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THE ANATOMY OF THE OSMUNDACEAE.

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(WITH PLATES XIV–XVII)

INTRODUCTORY.

THE cauline vascular system of the Osmundaceae has attracted considerable attention on the part of morphologists, since it is exceptional among the leptosporangiate ferns in exhibiting a type of structure presented by the phanerogams. Thus DeBary, the exponent of the "bundle system," states that "collateral bundles" are with rare exceptions characteristic of the stems and leaves of the phanerogams, but are likewise found in the Osmundaceae,¹ and that in their arrangement in the stems of the Osmundaceae they follow the "dicotyledon type."² Later we find Van Tieghem, the first enunciator of the "stelar theory" expressing himself as follows:³

La tige des *Osmundes* et des *Todées* diffère de celle des autres Fougères. La stèle axile et sans moelle du jeune âge, au lieu de se diviser en restant grêle, demeure simple en s'élargissant progressivement à mesure que la tige grossit; elle prend une moelle de plus en plus large, à la périphérie de laquelle sont rangé en cercle un certain nombre de faisceaux libéroligneux à bois séparés, mais à libers confluent, entourés d'un péricycle commun et d'un endoderme général. En un mot la tige de ces plantes demeure monostélisque à tout âge, comme celle de la plupart des Phanérogames.

¹ DEBARY: Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne 331.

² DEBARY: *op. cit.* 246.

³ VAN TIEGHEM: *Traité de Botanique* 1373.

Plainly enough, therefore, these eminent botanists, starting from very different conceptions, have arrived at the same conclusion, namely, that the central cylinder of the Osmundaceae resembles that of the phanerogams.

It is important to note, however, that heretofore all anatomical researches in this family have been confined to the tropical genus *Todea* and the cosmopolitan *Osmunda regalis*; and that hence the conclusion just stated has been based on the phenomena presented by these alone. When Van Tiegham proposed his "stelar hypothesis" several cryptogams besides the Osmundaceae were cited as exceptionally possessing medullated monostelic central cylinders. Since then more extended researches have been made which have yielded important results. Thus it has been shown that the central cylinder of *Ophioglossum* and of *Botrychium* instead of being medullated monostelic is in reality "gamodesmic;"⁴ that the central cylinder in the entire family Equisetaceae, some of whose species were included in the exceptions, is of the same kind;⁵ and that the central cylinder of the genus *Helminthostachys* is also of the "gamodesmic" type.⁶ It is true that Strasburger holds⁷ that the internal endodermis and endodermal sheaths about individual bundles are of intrastelar origin, and not of cortical as is the external endodermis, and that therefore these exceptions still stand; but this objection may be advantageously left for subsequent consideration. Of the apparent exceptions, the family Osmundaceae has remained untouched, and I have undertaken the present research on this anomalous case, with the primary object of furnishing data that will help determine the proper morphological interpretation of its vascular system.

The family Osmundaceae is a very limited one in point of numbers, consisting of but two genera, *Osmunda* with eight species, and *Todea* with six, and therefore constitutes a very

⁴ POIRAULT: *Ann. Sci. Nat. Bot.* VII. 18: 113. 1893.

⁵ JEFFREY: *Mem. Boston Soc. Nat. Hist.* 5: 155. 1899.

⁶ FARMER: *Ann. Bot.* 13: 421. 1899.

⁷ STRASBURGER: *Histologische Beiträge.* 3: —. 1891.

small part of the fern flora of the earth. But this does not seem to have always been the case,⁸ for the Marattiaceae, although overwhelmingly predominant in the Coal period, constituted but 4 per cent. of the total filicineous flora in the Lower Jurassic, the remainder being composed of Osmundaceae and Cyatheaceae, with the related families Matonineae and Protopolypodiaceae. As to distribution, the first genus is confined to the northern hemisphere, and the Todeas are with one exception found only in Australasia. Five Osmundas belong exclusively to restricted areas in east Asia and the adjoining islands; *O. Claytoniana* occurs in the Himalayas and North America; *O. cinnamomea* in eastern Asia, North and South America; and *O. regalis* in every continent except Australasia. Of the Todeas, *T. barbara* is a native of Australia, New Zealand, and South Africa; and the remaining species, the so-called "filmy" Todeas (*Leptopteris* of some authors), belong to oceanic islands in the eastern south-tropical region.⁹

Of these species I have had the opportunity of studying five, namely, *O. regalis*, *O. cinnamomea*, *O. Claytoniana*, *T. barbara*, and *T. superba*. Nevertheless, in the following pages most attention will be devoted to *O. cinnamomea*, not so much because its anatomy has not previously been described, as because the writer, for reasons which will become apparent, believes it retains a more primitive type of skeletal axis than any of the family so far investigated. The material of the species of *Osmunda* studied was collected from several different localities, and in large quantities. Of *O. cinnamomea* specimens from fully a hundred and fifty plants were preserved and examined, and of each of the others perhaps one-third of that number. The more important points were verified from specimens taken from three different localities.

Observations have been mainly restricted to the mature root, stem, and leaf trace. Some young plants of *Osmunda* were studied, and the growing points of the older stems have been

⁸ SCOTT: Studies in fossil botany 304. 1900.

⁹ DIELS: Engler and Prantl's *Natürlichen Pflanzenfamilien* 14: 377. 1900.

sectioned. But the mature stem, especially the region at which it branches, has proved to be of chief interest from the standpoint of questions of comparative anatomy.

THE STEM.

GENERAL ANATOMY.—The mature stems are very stout rhizomes, exceptionally so in *T. barbara*, which grow in a direction somewhat oblique to the horizontal. The leaves are in a closely set tuft at the anterior end, for they are annual and the internodes are very short. The broadly winged, overlapping bases with their sclerenchymatous sheaths resist decay long after the remaining portion of the leaf has perished, and these, together with the roots, which are very numerous, greatly add to the bulk of the stem. The stem usually bifurcates once into two branches of equal size, which lie in a horizontal plane. A few specimens of *O. regalis* were found, however, in which one of the forks was much larger than the other, but the larger almost immediately divided again, so that there were three branches of about the same size lying in the same plane. The forking bears no relation to the number of leaves produced, counting from the cotyledons, nor to the age of the plant. Occasionally there is no branching at all, though maturity has long since been attained, while in rare cases it has taken place comparatively early in the life of the fern.

The rhizome exhibits a very characteristic appearance in cross-section (*fig. 1*). The outer portion, the thick external cortex (*ex. c.*), consists of very resistant, dark-brown sclerenchyma, in *O. cinnamomea* of a rich red-tinted brown, in *O. regalis* and the *Todeas* of a black, and in *O. Claytoniana* of a dull brown hue. The cortex is marked by leaf-traces (*lt*), which form a close spiral, and at the nodes by the escaping roots (*r*). In *O. cinnamomea* sclerification of the cortical tissue is later in taking place than in the other species. The internal cortex (*i. c.*) is parenchymatous, comparatively narrow, roughly pentagonal, and its cells are heavily loaded with starch grains. Passing the pericycle and the bast region, which form a complete

sheath, the wood (x) of the stele is seen to be broken up into bundles of various shapes arranged in a circle, and separated from one another by the so-called medullary rays. These medullary rays extend out from a large pith. The pith or medulla in *O. Claytoniana* and *T. superba* is apparently homogeneous. In *O. regalis* it is often discolored and may contain one or more strands of brown sclerenchyma; in *O. cinnamomea* it is very frequently characterized by some brown sclerenchymatous tissue, and in *T. barbara* there is a large axial strand of this supporting tissue.

HISTOLOGY.—But we turn now to acquire a more intimate acquaintance with the stem as revealed by a study of its histological features. For this purpose several sets of transverse and longitudinal series were prepared, and a great many microtome sections examined. The material cut included stems of various ages. As development proceeds rather slowly, all the tissues are mature only at a considerable distance from the apex of the plant.

The cortical part of the stem has little of interest for us other than in the respects already mentioned. The sclerenchyma consists of elongated, thick walled cells, with a small lumen containing starch grains. The walls are brownish, and marked by simple pits, which are round or slit-like. According to Strasburger,¹⁰ the endodermis is not the innermost cortical layer, but I am unable to verify this. He has made the statement that the innermost cortical layer at a certain stage divides by tangential walls to form several layers of cells; of these, the outermost becomes differentiated as the endodermis, and the remaining layers lie between this and the phloem, filling the place of a pericycle. The somewhat elongated cells of the endodermis are marked in every case by the characteristic cuticularization of the radial walls, which in transverse section shows as the "radial dot" (*fig. 6, e, e*). The "radial dot" is distinctively brought out by treatment with phloroglucin and hydrochloric acid, and also with dilute sulfuric acid. In *O.*

¹⁰ STRASBURGER, *op. cit.* 449.

Claytoniana the radial markings are generally not as distinct as in the rest of the species studied, and the cells are reduced in size in comparison with those of the layers in contact (*fig. 8, e*). The contents in this species, too, are meager, consisting of granular protoplasm, a nucleus which as a rule stains a deeper red with saffranin than those of surrounding cells, and a few starch granules as shown by treatment with iodine solutions. Sometimes the endodermal cells of *O. cinnamomea* are likewise apparent by the lack of contents, in contrast to the heavily-laden cells, both ectad and centrad. Generally in this species, as in the remaining ones, *T. superba* excepted, the cells are filled with tannin, so that the endodermis stands out very distinctly.

The pericycle is entirely parenchymatous and consists of several layers—in *O. Claytoniana* and *Todea* of two or three, in *O. cinnamomea* of three or four, and in *O. regalis* of one to three. The cells are elongated, cylindrical, provided with large nuclei, and filled with finely granular contents, part of which is starch. Haematoxylin imparts to this tissue a light blue color. Tangential sections show that the orientation of the cells is very irregular (*figs. 3 and 9, p*). Immediately opposite the point of origin of a leaf trace, and for a short distance below, the long axes of the cells run parallel with the long axis of the stem, but for the most part in the remaining regions of the stem there is considerable disturbance, though only in tangential planes. This disturbance is commonly so marked that the long axis of the cell is at right angles to the stem axis, and between this and the parallel position there is every gradation. Therefore in transverse section these cells are either round or more or less tangentially lengthened (*fig. 8, p*). This variation in orientation is of interest, as it is connected with a similar phenomenon in layers lying nearer the cauline axis, namely in the phloem region.

XYLEM.—Before dealing with the phloem, however, it will be convenient to describe the xylem. The wood elements are of two kinds, namely, small ringed and spiral elements constituting the protoxylem, and scalariform tracheids which are of later development constituting the metaxylem. Occasionally a

parenchymatous cell is found among the tracheids. A transverse section shows, as mentioned before, a ring of variously shaped bundles; and by tracing these up and down, or by boiling a piece of stem in potash and then removing the softer tissues, there is shown to be a network forming the wall of a hollow cylinder, the strands being the "bundles" of DeBary, and the meshes the spaces occupied by the "medullary rays." Though there is a great deal of regularity in the apparent construction of this network, as proved by DeBary and Zenetti in *O. regalis*, yet a study of development shows that the "bundle theory" is inadequate for giving the right conception of the vascular system. In the young stem of the Osmundaceae the wood forms a completely closed cylinder, and Van Tieghem, basing his conclusions on *Todea* and *O. regalis*, has stated this to be the case for the whole family. I am able to state that the phenomena in the young stem of *O. cinnamomea* and *O. Claytoniana* are in accordance with his general conclusions in this respect.

Now directly above the point at which a leaf trace leaves the stele the wood is not developed for some distance. This gap is filled by parenchyma chiefly, except at the outer part, which is occupied by sieve tubes. There are exceptions in *O. cinnamomea* to be described later. Thus a transverse section of the stele, just above a node, shows a ring of wood broken at one place, the break being occupied by the tissues just referred to; in other words, the stele here has one medullary ray. *Fig. 23* shows a transverse section of the stem of *O. Claytoniana* through this region. Still further up the internode the ring is complete again. There is the same sort of gap above the second node. However, as the nodes become more frequent, that is, as the internodes become shorter, a leaf gap extends through more than one internode, and in a transverse section there is more than one medullary ray, until in the full grown stem, where a leaf gap extends through several internodes, a transverse section shows several gaps cut across, or in other words shows several medullary rays. It is therefore evident that the number of medullary rays seen in any transverse section depends on the frequency of

the nodes and the length of the gaps. In well nourished stems the number is greatest in *O. Claytoniana* (*fig. 17*), there usually being about twenty, and in *T. barbara* (*fig. 24*) the fewest. In this species the gaps are quite short, so that while the wall may be thin in many places at any given level, there are not more than two to six medullary rays seen in the cross section (*fig. 24*).

The persistent portions of the cylinder of wood, the "bundles," present various contours in cross section, the shape of any particular portion lying between two adjacent gaps, that is, of any strand, varying with the level at which it is cut. Just below where the leaf trace is given off, the wall is hollowed out on the side towards the pith, so that the transverse section of the strand presents a horseshoe shape (*fig. 17*). The middle of the inner surface of the strand at this level is occupied by protoxylem, which consists of about a half dozen small ringed and spiral vessels. Following the strand down, it is seen that the arms of the horseshoe thicken on the sides facing one another, especially towards the ends of the arms (*fig. 15, s*). Finally, the opening between the ends is fully closed and a small group of parenchymatous cells lying exactly centrad of the protoxylem is thereby enclosed (*fig. 17, s*). The parenchyma is more and more encroached upon by the xylem, until lower down it is seen no more. Not far below where the parenchyma vanishes, the protoxylem in that strand likewise disappears. Somewhat above the level at which the parenchyma is enclosed the strand begins to thin out on the outer side, a sharp trough-like indentation appearing, but not in the same radius as that in which the protoxylem lies. This trough continues to deepen until a few nodes down the strand is cut through, the point at which the break occurs being, indeed, the apex of a leaf gap. Thus neither the outer nor the inner surface of the cylinder of xylem is smooth; the lower part of a leaf gap can be traced as a hollow on the inner surface just below where the leaf is given off, ending as a blind tube amongst the tracheids, while the upper end of the gap may be traced as a furrow on the outer surface of the cylinder, gradually becoming more and more shallow

The protoxylem occurs in small groups of six to eight cells each, and a transverse section of the central cylinder shows from five to seven of these groups. Each group of protoxylem elements passes out in its entirety into a leaf trace, and on following back from the leaf trace each vanishes as already described. The protoxylem is therefore not continuous throughout the stem, but is in small, discontinuous strands. This fact has been recorded for *O. regalis* by Zenetti.¹¹

Lying externally to the wood are from four to six layers of elongated parenchymatous cells, rich in protoplasmic contents and in small starch grains. They are continuous with the parenchymatous cells of the medullary rays and do not materially differ from them. Those occupying the middle of the medullary rays have more meager contents, and towards the stem axis they become larger. That there is a "xylem sheath" characterized by cells of greater size and richer contents such as Zenetti describes for *O. regalis*, I cannot affirm, and certainly there is not such a sheath in *O. Claytoniana*.

PHLOEM.—The tissues that have just been described are bordered by the phloem, which consists chiefly of sieve tubes. Parenchymatous cells are sometimes met with in isolated positions in the metaphloem, and between the metaphloem and the protophloem they constitute a more or less broken layer, most pronounced in *O. Claytoniana*, and least constant in *O. regalis* and *T. barbara*. The sieve tubes are strongly developed and are of the "type vigne" of Lecomte. They are large, have thin walls of unmodified cellulose lined with a delicate layer of protoplasm, and are devoid of nuclei. They are provided with oblique terminal walls and are furnished with sieve plates both simple and compound. The sieve plates are covered with "globules brillants," and by treatment with proper reagents callus plugs may be demonstrated in them. The sieve tubes of the protophloem are smaller than those of the metaphloem and their terminal walls are not as oblique.

As there has been considerable difference of opinion regarding

¹¹ZENETTI: Das Leitungssystem im Stamm von *O. regalis*. Bot. Zeit. 53:63, 1895.

the disposition of the phloem in *O. regalis*, it will be well to define a sieve tube. Both Russow and Janczewski have studied sieve tubes very carefully, and Poirault has more recently reinvestigated the subject in the vascular cryptogams. The investigator last named summed up his observations on sieve tubes in the roots of vascular cryptogams in the following terms :¹²

Les tubes criblés peuvent se rapporter à deux types : le premier caractérisé par des cloisons transverses perpendiculaires aux faces principales et ne portant qu'un seul crible (*type Courge*, Lecomte) ; le second reconnaissable à ses cloisons transverses très obliques portant d'autant plus de cribles que leur obliquité est plus grande (*type Vigne*, Lecomte). On trouve, en outre, sur les faces longitudinales des punctuations isolées ou réunies en très petits groupes, constituant rarement des cribles aussi développés que ceux des faces transverses. Le contenu de ces tubes est un liquide hyalin tenant en suspension de nombreuses sphérules réfringentes, rassemblés surtout au niveau des cribles et des punctuations isolées. Il n'y a pas de noyau. La membrane est cellulosique.

He further adds that two substances occur as a rule — (1) the “globules brillants” already mentioned, and (2) “les bouchons calleux qui font corps avec la membrane et peut-être la traversent entièrement.”

In dealing with the sieve tubes of the stem and petiole he does not point out any other peculiarities, but deals at length with the callus plugs, and the perforation of the sieve plates.¹³ The observations of Russow, Janczewski, and Poirault agree for the most part, except in reference to the callus plugs.

The following criteria would seem to be distinctive in determining the presence of sieve tubes in the Osmundaceae; the existence of sieve plates, the absence of nuclei, and the presence of “globules brillants.” Less distinctive and rather as a confirmatory test I have sought for callus. Russow made this test one of paramount importance, but it seems best in dealing with the vascular cryptogams to give it a second place, and for the following reasons: (1) the callus, so-called, in the sieve tubes

¹² POIRAULT: Recherches sur les cryptogames vasculaires. Ann. Sci. Nat. Bot. VII. 18: 138. 1893.

¹³ POIRAULT: *op. cit.* 191.

of the vascular cryptogams may not be identical with that found in phanerogams; (2) it occurs in minute quantities only, and in some plants (*e. g.*, the Ophioglossaceae) probably does not occur at all; (3) its presence is determined by delicate microchemical means, and then only by limited color reactions.

Janczewski¹⁴ claimed to have found callus in *Pteris aquilina* alone of all the vascular cryptogams he examined, and states that it does not occur in *O. regalis*. The reagents he used were Schulze's solution (or chlor-zinc-iodin) and rosolic acid. On the other hand, Russow found callus in all of the sieve tubes he examined. The reagent he used was a mixture in variable proportions of chlor-zinc-iodin and potassium iodid-iodin. It should be stated that in the vascular cryptogams callus occurs in the wall of the sieve plate, appearing as if it were a part of the wall. After staining with a suitable iodine solution, the callus shows in face view as one or more round brown spots, and in section as rods or granules occupying the entire thickness of the lamella. Poirault has largely corroborated Russow's observations. He disagreed with Russow's generalization that it is a constant feature of sieve tubes, for he states that he has been unable to find any trace of callus in *Angiopteris* and *Ophioglossum*.¹⁵ In view of these investigations, therefore, it becomes a matter of interest to know if the sieve tubes of Osmundaceae show the phenomena of callus as described by Janczewski for *Pteris*, and by Russow and Poirault for many others of the vascular cryptogams.

Accordingly tangential and transverse sections about five microns thick, of the three *Osmundas* studied and of *T. barbara* were cut from mature pieces of stem embedded in celloidin. In the present research the writer has tried several stains, such as ruthenium oxid, Hofmann's blue, rosolic acid, and Russow's mixture. These have been applied to sieve tubes of plants from widely separated groups, such as *Vitis* (summer and winter sieve tubes), *Tilia*, *Pinus*, *Pteris*, and the mixture of chlor-zinc-iodine

¹⁴ JANCZEWSKI: Tubes cribreux. *Ann. Sci. Nat. Bot.* VI. 14: 50. 1882.

¹⁵ POIRAULT: *op. cit.* 192.

and potassium iodid-iodin proved to be by far the most satisfactory reagent for the demonstration of callus. The two constituents of this reagent were prepared fresh, and then mixed in different proportions until one giving the best results was obtained. The proportions vary with the different kinds of plants tested. In using this stain, though the presence of the celloidin is not a serious objection, it is preferable to dissolve out the celloidin, wash in alcohol, then in distilled water, and examine in stain on the slide.

In face view it is difficult to make observations on account of the "globules brillants," hence the most reliable observations can be made on sectioned plates. Almost at once after applying the stain, the callus plugs become evident, staining a dark red-brown (*fig. 7*). They appear as more or less fine rods, completely traversing the sieve plate, and their number in a sieve plate depends on its size. The cellulose is slower in staining; at first it is light blue or a violet, and later a deep blue. Hence the callus plugs are to be seen most clearly in the early stages of the staining process. The stain unfortunately is not permanent. Callus was clearly demonstrated in the species under investigation, but on account of the size of the cells and of the sieve plates, *T. barbara* proved the best subject for the purpose. As one of the characters of the sieve tubes of the Osmundaceae, we record, therefore, the regular occurrence of callus plugs in the sieve plates.

The "globules brillants" are exceedingly abundant in the sieve tubes, and especially in the older ones (*fig. 7*). While they adhere to the protoplasm of the cell and may be found in any part of the cell they are by far most abundant about the sieve plates, dotting their surface, filling the pits, and surrounding the entrance to the pits. They are evidently not homogeneous, but appear to consist of two substances, one of which is more refractive than the other, for by slight focusing up and down they change from a dark looking, opaque granule to a light semi-translucent spherule. Iodin solutions stain them brown, not appreciably different from the callus plugs. Occasionally

irregular fragments of matter are found in the cell, which also stain a similar brown. The relation between these fragments, the "globules brillants," the callus, and the disappearance of the nuclei calls for further investigation.

The sieve plates are very numerous, and vary in size and form. The walls of the pits are abrupt, and the number of pits varies with the size of the plate. The larger plates are irregularly oblong and the smaller ones are round. In *Todea* they are largest and most numerous. Having described the sieve tubes at some length, we shall now examine their distribution.

The phloem forms a continuous sheath, the outer portion of which is the protophloem. To this peripheral part of the phloem I find that DeBary and Zenetti alone make specific reference. The former states¹⁶ that this region of the central cylinder is characterized by "quergestreckte Zellen," but he offers no opinion as to the nature of the tissue in question. Zenetti divides the zone into strands of typical protophloem and connecting portions of "quergestreckte Zellen." The typical protophloem is in short strands one cell thick, lying ectad of strands of xylem which are about to give off the leaf traces. The "quergestreckte Zellen" he cannot recognize as sieve tissue; because of the "quergestreckt" form and the position of the cells. This tissue in *Osmunda regalis*, consequently, forms a cylinder interrupted by the strands of protophloem only, but Zenetti found it to be generally two cells in thickness and opposite the medullary rays often several cells deep.

I have ascertained that the "quergestreckte Zellen" are devoid of nuclei; their walls are of cellulose, staining violet or blue with iodine solutions. They are rounded, elongated elements, with more or less oblique terminal walls; and are characterized by the possession of sieve plates which show the callus reaction when treated with Russow's reagent; the cells contain an abundance of "globules brillants" which are aggregated especially about the plates; the protoplasm is reduced to a thin parietal layer. The characters of the typical protophloem cells

¹⁶ DEBARY: *op. cit.* 360.

are the same as those of the "quergestreckte Zellen" except in regard to orientation (*fig. 6*).

Transverse sections show that the long axes of the so-called "quergestreckte Zellen" are tangentially placed, and never radially to any degree. To determine the slant of the long axes, therefore, with reference to the axis of the stem, tangential sections must be made. If such be examined it is seen that some are exactly at right angles to the axis, others are almost or entirely parallel, and between these extremes there is every gradation. This at once explains the difference in "width" of the "quergestreckte Zellen" in transverse section. It is further to be noted from the tangential sections that the ends of typical protophloem cells never abut against the long sides of the "quergestreckte Zellen," but there is a gradual change in the direction of the latter so that their ends communicate with the protophloem and it is quite impossible to say where the typical protophloem ends and the "quergestreckte Zellen" begin.

The root and leaf have been examined for "quergestreckte Zellen," for if these elements constitute a characteristic textural feature of the Osmundaceae they would naturally occur elsewhere than in the stem. They are not present at all in the appendicular organs. Further, in the young sporophyte, where the leaf gaps are far apart, they are absent from considerable portions of the stem. The real nature of the "quergestreckte Zellen" will be discussed after observations on their development and their relation to the leaf traces have been described.

The "quergestreckte Zellen" and the typical protophloem cells form a continuous sheath in all the species studied. In *O. Claytoniana* the elements of this sheath are very much smaller, and so it is easier to distinguish them from the metaphloem. In *T. barbara* their histological characters are best studied because of their relatively large size. Frequently in *O. cinnamomea* and *O. regalis* it is difficult to decide in the mature stem whether or not certain cells belong to this sheath or to the metaphloem. But evidently in all of the species the sheath is rarely more than two cells in thickness, and often, especially in

O. Claytoniana, there is but a single layer. Opposite outgoing leaf traces the sheath is reduced to a single stratum.

The *metaphloem* forms a hollow cylinder consisting of large sieve tubes such as have already been described. They are thin-walled, and especially in *O. regalis* in the older parts of the stem have often collapsed. The sheath is one or two cells thick opposite the strands of xylem, and several cells in thickness opposite the medullary rays (*fig. 8, ph*). Most of the tubes run parallel with the long axis of the stem, but here and there "quergestreckte" examples occur.

This cylinder of metaphloem has a smooth outer surface, but the inner surface is rendered very uneven on account of the wedge-like proliferations of the sieve tissue opposite the leaf gaps. Since this is a phenomenon common to all the species studied, we naturally seek an explanation of this peculiar disposition of the phloem. In his memoir on sieve tubes Janczewski,¹⁷ who could hardly have been prejudiced by any stelar theories, noted that isolated sieve tubes occur occasionally here and there in the medullary rays of *O. regalis*. The writer has found undoubted cases of the same thing in *O. cinnamomea*.

Two such eminent botanists as DeBary and Strasburger have disagreed as to the topographical distribution of the layer of metaphloem sieve tubes in *O. regalis*. The former states¹⁸ that the sheath is continuous, while the latter states¹⁹ that he puts himself in opposition to DeBary on this point, for he considers the phloem to be interrupted opposite the medullary rays. Strasburger does not say for what reason he considers the cells opposite the medullary rays not to be sieve tubes. My own observations on *O. regalis* are precisely in accord with those of DeBary and Janczewski. The cells opposite the medullary rays differ in no way from the sieve tubes opposite the xylem strands. I have found the same to be true of the other species studied, with the additional observation that isolated sieve tubes occur sometimes in the tissues filling the leaf gaps of *O. cinnamomea*.

¹⁷ JANCZEWSKI: *op. cit.* 66.

¹⁸ DEBARY: *op. cit.* 360.

¹⁹ STRASBURGER: *op. cit.* 449.

To this last observation I have two others to add, namely, the occurrence of an internal phloem in which the sieve tubes form a more or less continuous ring (*figs. 21, and 22*), and in rare cases the union of external and internal phloem through a leaf gap. In a certain rich, moist situation about a dozen well nourished plants of *O. cinnamomea* grew, of which, on examination, five showed the phenomenon of a continuous layer of internal phloem. Search in an adjoining locality resulted in finding specimens which showed the same feature. To extend the range of observations, I visited a peat bog some twenty miles distant from Toronto, where I knew the cinnamon fern grew, and secured specimens characterized by the same peculiarity. *Fig. 21* shows a transverse section of a stem found in this last locality. The sieve tubes of this internal phloem are as typical as those of the external, and except for their position not be distinguished from them. They do not always form a continuous ring as do the sieve tubes of the external phloem, but are often in more or less detached groups, embedded in small celled parenchyma. The layer of sieve tubes is from one to three cells thick. It should be added that internal phloem occurs only near where the forking of the stem takes place.

O. cinnamomea shows likewise two other features which are constant throughout every part of the stem, and at once distinguish it from other species: (1) an internal endodermis, and (2) several layers of parenchyma between this and the xylem.

INTERNAL ENDODERMIS.—The internal endodermis possesses the characteristic radial dot, though sometimes not as clearly distinguishable as in the external endodermis (*i. e., fig. 2*). Its cells are usually larger than those of the latter, but are filled with similar contents, most frequently tannin (*fig. 15*). It is further to be noted that it bends outwards opposite the leaf gaps (*figs 10, etc.*), and not infrequently connects through them with the external endodermis. I have examined scores of stems of the cinnamon fern, and in every specimen there was an internal endodermis. On the contrary, it seems to be invariably absent from the other species studied. As the central cylinder of the

family Osmundaceae has heretofore been classed as monostelic, the existence of an internal endodermis in one of the species is therefore a matter of considerable moment, especially if it be regarded as a real phloeoterma.

Between the internal endodermis and the xylem there is a cylinder of elongated parenchyma, rich in starch and protoplasm, and from two to seven cells in thickness. This layer is continuous with the medullary rays. In *O. regalis*, *O. Claytoniana*, *T. barbara*, and *T. superba* a similar but thinner layer is found as a rule, and the cells are always smaller and richer in contents than those of the medulla on which they border.

THE MEDULLA.—The medulla is very large in this family, particularly so in *O. Claytoniana*, and consists of large-celled parenchyma. Most of the cells are partly filled with large starch granules, but frequently some of them contain tannin, especially in *T. barbara*. A brownish fluid may occur in intercellular spaces, and in *O. regalis* within the cells themselves. In these regards there is often a striking resemblance between the parenchyma of the medulla and that of the internal cortex in the same plant. But there yet remains to be described a still more significant phenomenon, namely, the occurrence in the pith of brown sclerenchyma of the same kind as is found in the external cortex (*figs. 14* and *20*). This is probably a primitive feature, and in this, as in many other respects, *O. cinnamomea* proves to be most interesting. Out of forty-four pieces of stem, chosen at random, and representing a corresponding number of different plants of this species, twenty-five of the examples showed brown sclerenchyma in one or both ends. It occurs as a central strand, varying in size from a few cells to almost the limits of the pith, or as several small strands irregularly arranged. *Fig. 14* is a photograph of the transverse section of a stem in which there is a large axile strand, and *fig. 15* of one in which the sclerenchyma is entirely absent from the pith. Further it has the peculiar habit of being present at one level, but perhaps not at another; so it is likely to be found in nearly every plant if the stem be sectioned from end to end.

This same habit is characteristic of its appearance in *O. regalis* (fig. 20), but more often it is not present at all. That brown sclerenchyma occurred in the pith of *O. regalis* did not escape the observant DeBary,²⁰ but elsewhere I find no reference to this fact. Strangely enough, however, out of thirty-five or forty plants harvested from one locality there was not a trace of sclerenchyma to be found in the medulla of any of them, while in one region not far distant 25 per cent. showed this phenomenon, and in another a still higher per cent.

Parenchyma is the sole constituent of the medulla of *O. Claytoniana* (fig. 17). This is probably true of *T. superba* too. Fig. 25 is a cross section of *T. barbara* taken too near the growing point to show sclerenchyma, but farther down the medulla was occupied by a large strand of this tissue (fig. 24).

Thus medullary brown sclerenchyma is usually present in *O. cinnamomea*, in *O. regalis* not uncommonly, and in *O. Claytoniana* not at all. In *T. barbara* it also occurs, but apparently not in *T. superba*. It is perhaps significant that such series can be arranged, but of greater importance is the fact that the occurrence in the Osmundaceae of brown sclerenchymatous tissue, apparently within the cauline central cylinder, has no parallel among existing ferns.

THE FORK.—There yet remains to be described the anatomy of one particular portion of the stem, the part in the region of bifurcation. It has been stated that it is peculiar to the stem of the Osmundaceae to fork once, and that in a horizontal plane. We shall treat first of the phenomenon in *O. cinnamomea*. Tracing the main stem forwards, it is seen to become flattened and then to become constricted in a median vertical plane. Immediately anterior to the point of bifurcation of the vascular axis, there is a wide ramular gap in the central cylinder of each branch (fig. 10). Sections of the main axis immediately below the fork show two bands of phloem, one on the upper and one on the lower internal surface of the central cylinder (fig. 13). Sections passing through just in front of the region of bifurcation

²⁰ DEBARY: *op. cit.* p. 290.

show similar bands of phloem along the inner wall of the central cylinder of each branch (*fig. 11*). Cases have been described above, in which there is a complete cylinder of internal phloem instead of the two isolated bands just referred to (*fig. 21*). The internal and external phloem connect through the ramular gaps (*fig. 11*). Likewise the internal and external endodermis are in textural continuity through these gaps, so that there is free communication between the cortex and the pith (*fig. 10*).

Sometimes the cortex lying between the two branches contains brown sclerenchyma which is continuous through the ramular gaps with strands of the same tissue occurring in the medulla of the branches. Frequently in less vigorous plants a transverse section of the main axis posterior to the point of ramification shows a diamond-shaped piece of cortex surrounded by endodermis (*fig. 12*). Posteriorly this included piece of cortex becomes continuous with the medulla of the main axis (*fig. 13*), and anteriorly with the general cortex (*fig. 11*).

Twenty-five forks of *O. cinnamomea* were selected at random and sectioned. Twelve of them presented the phenomenon of typical wide ramular gaps. Six of them were of the reduced kind just described. In five cases there were gaps in the xylem only, cortex and medulla never becoming continuous; and in two even the xylem did not open up (*fig. 16*). For reasons to be outlined later, the writer believes the wide gaps to be the most primitive.

O. regalis presents a much degenerated form of ramular gap, for here only the xylem opens (*fig. 19*). In *O. Claytoniana* the degeneration is carried still farther, for as a rule there are no branch-gaps at all (*fig. 18*). In *T. barbara* the xylem alone may open up.

The phenomena of the fork may be thus summarized:

- (1) Complete ramular gaps occur only in *O. cinnamomea*.
- (2) Internal phloem occurs only in *O. cinnamomea*. It is found in the branches just above, and in the parent axis just below the point of bifurcation of the central cylinder.

(3) The internal phloem may form an entire cylinder.

(4) Where gaps are complete, the cortical and medullary tissues connect through them.

(5) Thus sclerenchyma of the cortex is sometimes continuous with sclerenchyma in the medulla of the main axis, and of the branches.

(6) *O. cinnamomea* presents the following forms of ramular gaps arranged in order of degeneration, (*a*) complete gaps, (*b*), phloem and xylem only open, (*c*) the xylem alone opens, (*d*) no gaps at all.

(7) *O. regalis* and *T. barbara* show gaps in the xylem only, and in *O. Claytoniana* there are usually none at all. *O. Claytoniana*, therefore, presents the extreme case of degeneration.

THE LEAF TRACE.

The leaf traces pass very obliquely up through the external cortex. A section of a leaf trace shortly before it passes into the petiole presents some noteworthy characters. In the first place there is no pith, but a solid horseshoe-shaped mass of xylem with the convex side turned outwards (*fig. 5, x*). The xylem is made up of large scalariform tracheids with a protruding mass of a few small vessels constituting the protoxylem. The protoxylem is situated on the inner face of the single strand of xylem (*px*), and is continuous with that of the stem. In *T. barbara* it frequently breaks into two or three groups.

Surrounding the wood is a layer of parenchyma, which on the concave side of the xylem quite fills the space between the arms of the horseshoe. The phloem consists of a crescentic band of sieve tubes, one to three cells thick on the external side of the leaf trace (*ph*), and a smaller band on the opposite side (*ph*). The protophloem consists of small elements which form a ring, broken only on the concave side of the xylem. Here the ring is completed, however, by the inner band of metaphloem. In *O. cinnamomea* and *T. barbara* isolated protophloem cells have been observed by the writer on the side of the inner band of metaphloem towards the stem axis. On the convex

side the protophloem is separated from the metaphloem by parenchyma. There are no "quergestreckte Zellen." The pericycle consists of two or three layers of cells, and is bounded by a well developed endodermis continuous with that of the stem. With reference to the attachment of the leaf trace to the cauline vascular axis Zenetti has given a very careful and accurate description.²¹

Strasburger has held²² that the stele of the petiole of *O. regalis* is a collateral bundle. He has considered the inner band of metaphloem to be a parenchymatous tissue. However, the cells of this band prove to be characteristic sieve tubes, and are continuous with sieve tubes in the stem opposite the medullary rays. The leaf traces, therefore, are undoubtedly concentric. Several botanists have arrived at the same conclusion for *O. regalis*.^{23, 24}

In summary, the most important features of the leaf trace are: (1) the absence of a pith, (2) the endarch xylem strand, (3) the concentric type of stele, (4) the absence of "quergestreckte Zellen," and (5) the cylinder of protophloem completed on the inner face by a band of metaphloem.

THE ROOT.

The roots have a definite relation to the leaves, both in position and in numbers. Two roots invariably originate from the base of every leaf trace, or from the central cylinder immediately below. They come off at the same level, one opposite each arm of the horseshoe-shaped strand of xylem (*fig. 18*) in every case where there are just two roots to a leaf. They grow almost directly outwards, and so in a transverse section of the stem are cut longitudinally. In such a section it is seen, likewise, that the cortical tissues of the stem and root are entirely independent of each other, and that, therefore, the root is of endogenous origin. This fact is true of the secondary roots also.

²¹ ZENETTI: *op. cit.* 69.

²² STRASBURGER: *op. cit.* 448.

²³ SCOTT: *op. cit.* 319.

²⁴ ZENETTI: *op. cit.* 66.

The cortex is exceedingly thick, forming by far the main bulk of the root, and consists of large celled sclerenchymatous tissue. The cortical cells diminish in size towards the periphery, and become thicker walled. In *T. barbara*, however, there is a discontinuous ring of exceedingly thick walled brown sclerenchymatous cells immediately surrounding the vascular axis. The endodermis, which is continuous with that of the stem and leaf, is very pronounced in all of the species, and is at once noted by the radial dot, and by the fact that its cells are filled with tannin. In the second particular, exception must be generally made of *O. Claytoniana*.

The stele is comparatively small, and is typically protostelic, since there is no pith. The wood has a narrow elliptical form, consisting mainly of very large scalariform tracheids. At each end of the ellipse there are a few small protoxylem elements, which are especially evident in the young root, and which have no connection with the protoxylem of the stem or leaf. The root, therefore, is diarch. There are likewise two bundles of phloem alternating radially with the bundles of xylem. In all of the *Osmundas*, however, I have observed triarch steles in the larger roots, which exception is of comparative frequency in *O. cinnamomea*. The phloem consists of two flat bundles or bands. These bands are made up chiefly of thin walled sieve tubes which are of the same kind as occur in the stem. None of them are "quergestreckt." The phloem is separated from the xylem by three or four rows of parenchyma, and from the endodermis by a two rowed parenchymatous pericycle.

DEVELOPMENT OF THE TISSUES FROM THE GROWING POINT.

In discussing this subject there are two points in particular which will receive special consideration: (1) the statements of Strasburger and Zenetti regarding the origin of the endodermis, and (2) the real nature of the "quergestreckte Zellen."

The determination of the relation of the tissues to the apical cells seems of little concern, and moreover in the study of the apical region of the growing point there are serious difficulties.

Having described these for *O. regalis*, Professor Bower aptly remarks :²⁵

The meristem being thus at times irregular, and the subdivisions of the segments being variable, it is to be expected that the study of it (the apical region of the growing point) in longitudinal section would present difficulties, and I have not been able to trace any definite and characteristic mode of segmentation. Longitudinal sections cut from a considerable number of stems show that a conical apical cell is present. The relations of the surrounding tissues, and their reference to regularly succeeding segments are difficult to recognize.

To these observations on the extreme apical end of the growing point we have nothing to add, but pass further down the stem.

A short distance from the apex of the stem, the various tissues, though in embryonic form, become apparent. The cylinder of wood, whose thin walled, unligified cells are still provided with protoplasm and nucleus, can be distinguished from the pith, the parenchyma in the leaf gaps, and the immature phloem. The pericycle is rich in protoplasm, and its cells are radially arranged. At an earlier stage still, even before there is any evident differentiation in the vascular tissues, the leaf traces can be seen coming off from the cauline vascular axis.

When the protoxylem can be first demonstrated by phloroglucin and hydrochloric acid, the endodermis (both internal and external in the case of *O. cinnamomea*) is also demonstrable by the same reagents, though not before. Zenetti has claimed²⁶ that at the time the protoxylem is formed, the endodermis, pericycle, "quergestreckte Zellen," protophloem cells, and some cortical cells are all in the same radial rows; and that, therefore, all have originated from the same mother layer. Strasburger has asserted²⁷ that the tissue lying in the stem between the phloem and the endodermis and occupying the position of a pericycle arises by tangential divisions with the endodermis out of the innermost cortical layer. Therefore, not the entire phloeoterma, he claims, but the outer division product is that which gives origin to the endodermis.

²⁵ BOWER: The comparative examination of the meristems of ferns as a phylogenetic study. *Ann. Bot.* 3: 323. 1889.

²⁶ ZENETTI: *op. cit.* 64.

²⁷ STRASBURGER: *op. cit.* 449.

Now, at the time the protoxylem elements appear, I did not find, in the species examined, the cells of the endodermis corradial with those lying centrad. It is true that in younger stages the cells in this region are in radial rows; but nearer still to the *punctum vegetationis* this is approximately true of all the cells of the stem. At this earliest stage one would hesitate to say, because certain cells were corradial, that they were therefore division products of the same mother cells; so Zenetti's conclusion, based on this sole argument, scarcely seems conclusive, even granting the correctness of his observation. If, too, such a conclusion were correct there would be the curious anomaly of certain phloem and cortical tissues having a common origin.

Evidently the study of transverse sections cannot settle the matter. To attempt to follow these layers upwards is obviously only possible in median longitudinal sections. But in the stems of the Osmundaceae the leaf traces are exceedingly numerous, and at the growing point are closely packed together, and appear before the tissues of the cauline central cylinder become at all differentiated. Hence, no matter what be the plane of section, the endodermis cannot be traced continuously very far anteriorly to the point at which it is differentiated, for a leaf trace is certain to intervene; and I found it quite out of the question to pick out an undifferentiated endodermis on the side of the leaf trace turned towards the apex. Therefore, every attempt failed to refer the endodermis and the rows of cells "occupying the place of the pericycle" to the same initial layer.

The typical protophloem, and the "quergestreckte Zellen" begin to be differentiated simultaneously with the appearance of the protoxylem. They are best examined in tangential sections. Their walls at this time become pitted, and their contents much less granular than those of the surrounding cells. Here, as in the maturer parts of the stem, there appear to be no differences between the typical protophloem and the "quergestreckte Zellen." Their relation to the leaf traces seems to explain their irregularity in orientation. Immediately below the point of origin of a leaf trace they are arranged with their long axes parallel

to the long axis of the stem, and there is a gradual transition to the tangential position. More than this, the laterally placed protophloem cells of the leaf traces can be directly traced into the "quergestreckete Zellen" of the stem. There seems little doubt, therefore, as to their nature.

To summarize observations: (1) The "quergestreckte Zellen" are sieve tubes, as has been demonstrated above; (2) they become differentiated at the same time as the typical protophloem, and (3) occupy the same relative position; (4) they resemble the protophloem cells in form; (5) their orientation is not uniform; (6) they pass imperceptibly into the longitudinally orientated protophloem cells of the leaf traces. Hence there seems no reason to regard them as anything else than protophloem.

CONCLUSIONS.

The question now remains, how to interpret the vascular system of the Osmundaceae. To do this more intelligibly, it will be well to recapitulate the main fibrovascular theories. We shall begin with that of Sachs and DeBary.

These botanists regarded the bundle as the unit, and the vascular system as a more or less simple complex of bundles embedded in ground or fundamental tissue. Developmental studies have shown that this theory is inadequate, for the unit is wrong.

The hypothesis which at present obtains was supplied by Van Tieghem and Strasburger. In this conception^{28, 29, 30}, the stele is the unit. The primitive form of stele, the monostele, such as occurs for example in most roots and in the stems of lycopods, is a solid central strand of xylem, surrounded by a sheath of phloem, and marked off from the cortex by the differentiated internal cortical layer, the endodermis. Of this there are many modifications, of which mention is made of the most important. By the repeated bifurcation of the monostele, the polystelic type is

²⁸ VAN TIEGHEM: *Traité de Botanique* 673, 765.

²⁹ VAN TIEGHEM: *Sur la polystélie*. *Ann. Sci. Nat. Bot.* VII. 3: 275.

³⁰ VAN TIEGHEM: *Éléments de Botanique* 1:84, 179.

presented, as in *Primula* and *Pteris*, each segment being in every respect a stele. If these steles fuse laterally, thus forming a ring with internal and external phloem, the gamostele is produced as illustrated by *Marsilia*. Again, when parenchyma segregates in the axis of the monostele, and the vascular ring is broken into strands by ectad extensions of this pith (the medullary rays), we have the medullated monostelic type, such as is common in phanerogams. It is to be noted that the medullary and cortical tissues are considered by both these botanists to be of morphologically different value. Now by the bending in of the endodermis of the medullated monostele between the bundles, and the fusion of the ends of adjacent groups on the centrad side of the bundle, so that each bundle has its endodermal sheath, and medulla and cortex become continuous, the schizostelic or astelic type results. Of this phenomenon *Ranunculus* and *Equisetum* afford examples. A modification of this type, the gamodesmic-schizostelic, is produced by the lateral fusion of these endodermal sheaths, so that there is a common internal and a common external endodermis. If the internal endodermis degenerates, as it does in *E. arvense*, then there is evidently a simulation of the medullated monostele. It is fair to add that Strasburger dissents³¹ from the last two types described, the astelic and the gamodesmic, for he regards the endodermal sheaths about the bundles in the first of these, and the internal endodermis in the second, as not morphologically phloeotermal, but originating from specialized stelar cells.

The researches of Gwynne-Vaughan³² and Jeffrey³³ have shown that the phenomena said to lead up to polystely do not occur in *Primula* and *Pteris*. If the polystelic conception falls, obviously gamostely goes too. Further, astely has been shown, where it occurs in *Equisetum* and *Ranunculus*, to be preceded by the gamodesmic appearance. Later the internal and external

³¹ STRASBURGER : *op. cit.* p. 442.

³² GWYNNE-VAUGHAN : Polystely and the genus *Primula*. *Ann. Bot.* **11** : 307. 1897.

³³ JEFFREY : Morphology of the central cylinder of angiosperms. *Trans. Canad. Inst.* **6** : —. (1-40) 1900.

endodermis may fuse between the bundles, but in no case is there an inward looping of the endodermis. Finally, the stelar origin of the pith of the medullated monostele has been disputed, and the question raised as to whether the medullary and cortical tissues are in reality morphologically different. In other words, is the medullated monostelic type primitive, as its simplicity might indicate, or has it resulted by degeneration from more complex types?

It is interesting to note that Potonié had discussed this last question from the standpoint of fossil botany, and concludes³⁴ that it seems evident in the case of certain groups, such as the cycads, that the simple results from the complex (for example, the cycads from the *Medulloseae*). Hence for these groups at least he is inclined to reject this idea of segregation of parenchyma in the center of the protostele to form the medullated monostele, but holds that the medullated monostelic type has probably arisen by degeneration from his "pericaulom." Since this pericaulom was produced, according to his theory, by the lateral fusion of leaf bases in the stem surrounding the originally solid stele, the "urcaulom," the medullated monostele has been derived from a form of central cylinder such as Van Tieghem has described as polystelic, preceded or accompanied by the disappearance of the enclosed urcaulom. The paleontological evidence, however, appears not to be conclusive, for in the very group that Potonié cites, the cycads, so eminent a paleobotanist as Dr. D. H. Scott takes a directly opposite view. He points out³⁵ that the vascular system of the *Medulloseae* was typically polystelic, while in the recent cycads there is but one vascular cylinder, and that hence "we should involve ourselves in unnecessary complications if we endeavored to derive the simple, primary structure of the cycadean stem from the more elaborate organization of a *Medullosa*. It is far more natural to suppose that the monostelic cycads arose from monostelic ancestors."

³⁴ POTONIÉ: *Die Metamorphose der Pflanzen im Lichte paläontologischer Thatsachen* 22.

³⁵ SCOTT: *Studies in fossil botany* 395. 1900.

In 1897, Dr. E. C. Jeffrey put forward another view of the vascular system,³⁶ based upon a study of the young sporophyte. Here, too, the stele is the unit. According to this conception there are two primitive types of vascular axes; the first the same as Van Tieghem's primitive type, and designated "protostelic;" the second, one in which there is a hollow cylinder, or "siphonostele," whose external wall abuts on the cortex, and whose internal wall encloses the medulla, and which possesses internal as well as external phloem. This is the "amphiphloic siphonostelic" type, called by Van Tieghem the "polystelic." The commonly called "astelic" modification results from the amphiphloic type by a degeneration of the internal phloem, and the medullated monostelic type of Van Tieghem is derived from the astelic by the loss of the internal phloeotermia or endodermis. A study of development from the seedling is likely to show how these and other modifications in the stellar structure have been derived from the primitive types. Attention is also called to certain portions of the wall of the siphonostele in which the vascular tissues do not develop. These places lie above the points of exit of branch traces, and of leaf traces, and are known as ramular and foliar gaps respectively. Through these gaps the tissues outside and inside connect. In transverse section, the connecting tissues seen constitute the medullary rays, and the segments of the woody cylinder with adjacent phloem and parenchyma the bundles. A fact of great phylogenetic importance in dealing with "gaps" was further pointed out, namely, that in small leaved plants, as in the Lycopodiaceae, Equisetaceae, etc., only ramular gaps occur. These plants are grouped in the division Lycopsidea, and their steles are said to be cladosophonic. In all other vascular plants there is a gap for every leaf. These constitute the large leaved plants, the Pteropsida, and their steles are said to be phyllosiphonic.

As a matter of theory, it is suggested that the siphonostele arose from the protostele for mechanical causes, in the Lycopsidea to support the branches, and in the Pteropsida to support the

³⁶JEFFREY: Trans. Brit. Assn. Toronto. 1897.

leaves. Potonié also explains the origin of his second primitive type the "pericaulom," the homologue of the siphonostele, on mechanical grounds.

In the light of these theories we can now apply ourselves to an interpretation of the anatomy of the vascular system of the Osmundaceae, and likewise note if the facts already dealt with throw any light on the theories.

First, we are in a better position now to decide whether the internal endodermis of *O. cinnamomea* is phloeotermal or not. It has been noted that in similar cases, that is, in gamodesmic stems, Strasburger has denied the phloeotermal character of the internal endodermis. With regard to the internal endodermis the following facts have been observed:

1. There is present the characteristic cuticularized "radial dot."

2. The structure and contents of the cells are materially the same as of the external endodermis.

3. The sheath is continued into the portions which in some individuals present the phenomenon of internal phloem, just as in any form called by Van Tieghem and Strasburger gamostelic. In the gamostelic type the phloeotermal character of the internal endodermis has been admitted.

4. It generally connects with the external endodermis through ramular gaps, and by no means rarely through foliar gaps. When this occurs, there is no point at which it could be said that the one stops or the other begins.

Having verified these facts in a great many cases, I am therefore of the opinion that the internal and the external endodermis are homologous tissues.

Second, are the medullary tissues morphologically equivalent to the cortical? Again we recapitulate observations.

1. They do not differ in structure or in contents.

2. The medulla very often contains brown sclerenchyma, at least in three species studied, a tissue which, in other ferns, never constitutes a part of the stele.

3. Medulla and cortex connect more frequently than not

through the ramular gaps in *O. cinnamomea*, and occasionally through foliar gaps; and neither is there a transition in the nature of the connecting tissues, nor any line at which we can say, the cortical tissues lie externally to this and the medullary tissues internally.

4. The cortical and the medullary brown sclerenchyma sometimes fuse through ramular gaps in *O. cinnamomea*.

5. Portions of stem of *O. cinnamomea* have been found which are of the "gamostelic" type of Van Tieghem. The medulla in gamosteles is granted to be morphologically a cortical tissue.

The conclusion is evident for *O. cinnamomea* at least, and if it be granted that the medullary tissues of this species are morphologically equivalent to the cortical tissues, then biological principles alone would demand a like conclusion for the other species.

Third, of what type is the vascular system of *O. cinnamomea*? Again the facts must form the basis for a decision:

1. The young stem of *O. cinnamomea* possesses an entirely closed hollow vascular cylinder, sheathed with phloem and broken only immediately above the exit of a leaf trace; and at a level higher up the cylinder is entirely closed again. There is a medulla and an internal endodermis.

2. In older plants the leaves are more frequent, and the gaps extend through several internodes; but yet the cylinder is the unit. The cylinder of phloem is quite rarely broken, except where branching takes place.

3. There is an internal endodermis which is persistent throughout the entire central cylinder of the stem.

4. As a rule the internal endodermis bends out opposite leaf gaps.

5. There is an internal phloem in portions of some plants.

6. Not only does the cylinder of external phloem remain practically unbroken, but opposite leaf gaps there is on the inner side a proliferation of sieve tubes. In *O. regalis* Janczewski found isolated sieve tubes in the parenchyma filling the leaf gap; and the same thing is true of *O. cinnamomea*.

According to Van Tieghem's stelar theory, the last two facts can be explained only by considering the central cylinder of the Osmundaceae to be "gamostelic." The centrad extensions of the phloem opposite the medullary rays could then be explained by assuming that steles had united laterally, with the disappearance of phloem on the medullary side, but with the partial persistence of phloem on the radial planes. This would also explain the occurrence of internal phloem, the union of internal and external endodermis, and the homology of medullary and cortical tissue. But from the study of development there is not a shred of evidence to prove that there has been a union of steles. In fact, such a study shows distinctly that there is but one stele in the stem of *O. cinnamomea* from the very first. Van Tieghem's observations on *O. regalis* have already been quoted (see INTRODUCTION); so we cannot describe the cauline vascular system as "gamostelic," if this name implies a union of steles.

There remains yet another interpretation, namely, that the vascular system of the stem of *O. cinnamomea* is a siphonostele in which some degeneration from the primitive type has taken place. It has been pointed out in a description of the conception of the vascular system held by Dr. E. C. Jeffrey that the most primitive siphonostele is the amphiphloic siphonostele. In this there is an internal phloem and phlooterma, and in its phyllosiphonic form there are wide leaf gaps and branch gaps through which internal and external phloem, internal and external phlooterma, and medulla and cortex connect with each other. In *O. cinnamomea* the gaps in this primitive type have closed somewhat, so that medulla and cortex rarely connect except through ramular gaps. Also the phloem forms an almost unbroken cylinder, and the centrad proliferations opposite the medullary rays are the vestigial relics of connection between external and internal phloem. The internal phloem has also disappeared in greater part.

With such a conception of the cauline vascular system of *O. cinnamomea*, the centrad accumulation of sieve tubes opposite

the medullary rays, the occasional presence of sieve tubes in the medullary rays, the fact of the internal phloem, the connection of medulla and cortex through ramular and foliar gaps, the presence of sclerenchyma in the medulla, the bending out of the internal endodermis into the leaf gaps, and the facts of development, all become intelligible.

Fourth, which of the species studied possesses the most primitive type of central cylinder?

After a fairly comprehensive study there is one feature that stands out prominently, the great similarity and uniformity of vascular structure in the various species of *Osmunda* and *Todea*. According to Solms-Laubach the stems of fossil remains of this family, of which none earlier than the Tertiary have been found, do not present any striking differences from the living representatives. Paleobotany, therefore, offers no solution to the problem. In spite of the conservatism of the central cylinder, there are, however, minor anatomical differences. On the basis of these alone, without referring to the young sporophytes, I think there is sufficient warrant for placing *O. cinnamomea* at one end of the series, possessing as it does an internal endodermis, internal phloem, and wide ramular gaps. It is difficult to say which species is to be placed at the other end of the series. In view of the fact that *O. Claytoniana* never has sclerenchyma in the medulla, that there are small or even no ramular gaps, no internal sclerenchyma, and even a degenerated external endodermis, we may not be far astray in putting it in the position farthest from *O. cinnamomea*. Now of these two, which retains a central cylinder more nearly primitive? If *O. regalis* has a medullated monostelic central cylinder, as has hitherto been claimed for it, then *O. Claytoniana* has also, and therefore, according to Van Tieghem, a more primitive form than that of *O. cinnamomea*. Assuming the correctness of this for the moment, it will be in order next to see if such phenomena as presented by *O. cinnamomea* could be derived according to Van Tieghem's hypothesis from such a simple medullated monostelic form as that of *O. Claytoniana*.

The phloem sheath must have broken into bundles, and the endodermis must have looped in between the bundles, and connected around them on the centrad side. With the formation of this astelic type some of the cortex would have been included in the medulla, in evidence of which the sclerenchyma in the pith would stand as proof. Then next the bundles must have fused laterally to produce the gamodesmic type in which there is an external and an internal endodermis. Granting that the central cylinder could be so plastic in a single species, there are left yet to be explained the continuous sheath of phloem, the proliferation of sieve tubes opposite the medullary rays, the occurrence of isolated tubes in the medullary rays, the occurrence of internal phloem, and the phenomena of the ramular gaps. Further, there are no facts in development that point to such a series of changes.

Turning now to the other alternative, namely, the possibility that *O. cinnamomea* has the more primitive form of central cylinder, it will be granted that by the degeneration of internal phloem, endodermis, and medullary sclerenchyma, and by the closing of the ramular gaps the central cylinder such as we find in *O. Claytoniana* would result. In proof that such degeneration could have taken place, it is to be noted (1) that in *O. cinnamomea* itself, it has been pointed out that the amphiphloic condition is localized, that the internal endodermis has already begun to degenerate, that medullary sclerenchyma is not a constant feature, and that closed steles above the point of branching are not at all uncommon; and (2) in further proof, analogous cases of degeneration within the same genus are frequent. Thus within the genus *Equisetum* two species such as *E. arvense* and *E. hiemale* may be chosen, the first long considered medullated monostelic and more primitive, the second gamodesmic and considerably modified. But a study of development and of nodal portions of the stem has shown that *E. arvense* has a reduced central cylinder, the product of degeneration from a gamodesmic type, and that therefore *E. hiemale* is nearer the primitive. Similar cases of degeneration have been pointed out by Van

Tieghem, Poirault, and Jeffrey, in the genera *Ophioglossum*, *Botrychium*, *Equisetum*, *Ranunculus*, etc. Very lately Boodle,^{37, 38} has called attention to an interesting series of central cylinders in the family Schizaeaceae. *Aneimia Phyllitidis* has a ring of separate bundles, each with a band of xylem surrounded by a phloem, pericycle, and endodermis of its own; *A. Mexicana* has a complete ring of xylem in the internodes with external and internal cylinders of phloem and endodermis; *Schizaea* has a ring of xylem surrounding a central pith, but no internal phloem or endodermis. It is likely that here, too, the *Schizaea* type is derived from the *Aneimia* type by degeneration. In the Hymenophyllaceae likewise, every grade is found from the case in which the phloem of the solid stele forms a complete ring to that in which it is developed on one side only.

After examining a number of comparatively young specimens of *O. Claytoniana*, I am somewhat doubtful if the study of the development of this species will throw any further light on the subject of morphology; but for *O. regalis* I am more hopeful. Nevertheless, aside from further developmental proofs, I incline to the view that *O. cinnamomea* possesses the most primitive type of central cylinder. I again recapitulate the reasons:

1. The opposite view demands a very plastic central cylinder in one species alone, not differing very greatly in habit from the others.

2. There would still remain phenomena that the opposite view could not explain.

3. There are no facts of development even in analogous cases to support the opposite opinion.

4. The view adopted here demands only slight changes, and those are of degeneration, to explain all the phenomena.

5. There are precisely similar analogous cases of degeneration.

6. Within the species *O. cinnamomea* itself, every phase of

³⁷ BOODLE: Stem structure in Schizaeaceae, etc. Brit. Assn. Dover, 1899.

³⁸ BOODLE: On the anatomy of the Hymenophyllaceae. Ann. Bot. 14: 455. 1900.

degeneration except the entire disappearance of internal endodermis is observable in suitable specimens.

When we attempt to orient the other species amongst themselves, the task is more difficult, and of little importance. As already indicated, a closer study of development may afford more precise proofs. In the mature stems we have seen that *O. regalis* occasionally has sclerenchyma in the medulla, that there are ramular gaps, though usually small, and that the external endodermis is well developed. In *O. Claytoniana*, on the other hand, sclerenchyma is never found in the medulla, ramular gaps are infrequent, and the external endodermis shows indications of degeneration. In neither of these species is internal endodermis or internal phloem present. The probability, therefore, is that in the genus *Osmunda* there is a series, *O. cinnamomea* possessing the most primitive type of central cylinder and *O. Claytoniana* the most degenerate, *O. regalis* occupying a middle position, but nearer to the latter. It is merely interesting to note in passing that Professor Campbell concluded³⁹ from his study of the prothallia of *O. Claytoniana* and *O. cinnamomea*, that the gametophyte of the former was more specialized in many particulars, in other words, was less primitive in type than the latter.

Fifth, does a study of the vascular system help to determine the phylogenetic position of the Osmundaceae?

It was stated at the beginning of this paper that botanists have regarded the Osmundaceae as possessing an anomalous form of central cylinder among the Filicales, their reason being that it seemed to present more of the features of a central cylinder such as is typical for dicotyledons, that is, a medullated monostele in Van Tieghem's terminology. In determining the position of the family, therefore, in any natural system of classification, it was hopeless to try to reconcile this single dicotyledonous character with the remaining filicinean characters, and so the vascular system in the family was regarded as anomalous.

³⁹CAMPBELL: On the prothallium and embryo of *O. Claytoniana* and *O. cinnamomea*. Ann. Bot. 6: 49. 1892.

It is fair to note that Zenetti dissented⁴⁰ from the prevailing view, and evidently for the reason that he attached some value to the nature of the central cylinder from the phylogenetic standpoint. Hence he sought to find the same type amongst the vascular cryptogams. He rejected the ordinary fern type because it is "polystelic," and the lycopod type because there is no pith, obviously overlooking *Selaginella laevigata*, *Phylloglossum*, etc. So finding no living form with which comparison could be established he turned to paleophytology. Among the Lepidodendraceae he found the prototype sought for, especially in such of these fossils as *L. Harcourtii*, and the Sigillarians, because in these the wood is broken into bundles between which there are medullary rays. But he evidently did not grasp the significance of bundles and medullary rays in relation to leaf traces and branch traces. In *O. regalis*, too, the protoxylem is endarch, while in those ancient lycopods it was exarch. The stele of the Lepidodendraceae, as in all plants bearing palingenetically small leaves, was cladosophonic, while *O. regalis* is phyllosiphonic, as are all primitively megaphyllous plants. Hence any attempt to establish a relation between the central cylinder of modern ferns and of those ancient horsetails must fail. Indeed, of the early fossil forms preserved, the one with a central cylinder most closely resembling that of the Osmundaceae, as has been pointed out by Dr. Scott,⁴¹ seems to be the cycadofilicinean *Lyginodendron* (fig. 26).

Further, we dissent just as strongly from the view that the family is anomalous in the matter of its vascular system. The typical fern stem possesses an amphiphloic siphonostele, as is especially revealed by a study of development. But degenerated forms of this are to be met with in almost every family, some examples of which have been noted. The Osmundaceae, as has been shown above, all exhibit some degree of degeneration from this type. It is therefore evident that the cauline vascular system of this family is neither primitive nor anomalous among the Filicales.

⁴⁰ ZENETTI: *op. cit.* 73.

⁴¹ SCOTT: *op. cit.*

SUMMARY OF OBSERVATIONS.

1. An internal endodermis has been demonstrated in *Osmunda cinnamomea*, but in none of the other species examined. This internal endodermis is in textural continuity with the external endodermis through branch gaps, and sometimes through foliar gaps.

2. Internal phloem has been found in *O. cinnamomea* in the region of branching. This is continuous with the external phloem through ramular gaps.

3. The external phloem of the Osmundaceae forms a continuous cylinder, a fact which De Bary has stated for *O. regalis*; and is not broken opposite the medullary rays as Strasburger has affirmed of the same species. Isolated sieve-tubes have been found in the medullary rays of *O. cinnamomea*.

4. The xylem forms a cylinder broken only by foliar and ramular gaps.

5. Brown sclerenchyma has been shown to be usually present in the medulla of *O. cinnamomea*, not uncommonly in *O. regalis*, and not at all in *O. Claytoniana*. It occurs likewise in *Todea barbara*, but has not been observed in *T. superba*.

6. The medullary and cortical tissues of the Osmundaceae are histologically equivalent. Brown sclerenchyma, which is not an intrastelar tissue in other ferns, occurs in both medulla and cortex; and in *O. cinnamomea* the brown sclerenchyma of the medulla is in continuity with that of the cortex.

7. In *O. cinnamomea* the typical ramular gap is one through which internal and external endodermis, internal and external phloem, cortex, and medulla connect. Every stage of degeneration has been observed in *O. cinnamomea*, however, down to the completely closed steles. *O. regalis* has a gap in the wood only, and *O. Claytoniana* usually none.

8. The so-called "quergestreckte Zellen" pointed out by DeBary in *O. regalis*, and more fully described by Zenetti, have been found in all the species studied. They are sieve tubes, possessing all the characteristic features of sieve tubes, even that of callus plugs. Their irregularity of orientation is shared by the other peripheral tissues of the central cylinder, and is

apparently due to disturbance caused by the exit of the large leaf traces.

9. Callus plugs have been demonstrated in the sieve tubes.

10. A study of the growing point has further shown that the "quergestreckte Zellen" and the typical protophloem are of the same kind; but it has failed to verify Strasburger's statement that the pericycle and the endodermis arise from a common maternal layer.

11. The phloem forms a continuous sheath in the leaf.

12. The root possesses a protostelic, diarch, occasionally triarch, vascular axis.

SUMMARY OF CONCLUSIONS.

1. The internal endodermis in *O. cinnamomea* is to be regarded as phloeotermal in nature, a fact denied by Strasburger in homologous cases.

2. The medullary and cortical tissues seem to be morphologically equivalent.

3. Observations on the anatomy of the Osmundaceae have been confined heretofore to the cosmopolitan *O. regalis*, and the subtropical *Todeas*. From these observations it was concluded by Van Tieghem that this family possessed a type of central cylinder anomalous among the vascular cryptogams, a type (the medullated monostelic type) peculiar to the phanerogams. The writer dissents from this view. It appears to be the case that the central cylinder of *O. cinnamomea* is not medullated monostelic, for the medulla is obviously extrastelar. Further, it cannot be regarded as gamodesmic on account of the topographical distribution of the phloem. The most obvious interpretation seems to be that it is a degenerate form of the amphiphloic siphonostelic type of central cylinder (polystelic type of Van Tieghem). *O. cinnamomea*, *O. regalis*, *O. Claytoniana* form a series arranged in order of degeneration of their central cylinders, and the same is true of *T. barbara* and *T. superba*.

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Jeffrey, to whom I wish here to express my obligations for his advice throughout. My thanks are due to Professor R. Ramsay Wright for the facilities afforded in the department. For some of the material used I am indebted to Mr. Oakes Ames, Assistant Director of the Botanical Gardens, Harvard University; Sir William Thistleton Dyer, Director of the Royal Gardens, Kew; Dr. Brodie, Toronto; and Mr. R. B. Thomson, B. A.

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EXPLANATION OF PLATES XIV-XVII.

Abbreviations used.

<i>cp</i> , callus plugs.	<i>p</i> , pericycle.
<i>c</i> , cortex.	<i>ph</i> , phloem.
<i>e. c.</i> , external cortex.	<i>p. ph.</i> , protophloem.
<i>i. c.</i> , internal cortex.	<i>px</i> , protoxylem.
<i>e</i> , endodermis.	<i>qu</i> , "quergestreckte Zellen."
<i>e. e.</i> , external endodermis.	<i>r</i> , root.
<i>i. e.</i> , internal endodermis.	<i>s. s. s.</i> , strands.
<i>lt</i> , leaf trace.	<i>sc</i> , sclerenchyma.
<i>m</i> , medulla.	<i>x</i> , xylem.
<i>m. r.</i> , medullary ray.	

PLATE XIV.

- FIG. 1. Transverse section of the stem of *Osmunda cinnamomea*.
 FIG. 2. Transverse section of part of central cylinder of *O. cinnamomea*.
 FIG. 3. Tangential section of *O. regalis*.
 FIG. 4. "Quergestreckte Zelle" of *T. barbara*, showing sieve plates and callus plugs.
 FIG. 5. Transverse section of leaf trace of *O. Claytoniana* near the growing point.
 FIG. 6. Transverse section of part of central cylinder of *O. cinnamomea*.
 FIG. 7. Sieve tubes of *T. barbara*, showing sieve plates, "globules brillants," and callus plugs.
 FIG. 8. Transverse section of part of central cylinder of *O. Claytoniana*.

PLATE XV.

- FIG. 9. Tangential section of *Todea barbara*, showing "quergestreckte Zellen."
 FIG. 10. Transverse section of *O. cinnamomea*, immediately above point of ramification, showing open branch gaps.

FIG. 11. Transverse section of *O. cinnamomea* through nearly the same region in another plant.

FIG. 12. Transverse section of same plant as in *fig. 11*, but lower down.

FIG. 13. Transverse section of same plant as in *fig. 12*, but lower down.

FIG. 14. Transverse section of the central cylinder of *O. cinnamomea*, showing internal endodermis and brown sclerenchyma in the medulla.

PLATE XVI.

FIG. 15. Transverse section of central cylinder of *O. cinnamomea*, showing internal endodermis and an absence of brown sclerenchyma in the medulla.

FIG. 16. Transverse section of the stem of *O. cinnamomea* in the region of forking, showing absence of ramular gaps.

FIG. 17. Transverse section of the stem of *O. Claytoniana*.

FIG. 18. Transverse section of the stem of *O. Claytoniana* in the region of forking.

FIG. 19. Transverse section of the stem of *O. regalis* in the region of forking.

FIG. 20. Transverse section of the central cylinder of *O. regalis*, showing brown sclerenchyma in the medulla.

PLATE XVII.

FIG. 21. Transverse section of the central cylinder of *O. cinnamomea*, showing internal phloem.

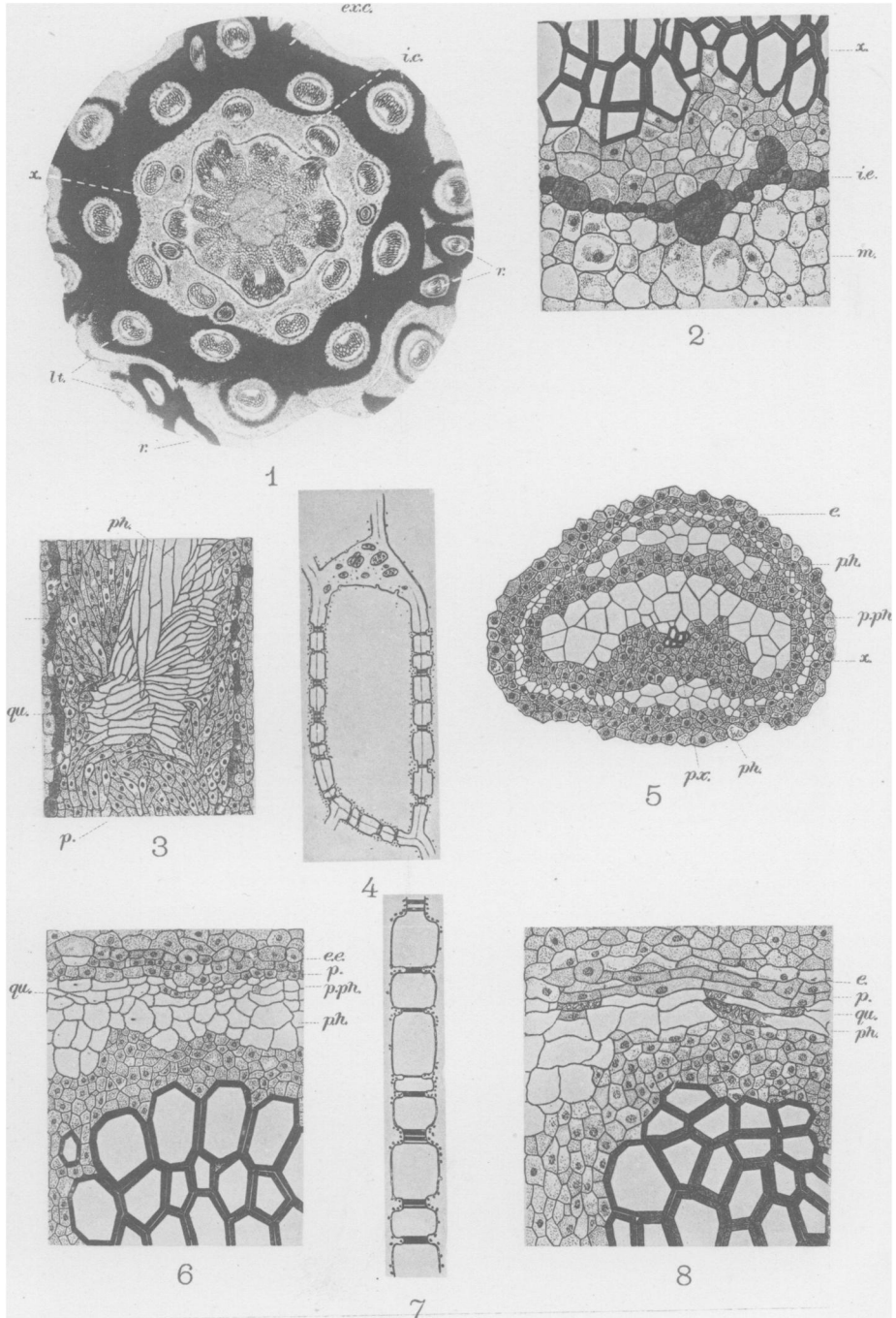
FIG. 22. A part of the central cylinder of *O. cinnamomea* shown in *fig. 21* more highly magnified.

FIG. 23. A transverse section of the young sporophyte of *O. Claytoniana*, showing one foliar gap, and the corresponding leaf trace opposite.

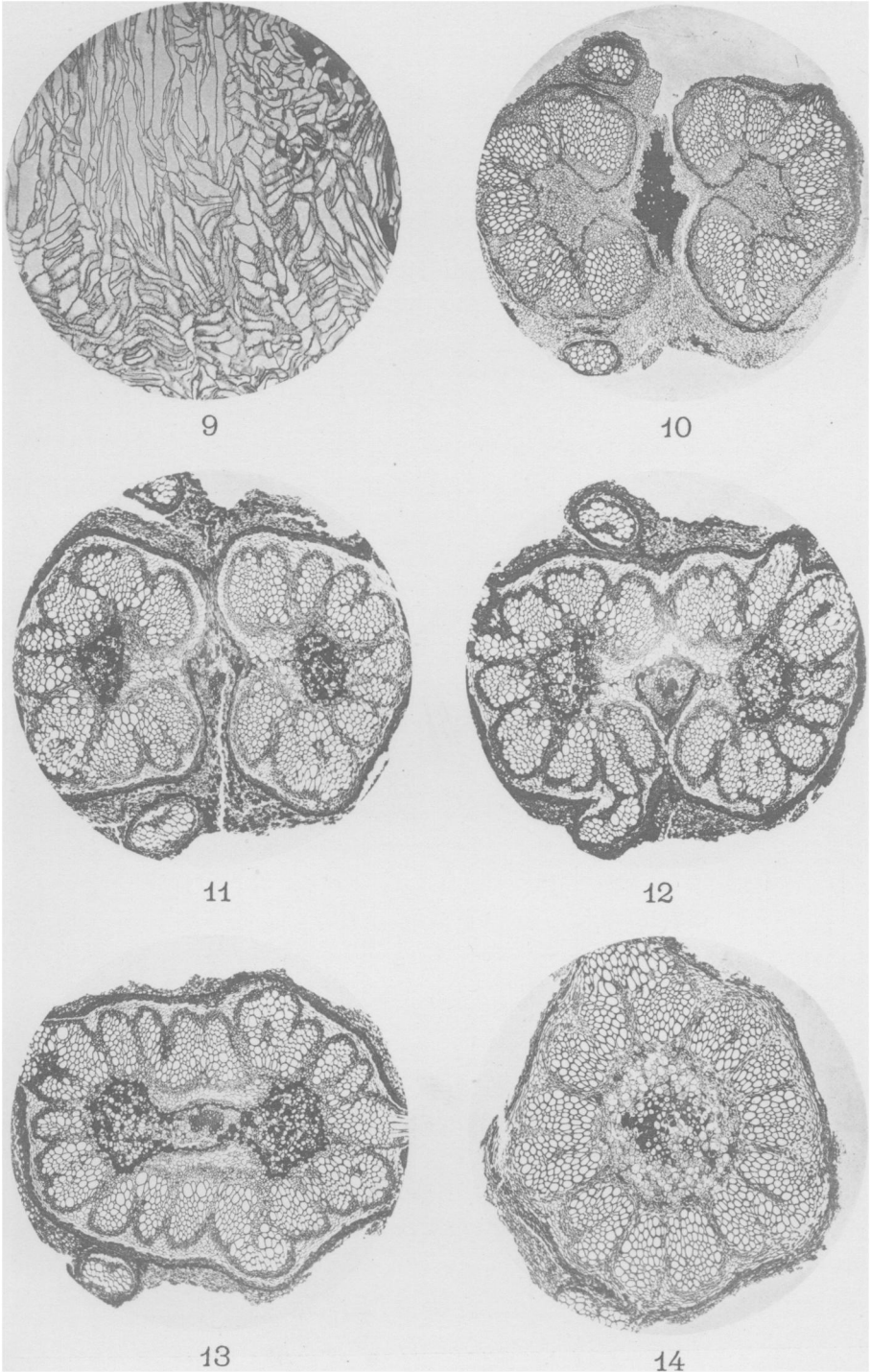
FIG. 24. Transverse section of the stem of *T. barbara*, showing brown sclerenchyma in the medulla.

FIG. 25. Transverse section of a part of the stem of *T. barbara* nearer the growing point.

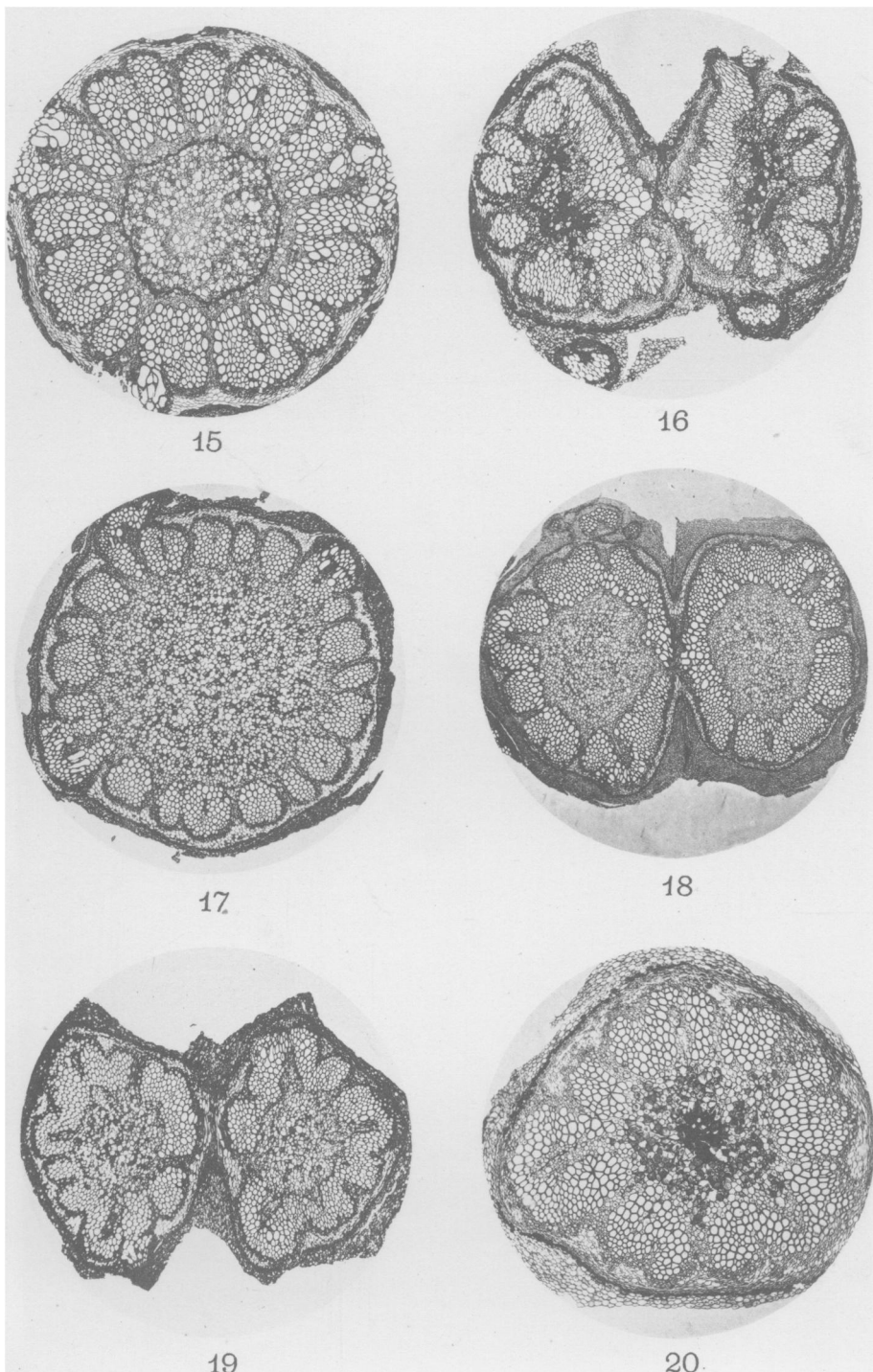
FIG. 26. Transverse section of *Lyginodendron Oldhamium*, showing a leaf gap, a leaf trace opposite, strands of sclerenchyma in the medulla, and strands of primary xylem centrad of the cylinder of secondary xylem.



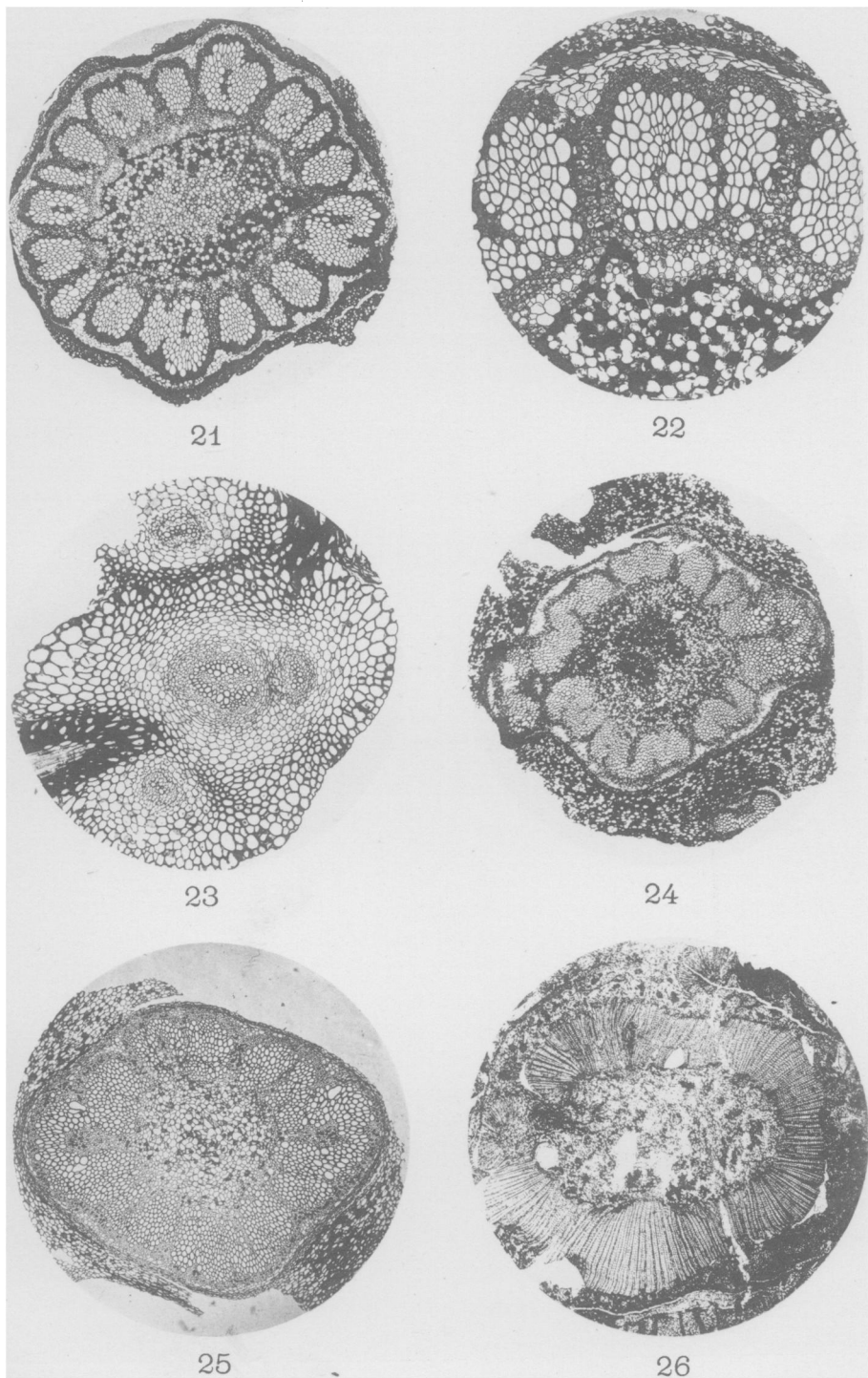
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