memoir on the genus *Equisetum*, to the universal absence of foliar gaps in the Lycopodiales, and the present photograph serves to illustrate this peculiarity.

The Lepidodendroceæ had the largest leaves of any Lycopodineous forms known to us. In *Lepidodendron Harcourtii* the stelar system is tubular with ramular gaps which correspond to the points of exit of the Halonial strands. Brongniart was the first to describe the structure of the central cylinder in this species. There are present in *L. Harcourtii*, and in *Lepidophloios fuliginosus* as well, ramular gaps, but no foliar ones. In *Lepidodendron brevifolium* ramular gaps, in the case of smaller branches, are apparently absent. (Scott, 'Studies in Fossil Botany,' fig. 53, p. 133.) Dr. Scott has assured me that he knows of no case of the occurrence of foliar gaps among the fossil Lycopodiales. *Tmesipteris*, *Psilotum*, and *Phylloglossum* have all a tubular central cylinder surrounded by a well marked endodermis. There are no foliar gaps present in any of these species. In some cases there are other gaps in the stelar system, but these have nothing to do with outgoing leaf-traces. I am indebted for material of these genera to Mr. L. Cockayne, of Christchurch, New Zealand, Professor Bayley Balfour, Mr. Baker, of the Technological Museum, Sydney, N.S.W., Australia, and to the authorities of the Royal Gardens, Kew.

There is obviously no endodermis (phlœoterma) distinguishable in *Lycopodium clavatum*. In *Lycopodium lucidulum* the endodermis is strikingly present. The difference between the two cases in the development of the endodermis is due to the presence and absence respectively of sclerenchymatous tissue surrounding the stele. Usually where sclerenchyma abuts on the central cylinder the phlœotermal layer cannot be readily distinguished. I have observed similar cases in the developing

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stem of Angiosperms. In the younger region of the stem where sclerenchymatous tissue does not occur, the endodermis can generally be made out without the use of reagents. In the later formed part of the axis, however, the appearance of sclerification in the pericycle and cortex causes the endodermis to be no longer apparent. Attention has been called to this feature in my memoir on the central cylinder of the Angiosperms. I have been able to confirm BERTRAND'S statement in regard to the presence of an endodermal sheath in *Phylloglossum*, *Tmesipteris*, and *Psilotum*.

Professor BOWER has stated that the endodermal sheath is not ("Morphology of Spore-producing Members. Pt. II. Ophioglossaceæ," p. 71, &c.) well defined in the Lycopodineæ, and has assumed that this is a primitive feature which they share with the simpler (reduced?) Ophioglossaceæ. I am unable to agree with this generalisation because my own studies, which confirm and supplement those of BERTRAND, lead to the conclusion that the phlœotermal sheath is well developed in the Lycopodiales. The Marattiaceæ and the Ophioglossaceæ, moreover, have the endodermis characteristically present in the stem of the young plant, even where it is absent in the adult. There is possibly a tendency at the present time to attach too little importance to the endodermal sheath. This layer is too constantly present in seedlings, even where it is absent in the adult, to be disregarded. It appears to be a primitive morphological boundary, if its occurrence in the stem of groups, which are generally regarded as ancestral, is to be considered significant.

III. GYMNOSPERMS.

It will be convenient to include under this head an examination of that interesting group recently erected by POTONIÉ ('Pflanzenpalæontologie,' p. 160), the Cycadofilices, which, from the anatomical standpoint, bridge over the gap between the Pteridophyta and Gymnosperms.

Cycadofilices.—Photograph 42, Plate 6, shows the structure of the central cylinder of *Lyginodendron oldhamium*. There is obviously a large amount of secondary wood present, the elements of which are arranged in radial rows. The magnification is not sufficient in the present instance to show the structure of the clusters of primary wood which are scattered along the border of the pith. On the left, a leaf-trace is passing off, leaving a wide gap in the central cylinder. Numerous dark clusters of sclerenchyma may be seen scattered in the medulla. Similar sclerotic nests appear in the cortex. They may be found also in the foliar gaps. This is very well shown in one of the figures of WILLIAMSON and SCOTT ('Phil. Trans.,' B, vol. 186, Plate 21, fig. 1).

Photograph 43, Plate 6, illustrates the structure of a part of the woody cylinder of *Lyginodendron oldhamium*. On the lower side of the photograph and next to the medulla is to be seen one of the clusters of primary wood. The protoxylem instead

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of appearing directly on the margin of the pith is separated from it by a large mass of primary metaxylem. The primitive elements of the wood are separated from the internal primary metaxylem by parenchyma. Outwardly they are continuous with the external primary metaxylem, and finally with the radial rows of secondary wood. This peculiar cryptogamous type of bundle has been termed "mesarch" by Solms-Laubach, and its constant occurrence in the Cycadofilices and Cycads affords one of the strongest arguments for regarding these groups as nearly allied to cryptogamous ancestors. The leaf-traces of *Lyginodendron* become concentric in their upward course, thus presenting an interesting parallel to those of the Osmundaceæ, which are collateral mesarch in the stem and concentric in the petioles.

The occasional occurrence of concentric bundles in the stelar tube has already been described in the case of the Osmundaceæ. Williamson and Scott (*op. cit.*, Plate 23, fig. 8) mention a similar phenomenon in *Lyginodendron oldhamium*. I have examined the original preparations in the British Museum. In these examples there is internal phloem as well as internal secondary wood. Dr. Scott considers these features to be mere anomalies, but in view of the condition found in the Osmundaceæ they are probably to be regarded somewhat more seriously. This probability is strengthened by the fact that in another species, *Lyginodendron robustum*, described by Mr. Seward ('Ann. Bot.,' vol. 11, p. 65), the presence of internal secondary wood is quite constant. *Cycadoxylon fremyi*, another species close to Lyginodendron, has also internal secondary xylem and phloem. In both the last-mentioned examples the primary centripetal wood is largely abortive. Of less interest in this connection is a monostelic genus *Heterangium*, which has secondary wood but no pith.

One of the most important genera of the Cycadofilices is *Medullosa*. In this genus the fibro-vascular system is polystelic, *i.e.*, made up of a number of anastomosing concentric strands. It differs strikingly from the ferns, however, in the fact that its "steles" are surrounded with secondary wood, and the primary wood is often largely abortive, being replaced by parenchyma and constituting the so-called partial piths. The concentric strands have a varying configuration. The external ones which, on the basis of the stelar development of the Ferns and polystelic Angiosperms we may probably regard as primitive, often form continuous zones, while the medullary bundles are star-shaped. The former are generally called "plate-rings," the latter "star-rings." An interesting feature of the same genus is the fact that the internally formed secondary wood of the plate-rings is often a very thin layer as compared with the outer zone. In a *Medullosa* with a single layer of plate-rings only, this would lead to a condition closely resembling that described above in *Lyginodendron robustum*, &c.

Potonié is of the opinion that the modern Cycads arose from Medullosan ancestors by the abortion of the primary cryptogamic wood and the disappearance of the centripetal secondary xylem of the cauline bundles. He thus regards the Cycads as resulting by a process of reduction from polystelic ancestors, just as appears to have

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been ('Metamorphose d. Pflanzen im Lichte Palæontologischer Thatsachen,' Berlin, 1898, p. 23. Also 'Pflanzenpalæontologie') the case in the Osmundaceæ. This conclusion is all the more striking because he is inclined to agree with ZENETTI in considering *Osmunda* to possess a very primitive form of central cylinder.

Dr. SCOTT takes a somewhat different view of the relationship of such types of stem as those of *Heterangium*, *Lyginodendron*, and *Medullosa*. He regards the cauline central cylinder of *Heterangium* and *Lyginodendron* as belonging to the same morphological category, the medullated central cylinder of *Lyginodendron* being derived from a pithless state, such as that of *Heterangium*, by expansion of the stele, and the formation of an intrastelar pith. He compares the central cylinder of *Lyginodendron* explicitly with that of *Osmunda*, which according to the anatomical ideas of VAN TIEGHEM and STRASBURGER is also medullated monostelic. The type of stem presented by *Medullosa* he regards as polystelic, and resulting from the repeated division of such a stele as is found in *Heterangium*. The *Lyginodendron* type, he believes, gave rise to the modern Cycads, while the Medullosæ are off the main line of descent. Dr. SCOTT, however, repeatedly calls attention to the difficulty which often arises in distinguishing between the monostelic and the polystelic types of central cylinder. I believe it to be extremely significant that in all cases of this kind we have to do with the so-called medullated monostelic central cylinder. Throughout the whole range of the higher vascular plants the histological resemblance between the medulla and cortex is in general very striking. This is not easy to explain on the hypothesis of the enlargement of a pithless stele and the formation of a median intrastelar medulla. The pith is too obviously different from the stelar parenchyma, and too strikingly like the cortical fundamental tissue, for this to be a very satisfactory explanation of its origin.

The late Professor HUXLEY considered that in the almost complete geological sequence from the pentadactyl early horses to the monodactyl horses of the present day, existed one of the strongest proofs in favour of the general principle of evolution by reduction and specialisation. We find apparently a similar series of reduction and specialisation in the Osmundaceæ which may be applied to the elucidation of the general problem of the evolution of the central cylinder in the higher plants. The medullated central cylinder of *Osmunda regalis* seems beyond reasonable doubt to have been derived through a quasi-polystelic phase, such as is presented by *O. cinnamomea*, from typical polystelic ancestors. This hypothesis alone appears to offer a satisfactory explanation of all the structural peculiarities of the central cylinder of the Osmundaceæ. If it be adopted for the Osmundaceæ, it applies equally to the Lyginodendreæ, which possess, as Dr. SCOTT has pointed out, so many striking features of resemblance to the Osmundaceæ. The present work has, in the case of the Osmundaceæ, brought out further points of agreement in the presence of internal phloem and medullary brown sclerenchyma, &c. This view of the matter, moreover, harmonises in a satisfactory way the somewhat divergent hypothesis of POTONIÉ and SCOTT in regard to the origin of the Cycads. Dr. SCOTT considers them to be

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derived from ancestors resembling *Lyginodendron*, and Professor Potonié believes them to be descended from polystelic forms like *Medullosa* by reduction. If the type of central cylinder presented by *Lyginodendron* has originated by reduction from that of polystelic ancestors, obviously the views of these Palæobotanists are reconciled on the basis of a fuller knowledge of stelar morphology.

Before taking leave of the Cycadofilices, it is necessary to make some reference to the structure of their leaf-traces. Those of *Heterangium* and *Lyginodendron* became concentric shortly after leaving the central cylinder of the stem. In *Medullosa* they generally assumed a peculiar sort of collateral structure of a cryptogamous type. The protoxylem, instead of being separated from the phloem by the whole width of the metaxylem, lies next the phloem. In other words, the wood instead of being formed centrifugally as in most Phanerogams, is produced centripetally. In some species of *Medullosa*, the wood of the leaf-bundles became mesarch by the formation of primary metaxylem on the side next the phloem as well as centripetally.

Cycadales.—The stelar tube of the Cycads is collateral, and is interrupted by foliar lacunæ. The medulla and the cortex are occupied by numerous mucilage ducts which communicate through the foliar gaps. Photograph 44, Plate 6, shows some of the concentric bundles which are present in the cortex of *Cycas revoluta*. In Photograph 45, Plate 6, appears one of these more highly magnified. These peculiar cortical bundles were first adequately described by Mettenius ('Beiträge zur Anatomie d. Cycadeen,' p. 589), who showed that they terminated above in the leaf-traces. De Bary ('Comparative Anatomy,' Eng. Ed., p. 340) found concentric bundles still higher up in the actual petiole of *Dion edule*, and Scott ('Ann. Bot.,' vol. 11, p. 399) subsequently described their existence in the reproductive axis of certain Cycads. Worsdell ('Brit. Assoc. Rep.,' 1900, p. 938) has quite recently called attention to their persistent presence in the Cycads and their allies.

In Photograph 46, Plate 6, is shown one of the petiolar bundles of *Cycas revoluta*. Like that of the petiole of *Medullosa anglica*, &c., its wood is mainly centripetal. There is a small amount of centrifugal wood formed on the side next the phloem. Dr. Scott has made the interesting discovery that similar mesarch bundles occur in the peduncles of the *cones* of *Stangeria* and other Cycads. Potonié derives the centrifugal part of the xylem in these cases from the similar structure existing in the bundles of the stem of the living Cycads, the centripetal on the other hand, from the centripetal wood present in the *stem* of the ancestors of the group. This conclusion he considers warranted by a study of the anatomy of the *Medullosæ*.

The evidence in the form of characteristic and very constant anatomical features seems to be very strong for the near connection of the Cycads with a cryptogamic ancestry. When this evidence is considered in the light ot what is known of the anatomy of the Cycadofilices, it becomes doubly convincing. It has been argued in a former paragraph that the central cylinder of *Lyginodendron* is derived from an ancestor with a concentric tubular fibro-vascular cylinder by reduction. The step

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from *Lyginodendron* to the modern Cycads is not a very great one. The leaf-trace and reproductive axes of the living Cycads retain most persistently the ancestral features of the stock. The anatomical structure of the Bennettitales does not appear to have differed greatly from that of living Cycads, except in the greater simplicity of the course of the leaf-traces.

Cordaitales.—It is unnecessary to refer at length to this group. Mesarch bundles have long been known to exist in the leaves. Quite recently Dr. Scott ('Brit. Assoc. Rep.,' 1900, p. 945) has found them also in the stem. The relationship of this group through such forms as *Poroxylon* with Cycadofilicinean ancestry seems by this interesting discovery quite established. There were well-marked foliar gaps in *Poroxylon* as Dr. Scott ('Studies in Fossil Botany,' p. 408) has recently pointed out. The same was true of the Cordaites.

Ginkgoales.—Photograph 47, Plate 6, illustrates the structure of the young stem of *Ginkgo biloba*. Two cotyledonary traces may be seen in the cortex subtending gaps in the central cylinder. Foliar gaps are likewise present in connection with the double traces of the adult.

Coniferales.—I have found foliar gaps in all the numerous Coniferales which I have examined, even in those of extremely xerophytic habit and reduced foliage. In Photograph 48, Plate 6, is seen a transverse section of a small branch of *Thuja occidentalis*. Two leaf-traces may be distinguished subtending very marked foliar gaps. The Coniferales present this marked difference from the Lycopodineous series from which they have been derived by Renault, Potonié, and Campbell, that they invariably possess foliar gaps which are constantly absent in the Lycopods.

Gnetales.—I have examined several species of *Ephedra*. Well marked foliar lacunæ are present corresponding to the double leaf-traces. In *Gnetum gnemon* numerous leaf-traces come off opposite distinct foliar gaps. The resemblance between cortical and medullary tissues is very marked in this genus.

Conclusions.

The observations recorded in the foregoing pages seem to warrant certain general conclusions in regard to Morphology and Phylogeny.

Morphology.—Anatomical work has for some years past been dominated by the morphological ideas which are due in the first place to Van Tieghem, but have been modified to some extent by Strasburger. These morphological conceptions are too well known for it to be necessary to more than recapitulate them in the briefest way.

In some cases the fibro-vascular conductive tissue of stems consists of a solid core of xylem surrounded by phloem and pericycle, and shut off from the general fundamental tissue by a well marked layer of the latter called by Van Tieghem the endodermis. To this fibro-vascular cylinder Van Tieghem has applied the designation "stele." Where the stem contains but a single such stele it is known as monostelic.

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In the axes of many ferns there are apparently several or many such steles present. This type of stem VAN TIEGHEM calls polystelic, and states that the numerous steles arise by the repeated bifurcation of the originally single stele of the young plant. These numerous steles are considered sometimes to fuse together, and the gamostelic (solenostelic) condition results.

Again, the monostelic central cylinder, instead of dividing repeatedly or continuing unchanged, may become expanded and form an internal pith, which is quite different morphologically from the fundamental tissue outside the stele. In this case the result often is the formation of a number of collateral bundles surrounding the medulla and separated from each other by parenchymatous medullary rays. In some instances the individual collateral fibro-vascular strands of such a medullated monostelic cylinder are surrounded by sheaths resembling the sheath (here absent) which ordinarily surrounds the whole complex of bundles. VAN TIEGHEM calls this condition astelic or schizostelic, and considers it to arise by the sinking-in of the common endodermis between the individual collateral bundles, with the final uniting of the loops to form individual bundle sheaths. The pith, as a result of such a process, is considered to become part of the cortex. Sometimes the whole fibro-vascular complex has a common inner as well as an outer sheath. This condition is conceived to arise from that just described by the lateral fusion of the individual bundle sheaths. VAN TIEGHEM calls such a type of central cylinder gamodesmic or gamomeristelic. A single genus, *e.g.*, *Ranunculus*, may present all the modifications just described, viz., medullated, monostely, astely, and gamodesmy. In the first case the pith, according to VAN TIEGHEM'S view, is intrastelar; in the two latter, extrastelar.

STRASBURGER has adopted VAN TIEGHEM'S conceptions in regard to monostely, polystely, and medullated monostely. In regard to astely and gamodesmy, he does not agree with VAN TIEGHEM, for he considers it improbable that the pith in different species of the same genus, *e.g.*, *Equisetum* or *Ranunculus*, should lie sometimes within and sometimes without the stele. He accordingly considers the sheaths which are present in VAN TIEGHEM'S astelic and gamodesmic condition as merely histological layers of no morphological importance. He consequently regards the astelic and gamodesmic conditions of the central cylinder as in reality medullated monostelic. STRASBURGER suggests the name Phlœoterma for the morphologically innermost layer of the fundamental tissue which constitutes the stelar sheath. The phlœoterma so defined may have various modes of histological differentiation; it may appear as an endodermis, or a lignified zone, or as an amyliferous layer.

It is a curious consequence of STRASBURGER'S conception of the morphological nature of the medullated monostelic central cylinder that, wherever VAN TIEGHEM'S astelic condition is present, all histological evidence of a phlœoterma is absent. The writer has shown in his memoir on the Angiosperms that if we subject this conception to the test of development, the result is unfavourable to STRASBURGER'S views; but it will be well to re-state the argument briefly in the present connection.

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In *Ranunculus acris*, according to STRASBURGER, there is present a true phlœoterma. In a section through the subterranean stem it may be seen as a dark line following the outer margin of the bundles. Where the latter are separated by leaf-gaps, curiously enough, the interrupted phlœoterma passes inwards on the flanks of the bundles. It also passes round the central cylinders of emerging roots, so that there can be no doubt as to its identity. In the quite young stem, where a leaf-gap is present, the external phlœoterma, which is obviously the same layer as that higher up, passes around the margins of the gap to become continuous with a similar layer on the inside of the fibro-vascular ring. We have here a clear indication of the significance of the sinking-in of the phlœoterma on the flanks of the bundle in the older stem. Successive sections between the two regions demonstrate that the internal sheath gradually disappears. In an intermediate region, by the overlapping of the foliar gaps, the collateral fibro-vascular ring which is primitively continuous is broken up into a series of separate strands, each completely surrounded by a phlœotermal sheath. If this condition, or the earlier condition referred to above, were present in the adult stem, STRASBURGER would not admit that the sheaths in either case merited the name phlœoterma.

A very strong argument against the validity of STRASBURGER'S interpretation of this and similar cases is that it takes no account of the facts of development, and makes the same sheath in the upper part of the stem a true phlœoterma, and in its lower, presumably more primitive and typical region, a mere histological layer of no morphological importance. It further offers no explanation of the fact that, even in the case of the adult, the layer which he regards as the phlœoterma is not continuous, but passes inwards on the flanks of the bundles. It seems difficult to retain a morphological hypothesis which is so obviously in opposition to the facts of development. The above reasoning in regard to the endodermis is obviously not affected by the question as to whether this layer is in all cases really the innermost stratum (Phlœoterma) of the cortex, because if it be not the most internal layer of the fundamental tissue, then, *à fortiori*, it follows that everything outside is cortical tissue.

As a result of developmental study recorded in an earlier memoir, as illustrated in the above example, the writer has come to the conclusion that in the Angiosperms the pith is to be regarded as always belonging to the fundamental tissue, and that as a consequence VAN TIEGHEM'S hypothesis of medullated monostely cannot be maintained.

For the real explanation of this anatomical condition we have to go (as is so generally the case in morphological problems) to the structure and development of the higher Cryptogams. In the earlier part of this essay attention has been called to the primitively tubular condition of the central cylinder in the so-called polystelic ferns. The tubular condition becomes less obvious subsequently by the overlapping of the foliar gaps, and sometimes by the formation of a more or less complex system of medullary strands. The polystelic condition of VAN TIEGHEM,

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consequently does not originate by the successive bifurcation of the primitive stele, as in the absence of developmental data he was led to suppose; but, on the contrary, by the breaking up and modification of a stelar tube. The writer has suggested already (*opera citata*) that the stelar system of the so-called polystelic ferns should on that account be designated siphonostelic. The term gamostelic is scarcely applicable, because it implies the fusion of strands originally separate, whereas the real condition of affairs is actually the reverse. Quite recently Gwynne Vaughan ("Observations on the Anatomy of Solenostelic Ferns.—*I. Loxsoma*." 'Ann. Bot.,' vol. 14) has reached a similar conclusion in regard to the so-called polystelic type of central cylinder, adopting for it the term solenostelic, which corresponds to the writer's siphonostelic with internal phloem. The designation adelosiphonic may conveniently be used in the cases where the central cylinder of the adult no longer presents the more primitive tubular condition.

The facts described in an earlier part of this memoir in the case of the Osmundaceæ and Polypodiaceæ seem to leave little room for doubt, that the siphonostelic type of central cylinder with internal phloem *may* give rise by reduction to a modification not distinguishable in any way from the medullated monostelic type of Van Tieghem. It seems reasonable on that account to derive the siphonostelic central cylinder *without* internal phloem (*i.e.*, the medullated monostelic type of Van Tieghem and Strasburger) from the condition *with* internal phloem, until some definite evidence from development, anatomy, or phylogeny, is forthcoming to show that it is originated in some other way. This hypothesis appears further to have the advantage of affording a single explanation for a large number of facts, *e.g.*, the peculiar anatomical structure of *Lyginodendron*, as well as that of the lower Gymnosperms, and also the peculiarities of sporelings and seedlings of the Marattiaceæ, Ophioglossaceæ, Equisetaceæ, Dicotyledons, and Monocotyledons.

Boodle (*op. cit.*, p. 403) has recently made some novel and interesting theoretical suggestions in connection with his work on the Schizæaceæ. After criticising the anatomical views advanced by the writer in an earlier memoir on the anatomy of the Angiosperms, he states his opinion that the monostelic, medullated monostelic, solenostelic, and dialystelic types of Van Tieghem are all reducible to one. He regards the cauline fibro-vascular system as morphologically always circular in outline, and the pith, where present, as always part of the stelar tissues, irrespective of the distribution of the endodermal sheaths. He reaches this conclusion by extending the reasoning applied by Strasburger to prove that the sheaths surrounding the bundles in Van Tieghem's astelic type are merely histological layers, and of no morphological importance. He follows Strasburger in the view that the endodermis has the physiological function of an air-tight sheath, but he adduces no experimental evidence that such is the case. In the Selaginellas the endodermis instead of being air-tight is actually lacunar tissue. Moreover, in a large number of cases, as has been noted above, the endodermis is well-developed in the sporeling or seedling, even

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when obsolescent or absent in the adult. These considerations, among others, make it very difficult to accept the hypothesis that the endodermis is a cenogenetic adaptation for the purpose of rendering the bundles air-tight.

Further, Mr. Boodle's view is entirely subversive not only of the results of Van Tieghem, Strasburger, and more recent authors, but also of the well-established classification of the tissues of the Vasculares due to Sachs and De Bary. If there is in general no morphological boundary between the bundles and the fundamental tissue, it is apparently quite useless to discuss the fibro-vascular system of the higher plants from the morphological standpoint. Further, if in accordance with Mr. Boodle's views we regard the very complex arrangement of bundles in the adult stem of *Pteris aquilina* as included in a single circular central cylinder, it is not easy to see why a similar view should not be taken of the equally complex arrangement of bundles in the petiole.

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. In the case of the Osmundaceæ, Polypodiaceæ, and Lyginodendron, the stages of degeneracy may be seized *in flagrante*. There are, further, the strongest reasons for deriving the Gymnosperms generally from such a type as Lyginodendron by a process of progressive loss of cryptogamic features. It appears, likewise, not unreasonable to consider the Angiosperms as descended from the higher Gymnosperms or from some other Filicinean stock now extinct. In the Angiosperms, however, all cryptogamic anatomical features have long disappeared.

Phylogeny.—Attention has been called repeatedly in the course of this essay to the constant and characteristic features of the siphonostelic central cylinder, viz., that unfailingly in certain great groups foliar gaps are present, while in others they are invariably absent. Foliar lacunæ are a characteristic feature of the siphonostelic central cylinder of the Filicales, Gymnosperms, and Angiosperms. They are invariably absent in the Lycopodiales and Equisetales. The writer has suggested in the memoir on the Angiosperms that the siphonostelic nature of the fibro-vascular skeletal tissues has arisen in connection with the function of support.

In the case of the Filicales, Gymnosperms, and Angiosperms the stelar gaps are characteristically foliar, at least in the young plant, while in the case of the Lycopodiales and Equisetales there are ramular gaps only. The tube with foliar gaps may appropriately be called phyllosiphonic, while that with the ramular gaps only, may be designated cladosiphonic.

Emphasis has been laid in the introduction on the small use made by Botanists, as distinguished from Palæobotanists and Zoologists, of skeletal characteristics. The present and the two earlier memoirs are devoted to an attempt to show that these characteristics are of great phylogenetic value, especially in connection with the larger groups, and in the case of the higher plants where the characters of the

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gametophyte and the sporangium so generally used as the basis of phylogeny have by the appearance of heterospory, and the seed-habit suffered such a profound modification. Stelar anatomy and development, in other words, help to bridge over the gulf which exists between the vascular Cryptogams and Phanerogams. If the latter are descended from the former, anatomy is, for the present at least, practically the only guide to the cryptogamic ancestry from which they have come.

Anatomical data lead us to the conclusion that the vascular plants at present existing on the earth and their fossilised predecessors, as far as we know them, have come from two great stocks which appear to have been separate back to the beginning of the period when the palæontological record begins. One stock was palingenetically microphyllous, and gave rise to the Lycopodiales and Equisetales; the other had from the earliest times large leaves, and was the progenitor of the Filicales, Gymnosperms, and Angiosperms. I have already suggested ("The Morphology of the Central Cylinder in the Angiosperms," 'Canadian Inst. Trans.,' vol. 6, 1900) that the former group should be named the Lycopsida, and the second the Pteropsida. This classification harmonises with all the evidence derived from other sources.

Summary.

Morphology.—1. There are two types of cauline central cylinder, protostelic and siphonostelic.

2. The protostelic central cylinder is more primitive, and in its single concentric vascular strand no medulla is present.

3. The siphonostelic central cylinder is tubular, and has a medulla derived from the fundamental tissue. It is characterised by the presence of foliar and ramular lacunæ, or by ramular lacunæ only.

4. The siphonostelic central cylinder sometimes ceases to be obviously tubular in the adult, and in such cases may be termed adelosiphonic.

5. The siphonostelic central cylinder is primitively concentric, but in the Angiosperms, Gymnosperms, Osmundaceæ, &c., has become collateral by reduction.

6. The pith is to be regarded as an inclosed portion of the fundamental tissue.

Phylogeny.—1. There are two phylogenetic types of tubular central cylinder, viz., that in which only ramular gaps are present and that in which both ramular and foliar gaps occur. The former may be termed cladosiphonic, and the latter phyllosiphonic.

2. The use of these constant and characteristic anatomical features results in the division of the Vasculares into two great primitive stocks—the Lycopsida, which are cladosiphonic and palingenetically microphyllous, and the Pteropsida, which are phyllosiphonic and palingenetically megaphyllous. The Lycopsida include the Lycopodiales and the Equisetales. The Pteropsida include the Filicales, Gymnosperms, and Angiosperms.

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In addition to the acknowledgments made in connection with the various groups considered in this memoir, I wish to express my special thanks to Sir William Thiselton-Dyer, Director of the Royal Gardens, Kew, Professor Bayley Balfour, Director of the Royal Gardens, Edinburgh, Professor G. L. Goodale, Director of the Botanic Garden, Harvard University, and Mr. Oakes Ames, Assistant-Director of the same Garden, for their great kindness in supplying much of the material employed in this research. To Dr. D. H. Scott I am under obligations not only for material, but also for the privilege of examining his private collection of fossil plants while working at the Jodrell Laboratory at Kew.

Explanation of the Plates.

PLATE 1.

Photograph 1. Transverse section of the young stem of *Danæa alata*. × 25.
Photograph 2. The same. × 25.
Photograph 3. An older stage. × 20.
Photograph 4. A still older stage. × 25.
Photograph 5. The same stage. × 30.
Photograph 6. Mature stem of *D. alata*. × 2.
Photograph 7. Young stem of *D. simplicifolia*. × 25.
Photograph 8. The same. × 20.

PLATE 2.

Photograph 9. Older stage of *D. simplicifolia*. × 25.
Photograph 10. Transverse section of the stem of an adventitious plant of *Marattia alata*. × 4.
Photograph 11. Young stem of *Angiopteris evecta*. × 30.
Photograph 12. Transverse section of central cylinder of *Osmunda cinnamomea*. × 19.
Photograph 13. The same. × 10.
Photograph 14. Older region of the same specimen. × 10.
Photograph 15. Transverse section of forking central cylinder of *O. cinnamomea*. × 6.
Photograph 16. Same, lower down. × 8.

PLATE 3.

Photograph 17. Forking stem of another specimen of *O. cinnamomea*. × 10.
Photograph 18. The same specimen lower down. × 10.
Photograph 19. The same specimen at a still lower plane of section. × 10.

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Photograph 20. Bundles of *O. cinnamomea.* × 25.
Photograph 21. Central cylinder of *O. cinnamomea*, showing internal phloem. × 10.
Photograph 22. Part of the same. × 25.
Photograph 23. Wood bundle of *O. cinnamomea.* × 40.
Photograph 24. A closed fork of *O. cinnamomea.* × 10.

PLATE 4.

Photograph 25. Central cylinder of the stem of *O. regalis*, showing medullary brown sclerenchyma. × 10.
Photograph 26. Fork of *O. regalis.* × 10.
Photograph 27. Central cylinder of the stem of *Todea barbara*, showing medullary brown sclerenchyma. × 6.
Photograph 28. Young stem of *O. claytoniana*, showing foliar gap. × 40.
Photograph 29. Older young stem of *O. cinnamomea.* × 50.
Photograph 30. Foliar trace of *Gleichenia flabellata.* × 25.
Photograph 31. Petiole of *G. circinata.* × 25.
Photograph 32. Young stem of *Cyathea macarthuri.* × 35.

PLATE 5.

Photograph 33. Older region of the same. × 10.
Photograph 34. Young stem of *Polypodium aureum.* × 70.
Photograph 35. Cauline central cylinder of *Antrophyum semicostatum.* × 40.
Photograph 36. The same. × 80.
Photograph 37. Part of the same. × 200.
Photograph 38. Cauline central cylinder of *A. plantagineum.* × 25.
Photograph 39. Cauline central cylinder of *A. reticulatum.* × 25.
Photograph 40. Part of cauline central cylinder of *Adiantum pedatum*, just above the foliar gap. × 80.

PLATE 6.

Photograph 41. Cauline central cylinder of *Selaginella lævigata.* × 30.
Photograph 42. Cauline central cylinder of *Lyginodendron oldhamium.* × 8.
Photograph 43. Part of the vascular zone of the same. × 30.
Photograph 44. Concentric cortical bundles of *Cycas revoluta.* × 10.
Photograph 45. Section of a cortical bundle of *Cycas revoluta.* × 30.
Photograph 46. Petiolar bundle of *Cycas revoluta.* × 200.
Photograph 47. Young stem of *Ginkgo biloba.* × 10.
Photograph 48. Branch of *Thuja occidentalis.* × 40.

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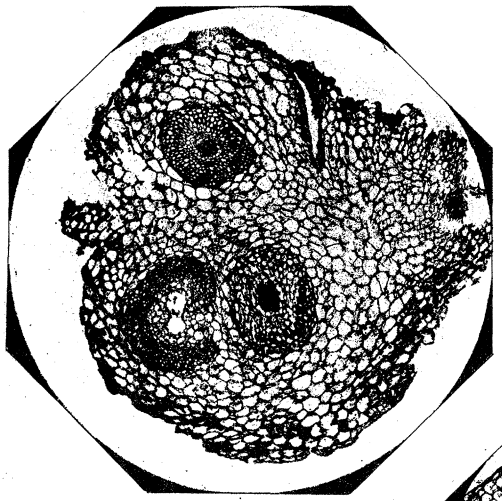

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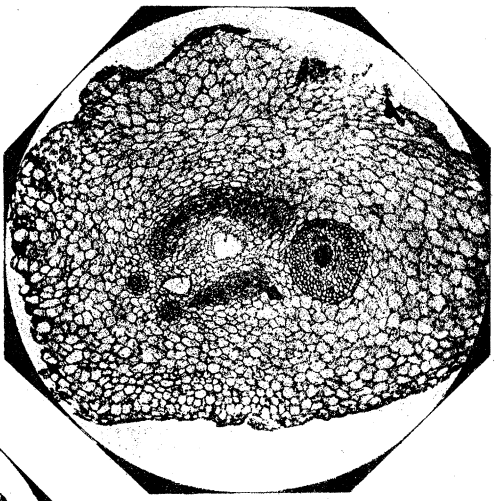

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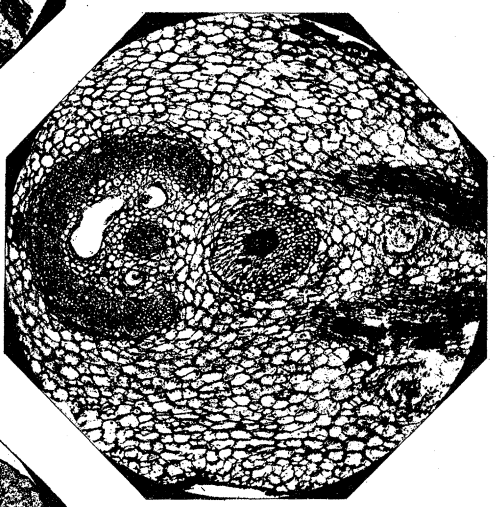

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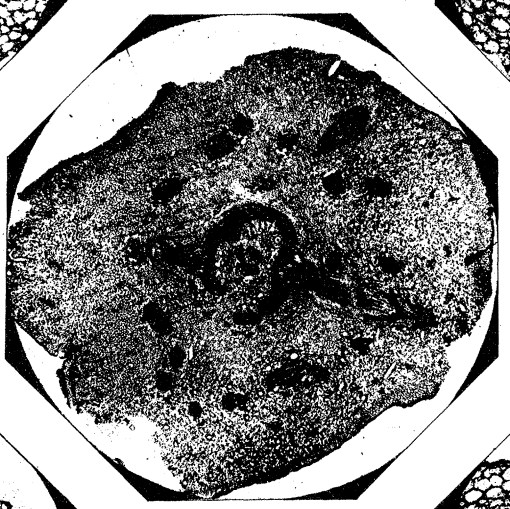

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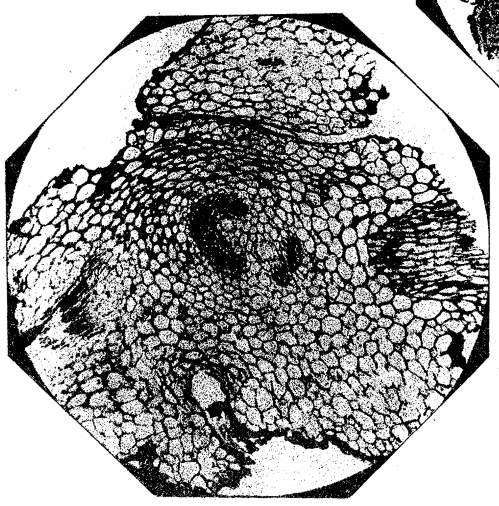

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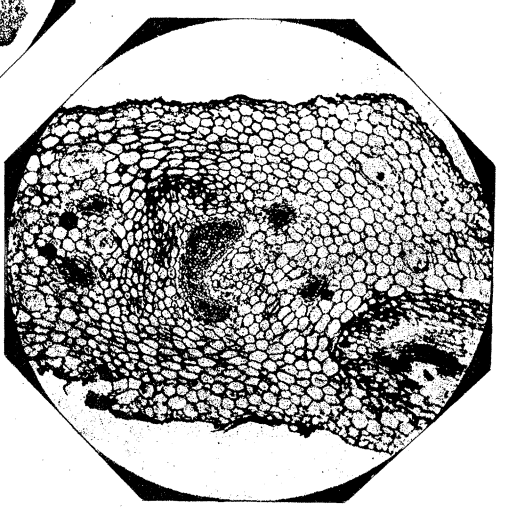

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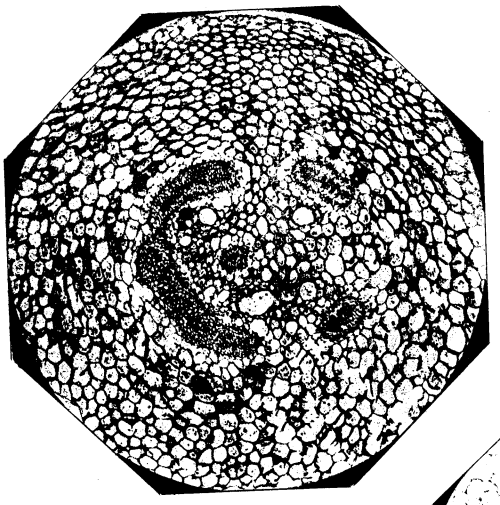

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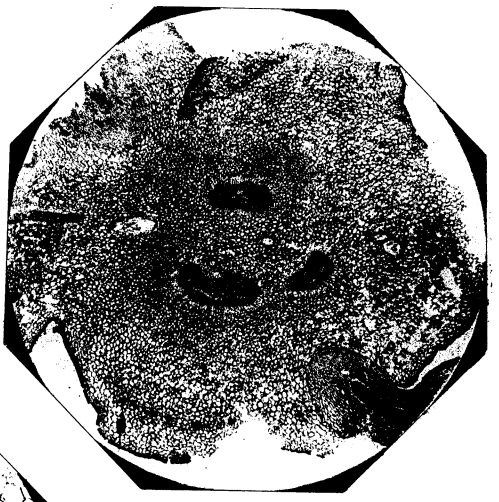

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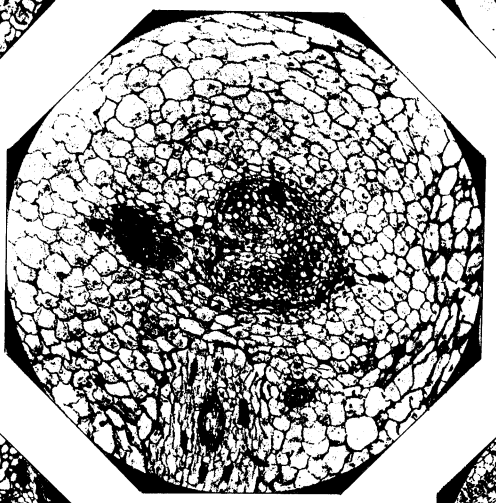

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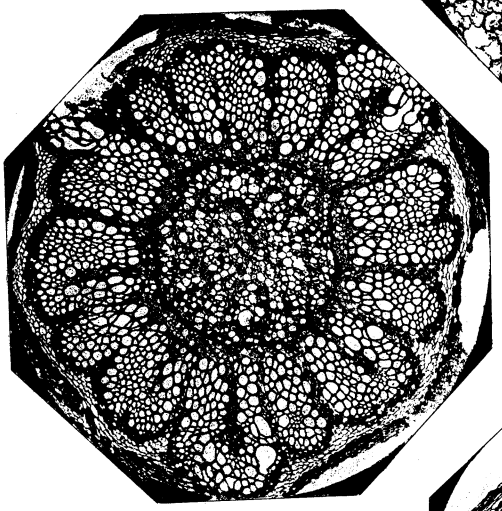

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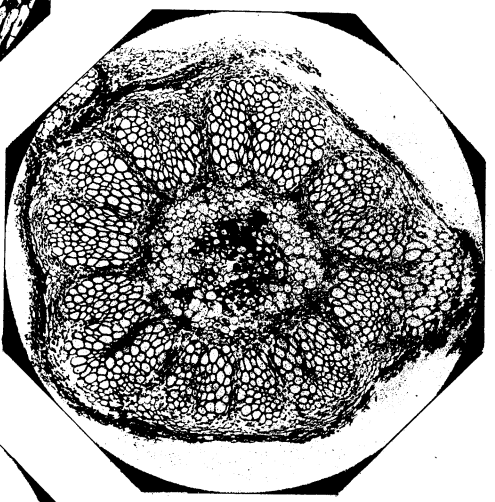

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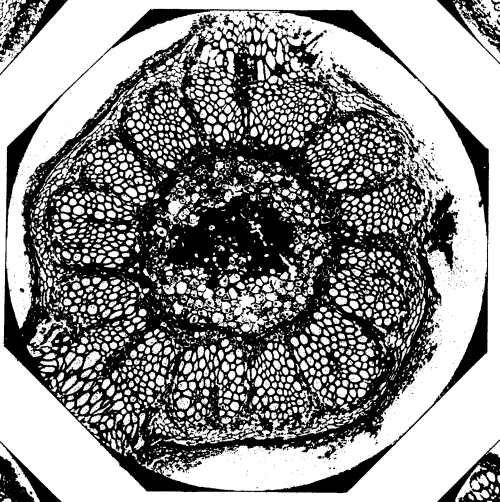

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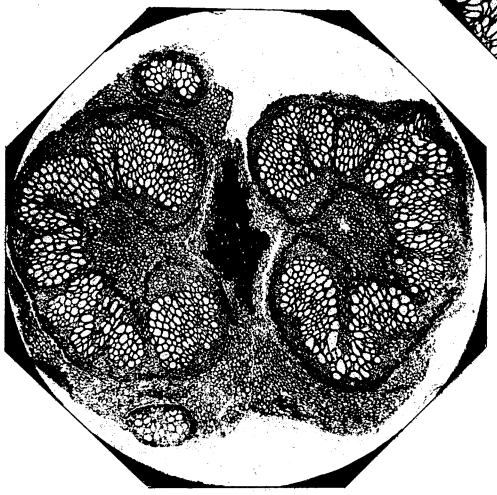

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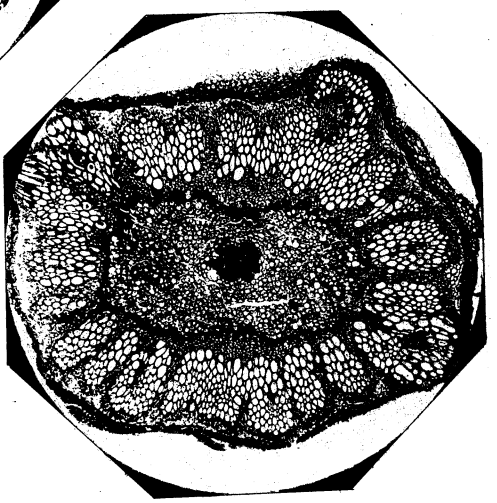

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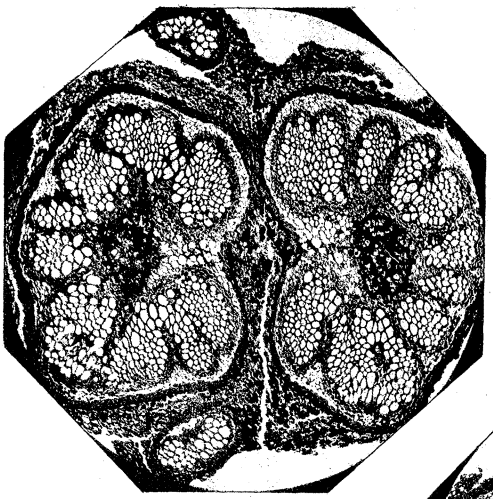

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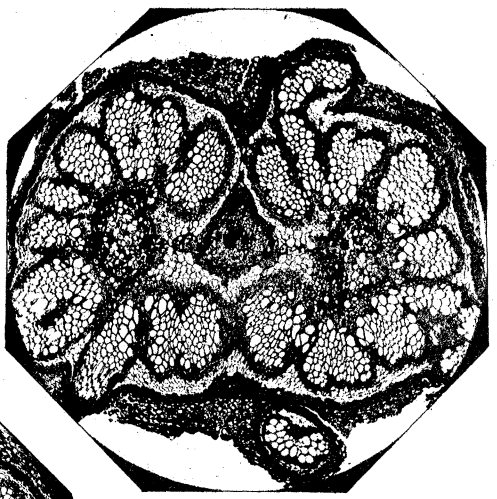

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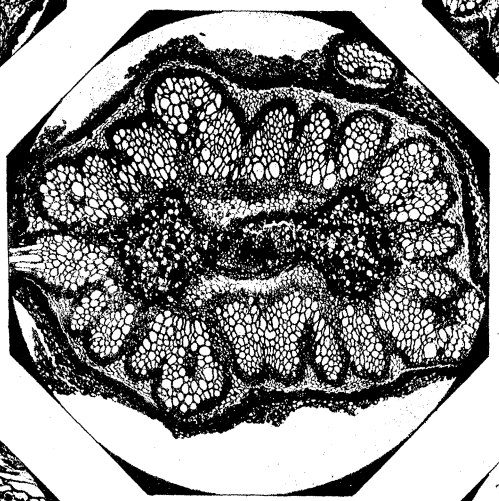

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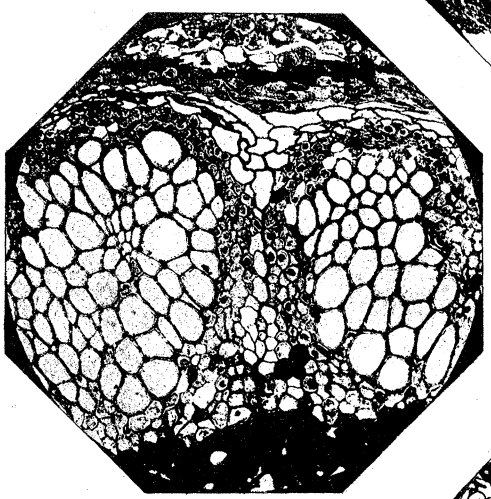

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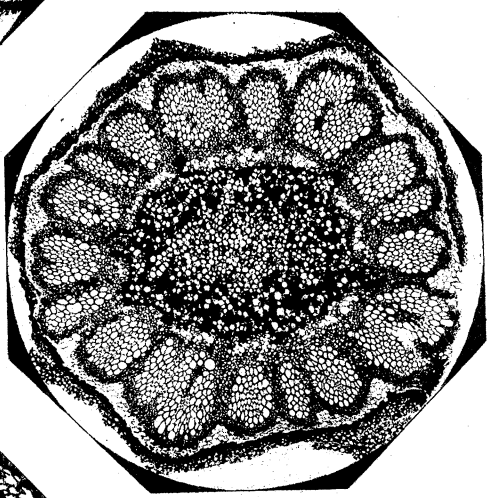

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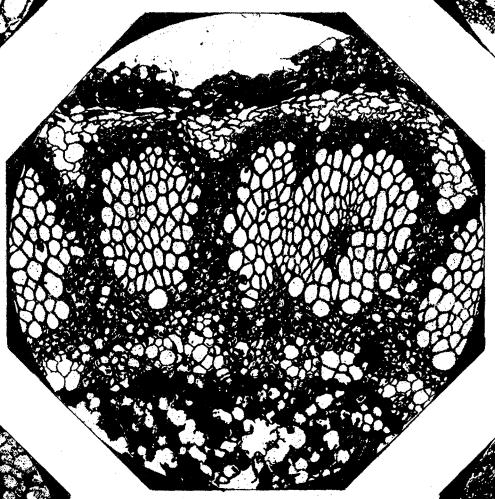

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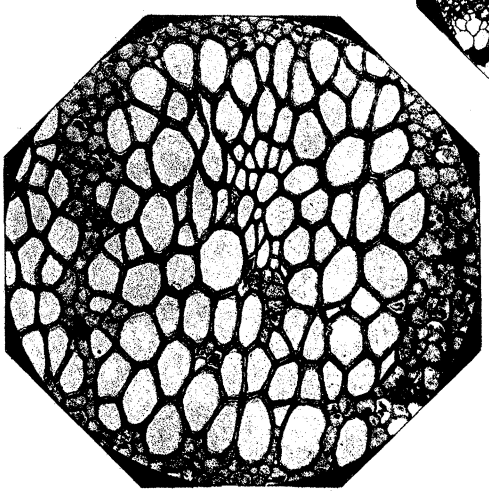

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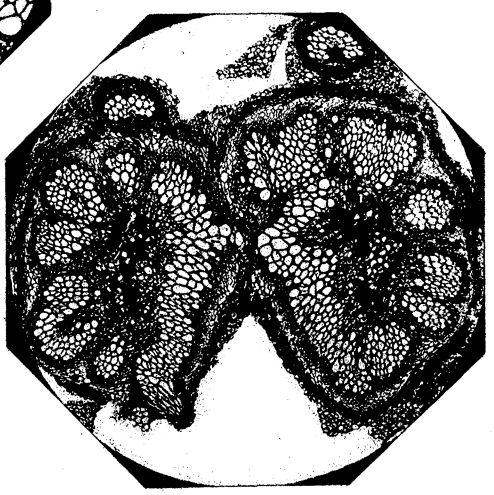

24.

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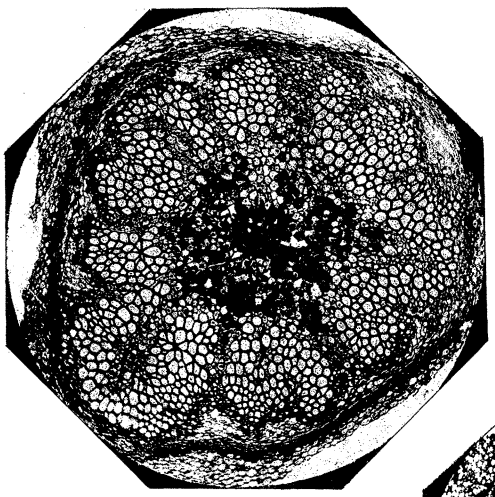

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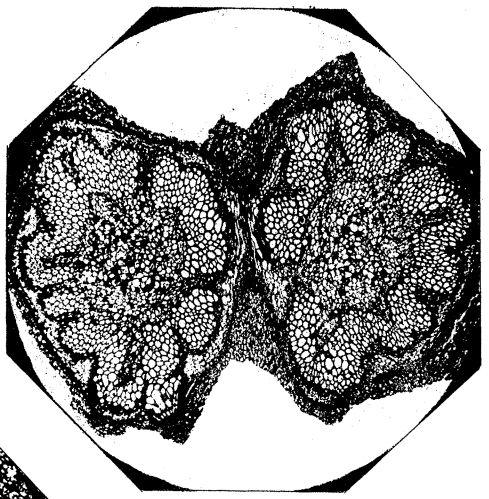

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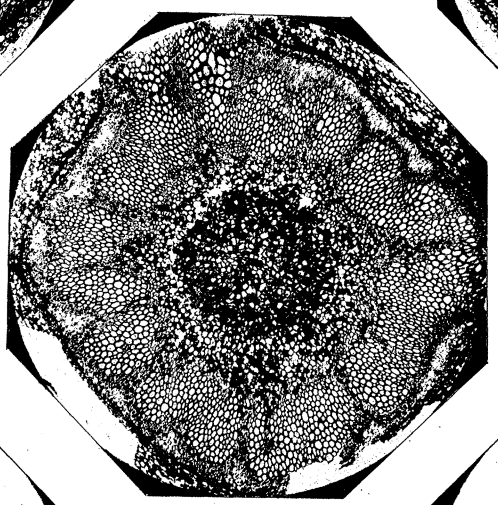

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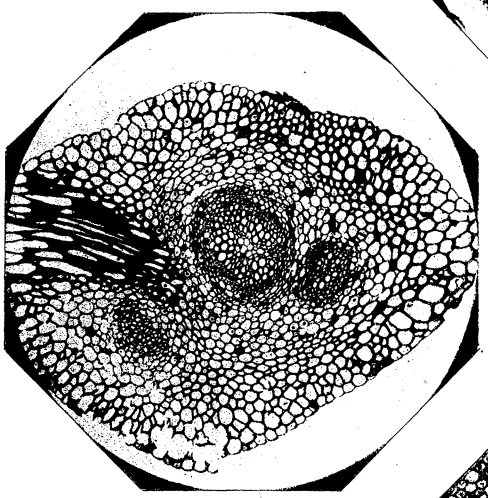

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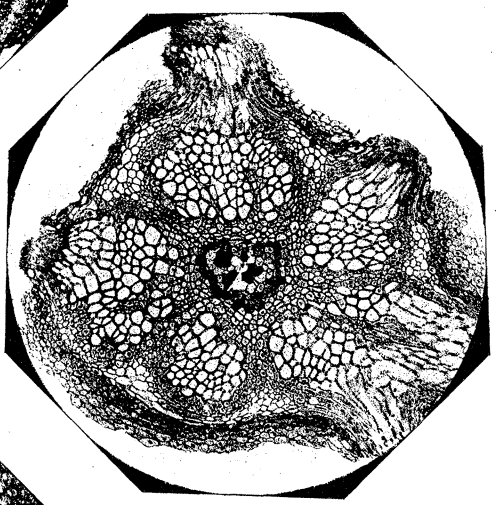

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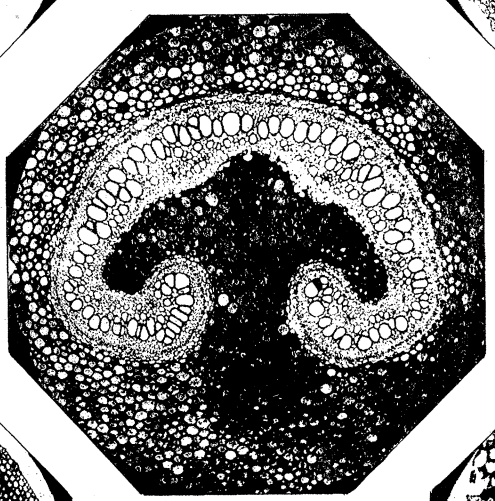

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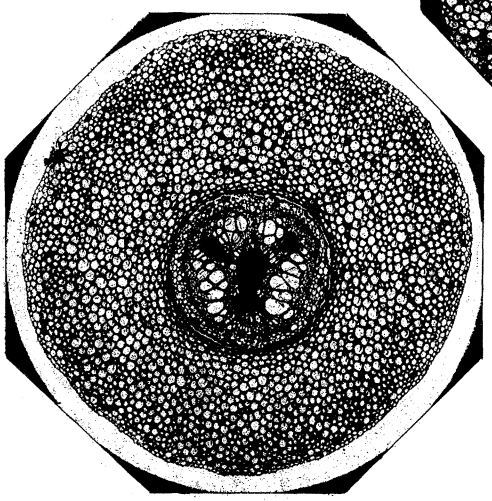

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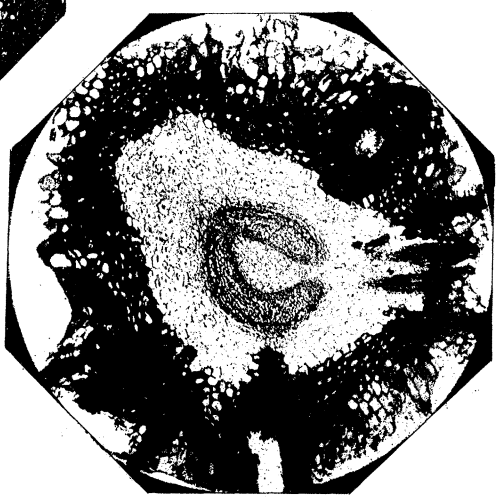

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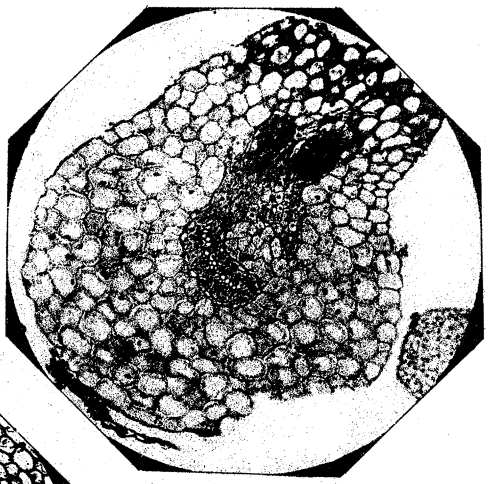

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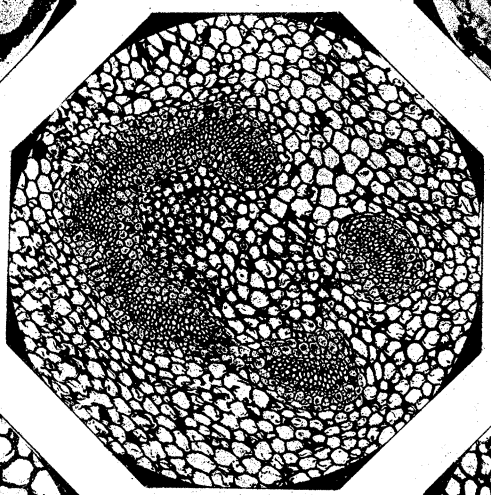

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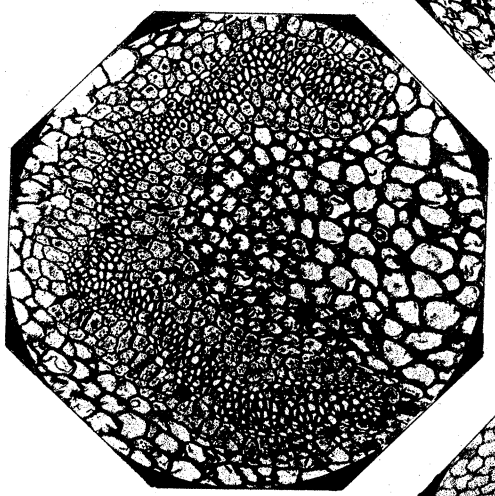

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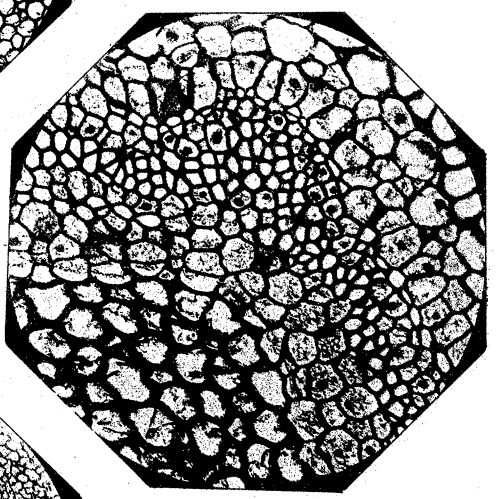

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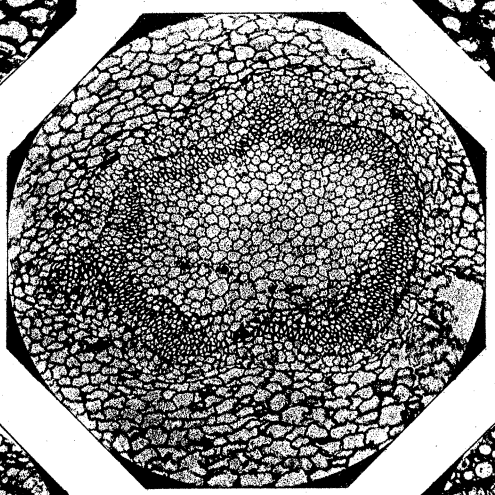

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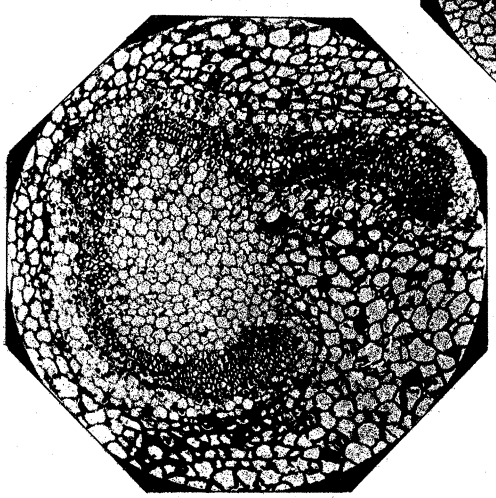

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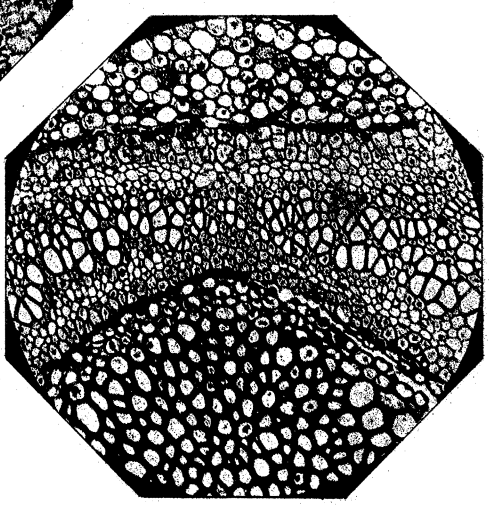

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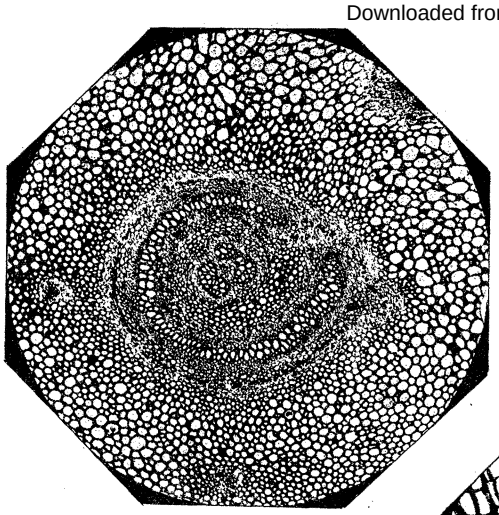

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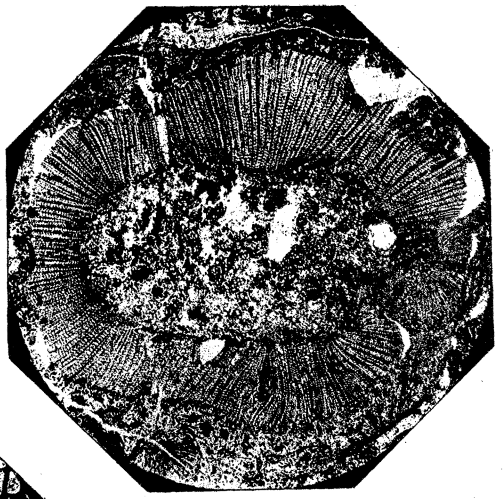

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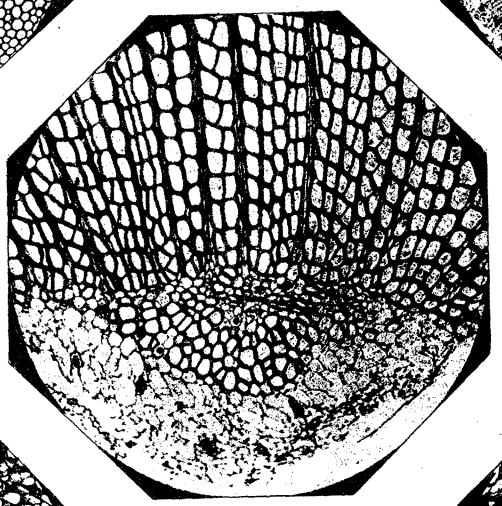

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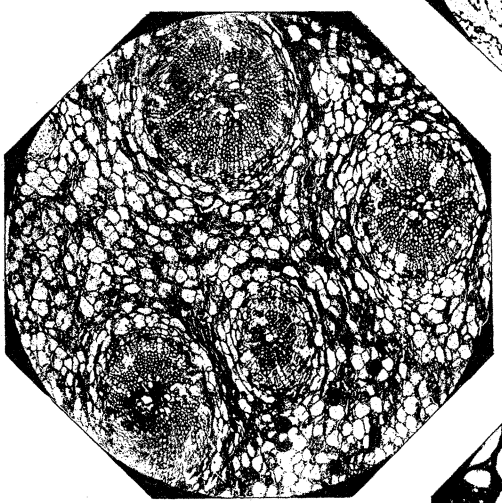

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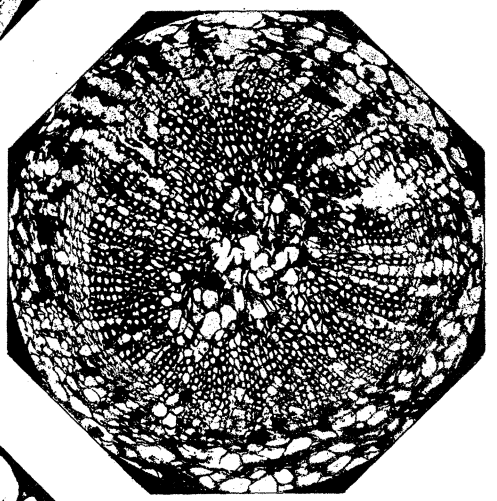

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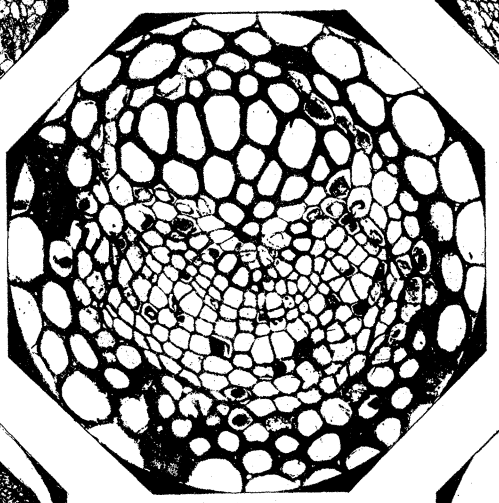

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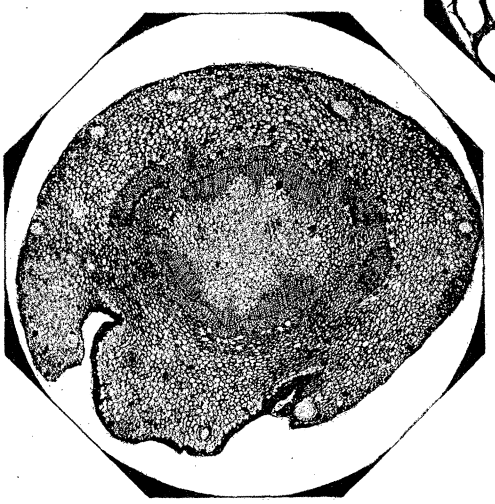

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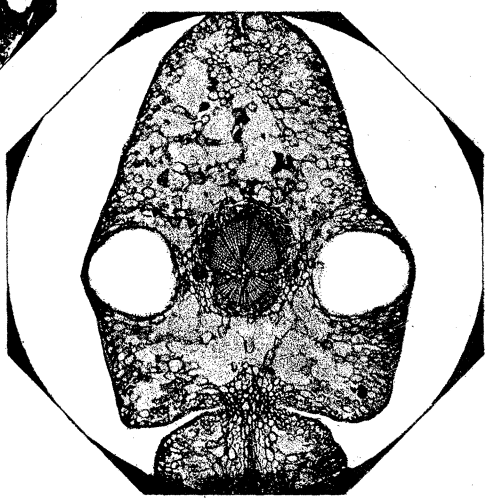

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