# Foliar Gaps in the Osmundaceae.<sup>1</sup>

BY

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#### With Plates XI and XII.

I N 1900 Jeffrey (1) proposed the division of all vascular plants into two great phyla: the *Lycopsida*, comprising the Lycopodiales and Equisetales, and characterized by ventral sporangia, small leaves, and the absence of foliar gaps in the central cylinder; and the Pteropsida, including the Filicales, Gymnosperms, and Angiosperms, all of which have dorsal sporangia, large leaves (at least primitively), and foliar gaps. That these two phyla differ in the position of their sporangia and in the size of their leaves, as far back as we have geological record, is now generally agreed. That they are clearly divided in the manner of departure of the leaf-trace is not, however, universally admitted. The question as to whether there are foliar gaps in the Lycopsida has been thoroughly discussed by Jeffrey in a recent paper (2). In the other main group, the Pteropsida, gaps are unquestionably present in all the families save one, the Osmundaceae. That there are numerous cases of the absence of foliar gaps, both in the fossil and the living members of this group, has recently been strongly urged by several writers, notably Kidston and Gwynne-Vaughan (3). The present investigation was undertaken to clear up the relation of leaf-trace to central cylinder in this interesting family.

More or less complete material of seven members of the group was obtained. These are the three common American species of Osmunda, O. regalis, L., O. cinnamomea, L., and O. Claytoniana, L.; Todea barbara, Moore; and the three filmy Todeas, T. superba, Colenso, T. hymenophylloides, Rich, and T. Frazeri, Hook. and Grev. Only portions of the mature leaves could be secured in the last species.

The central cylinder of the stem in the Osmundaceae consists, as is well known, of a ring of xylem strands, separated by parenchymatous 'rays', and surrounding a pith. Outside the xylem is a more or less continuous ring of phloem. The method of departure of the leaf-trace from the cylinder has been worked out by several investigators, among the foremost of whom is Zenetti (4). The first indication of the formation of a foliar

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strand is the appearance, usually near the outer margin of one of the xylem bundles, of a group of small protoxylem elements. Just inside this, a cluster of parenchyma-cells soon arises, which gradually increases in size towards the centre of the stem until it unites with the parenchyma of the pith, leaving the xylem-bundle in the shape of a horseshoe, with the protoxylem group near the middle of its inner face. The outer part, or curve, of the horseshoe now separates itself from the rest of the bundle and departs (with the phloem, which now surrounds it) as the leaf-trace, leaving the original bundle divided into two by a 'ray' of parenchyma. This ray is a foliar gap in the xylem caused by the departure of a leaf-trace. The two bundles eventually unite, closing up the gap thus formed.

This mode of separation of the leaf-trace from the cylinder was found to be by far the most common one in the group. Certain exceptions to it, however, were noted. In the stem of O. cinnamomea numerous instances were observed in which the cluster of parenchyma, after its appearance in the xylem-strand, instead of becoming continuous with the pith, broke first through the outer part of the xylem, on either side of the departing leaftrace, and thus separated the trace from the original bundle. A transverse section cut through this region seems to show clearly a leaf-trace leaving the cylinder without causing a break in the continuity of the xylem. Continuous serial sections were cut through such places as this, however, and it was found, in every case where a complete series could be obtained, that the xylem-bundle was soon much constricted and finally broken into two by a 'ray' of parenchyma opposite the outgoing trace. This 'ray' is often only a few cells wide, but is nevertheless a true foliar gap, differing from the others only in its relatively late appearance. It soon closes up, as do the other gaps. Pl. XI, Fig. 1, shows a leaf-trace departing from the cylinder of O. cinnamomea, apparently without making a break in the xylem. Fig. 2 shows the same trace at a slightly higher level. The gap opposite to it is now plainly discernible.

*O. regalis* shows much the same condition of affairs. With most of the traces the gap in the cylinder is formed when the foliar strand separates from the stem-bundle, but in a number of instances observed the parenchyma of the pericycle and of the pith came into communication only after the trace had progressed a considerable distance into the cortex. Fig. 3 exhibits a trace just departing from the cylinder. In Fig. 4 the very narrow gap is shown which eventually appears in the xylem opposite this bundle.

In O. Claytoniana these cases of apparent absence of gaps, though occurring, are not as frequent, and almost all the traces go off in the usual manner.

The mature stems of three species of the genus *Todea* were examined those of *T. barbara*, *T. superba*, and *T. hymenophylloides*. In the first of these, well-marked gaps were found in every case, and no temporary

apparent absence of a gap was observed. Gwynne-Vaughan, however, claims to have found instances in this species where the leaf-trace departed in what he designates as a 'protostelic', or gapless, manner. The interruptions are all short, and the lateral continuity of the xylem is therefore relatively great, but no instances of such a gapless condition were observed by the present writer.

In T. superba the leaf-gap in almost every case is narrow, and there were numerous instances noted where the trace was well into the cortex before a break opposite to it appeared in the central cylinder. Fig. 5 shows a trace apparently departing in a so-called 'protostelic' manner. Fig. 6 exhibits the condition of affairs a little higher up, where a wellmarked gap has been formed. Long series of sections were cut through the stem of this species and in no case was the absence of a leaf-gap observed. In their paper on the anatomy of Todea, Seward and Ford (5) figure a section of the stem of this species showing a leaf-trace departing apparently without leaving a gap. This figure is referred to by Kidston and Gwynne-Vaughan and by Tansley (6) as a probable example of the 'protostelic' exit of a leaf-strand. In view of the facts above described, however, it seems highly probable that a condition is present similar to that shown in Fig. 5, and that a gap in the xylem would subsequently appear. Seward and Ford do not call attention to the absence of leaf-gaps in this species in any other way than by the abovementioned figure.

In *T. hymenophylloides*, also, the gaps, or 'rays', are narrow in proportion to the size of the bundles. The great majority of traces depart in the usual manner. A number of instances were observed, however, where the gap was apparently absent for a while, but later appeared. Figs. 7 and 8, two stages in the passing off of a leaf-trace from the cylinder, show such a condition. In this form, also, Kidston and Gwynne-Vaughan mention finding cases where gaps were absent. None of these were observed by the present writer.

It would appear, therefore, that as far as the living Osmundaceae are concerned, foliar gaps are characteristically present, for in all the species where the whole course of a trace could be followed till it was far out in the cortex a break in the xylem ring opposite to it invariably appeared. The question now arises as to whether this family is *primitively* phyllosiphonic—whether, as Jeffrey maintains, their ancestors belonged to the phylum Pteropsida and had foliar gaps, or whether, in the ancient members of the group which possessed siphonostelic central cylinders, the leaf-trace departed without causing a break in the continuity of the xylem ring.

There are two general ways in which the answer to this question may be sought. The first, and by far the most satisfactory of the two if it can be successfully pursued, is to study the actual fossil progenitors of the

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family. The second is to examine the structure of those portions of the living forms which are known to be retentive of ancestral features.

Without going into the vexed question of the origin of the Osmundaceae, and leaving aside all such protostelic members of the group as Zalesskya and Thamnopteris, in which, obviously, leaf-gaps cannot occur and which therefore have little bearing on the present question, we find in the genus Osmundites, which possesses a medullated cylinder with a parenchymatous pith, a close and suggestive parallel to the conditions in living forms. There are five species at present included in this genus, the structure of all of which is now well known. Of these, perhaps O. Skidegatensis is the most striking. This fossil was first described from the Lower Cretaceous of Canada by Penhallow (7), and has also been investigated by Kidston and Gwynne-Vaughan (3). It is very large, possessing a wide pith surrounded by a central cylinder which has internal as well as external phloem. The method of departure of the leaf-trace from the cylinder is particularly noteworthy. It differs from the condition found in any of the other Osmundaceae in that the continuity of the whole central cylinder is interrupted, and the tissue of the pith becomes directly continuous with that of the cortex, and not, as in the other forms, with the pericycle-parenchyma only. The leaf-trace thus goes off in a fashion very similar to that found in Adiantum pedatum or any other of the ordinary siphonostelic ferns.

Osmundites Gibbiana of Kidston and Gwynne-Vaughan, O. Dowkeri of Carruthers, and O. chemnitziensis of Unger closely resemble one another in stelar structure. The general type of cylinder is very similar to that found in O. regalis or T. hymenophylloides. Foliar gaps are always present, though they are usually rather narrow, and the stem-bundles are consequently close together.

In O. Dunlopii of Kidston and Gwynne-Vaughan, however, a nearly continuous and unbroken ring of xylem appears at first sight to be present around the pith. The figures presented by the authors show this ring to be deeply constricted at intervals, and it seems entirely possible that very narrow 'rays', such as we have described in several species of Osmunda and Todea, might have originally occurred at these constrictions but might be undemonstrable in the present indifferent state of preservation. There are, moreover, a number of actual breaks in the ring which, according to these investigators, are probably due to accident. Some of these may also possibly represent true foliar gaps, or 'rays'. Several figures are presented showing the departure of the leaf-trace from the cylinder. They strikingly suggest the condition in some of the forms which we have above described, where the gap does not appear for some time after the trace has broken away from the stele. It is noteworthy that where the trace is figured as just departing from the cylinder there are but slight indications of a gap, but that

where it is well out into the cortex a deep constriction appears opposite to it in the xylem ring. Thin serial sections were of course impossible to obtain, as in the living species. On the whole, it seems very probable that we have here to deal with a form somewhat resembling T. superba, where foliar gaps are always present, though sometimes so narrow that they are hard to make out. It would not be at all surprising if in the process of fossilization the structure of these rows of thin-walled cells should be entirely lost to view. The theory that such a form as O. Dunlopii has been derived from one with a stele of the type represented by Thamnopteris Schlechtendalii, by the gradual alteration of the central tracheides into pithparenchyma, is at present supported by too little evidence to warrant its acceptance. Most probably, if this were the course of evolution, the transitional forms between the two types would show leaf-traces departing without the formation of gaps in the xylem. These transitional forms are lacking, however, and, as we have shown above, wherever there is a ring of xylem around a pith of parenchyma, a departing leaf-trace, either at or soon after its separation from the stele, subtends a foliar gap.

As far as it goes, therefore, the fossil evidence seems to support the view that foliar gaps are a primitive feature for the Osmundaceae. This testimony is not entirely sufficient, however, and we must turn to our other source of information, the structure of the conservative regions of the living members of the family.

Of these portions of a plant which retain ancestral features, the seedling has long been recognized, in connexion with the theory of recapitulation, to be one of the most important. The structure of the young plant in various members of the Osmundaceae has been investigated by Leclerc du Sablon, Faull, Seward and Ford, and Chandler. The first of these writers (8) worked out the structure and development of the vascular system in a young specimen of O. regalis. He found that there are originally two separate strands of xylem which fuse into a single protostele, surrounded by phloem. In the centre of this appears very soon a cluster of parenchyma-cells constituting a pith. Whenever a leaf-trace leaves the cylinder, it causes a break, which is soon repaired, in the continuity of the xylem ring. A little higher up in the stem, however, where the departing leaf-traces are numerous, gaps are formed more rapidly than they become closed, and the ring is consequently broken into a number of bundles, separated by 'rays' or foliar gaps. In no case, after the stele had assumed the tubular condition, was the absence of a foliar gap observed.

Faull (9), who investigated young plants of *O. cinnamomea* and *O. Claytoniana*, found a very similar state of affairs. The young stele possesses a continuous ring of xylem, which, however, is *always* broken at the departure of a leaf-trace. This break is subsequently closed, as in *O. regalis*.

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Seward and Ford (5) observed conditions in a young plant of T. hymenophylloides. They remark that in its essential features it agrees with O. regalis, as described by Leclerc du Sablon. After the appearance of the young pith, however, these authors observed that the first leaf-traces did not necessarily cause a break in the xylem ring, though well-marked gaps were formed by all the subsequent traces. The figure which they present of such a gapless condition resembles very much the early stage in one of those cases of delayed gaps to which we have above called attention. Another section, through the very base, or youngest part, of a mature stem, shows a ring of xylem broken at one point by the departure of a leaf-trace, thus presenting a state of affairs identical with that found in the species of Osmunda. These observations of Seward and Ford have been rather widely cited by other authors as evidence that the primitive method of departure of the leaf-trace in the Osmundaceae is a gapless one. Careful serial sections should be made through the region in question, however, before we may feel sure of the actual state of affairs.

Chandler (10) studied young plants of T. hymenophylloides and T. Frazeri. He simply states that his results in the former species confirm those of Seward and Ford, but gives no detailed account of the anatomy of the stem. In T. Frazeri he investigated only the very young stem, before the appearance of the pith. The single leaf-trace whose departure he observed was simply constricted off from the protostele. He examined the 'seedlings' of a large number of species of ferns and found that in every case, where the young stele is tubular, the departure of a leaf-trace causes a break in the continuity of the xylem ring.

The writer was able to examine the stems of young plants of O. regalis and of O. cinnamomea. They were too old, however, to show the continuous ring of xylem described by Leclerc du Sablon and Faull. Wherever the trace leaves the cylinder, in either of the two species observed, a wide gap results (Fig. 9).

The slender bases of mature stems of T. hymenophylloides and of T. superba were also examined, and in every case pronounced, though narrow, gaps were observed. Fig. 10 shows this young condition in the former species. Several gaps are visible, as well as two leaf-traces in different stages.

As far as the evidence from the young plant goes, therefore, it seems clearly to sustain the view that leaf-gaps are primitive structures in the Osmundaceae. Kidston and Gwynne-Vaughan, however, have used the structure of the 'seedling' to support the theory that the original condition in the family is a gapless ring of xylem. They cite the observations of Seward and Ford on *T. hymenophylloides*, which, as we have seen, would be much more reliable had they been made from a study of careful serial sections; those of Chandler on *T. Frazeri*, which could have nothing to do with the question of leaf-gaps, as the plants he examined had not progressed beyond the protostelic stage; and of Faull on *O. cinnamomea* and *O. Claytoniana*, which distinctly show that, although the young condition is a tubular stele, the continuity of the xylem ring is *always* broken at the departure of a leaf-trace.

Another region of the plant which is rapidly coming to be recognized as very retentive of ancestral characters is the vascular supply of the leaf. The occurrence of centripetal wood in the leaves of *Cycas* and *Prepinus*, and in the cotyledon of *Ginkgo*, when it has almost, if not quite, disappeared from the rest of the plant, are good illustrations of this. A still more striking case was recently investigated in this laboratory by Mr. A. J. Eames (11), who has found centripetal xylem in the vegetative and reproductive leaves of species of *Equisetum*, though it disappeared ages ago from the stem of the ancestors of living *Equiseta*.

In the Osmundaceae the leaf-bundle is somewhat like a flattened arch in shape, with incurved ends, and consists of a band of xylem elements more or less completely surrounded by phloem. It thus presents a rough resemblance to a portion of a siphonostelic central cylinder. It was thought that the relations of the vascular supply of the pinnae to this leafbundle would be of interest as showing the probable primitive method of departure from the stele of a foliar trace. The structure of the bundle in the rachis was consequently investigated in the three species of Osmunda, and in the four species of Todea already mentioned in this paper.

In all the species, traces to the pinnae go off from the leaf-bundle near the incurved ends of the arch. In O. regalis the first indication of this separation is the bending out of the arch at either end. This progresses so far that the xylem is broken at the adaxial end of the young trace. Such a condition is shown in Fig. 11. The trace to the pinna remains connected at its other end with the foliar strand for a long time, however, even until the gap in the leaf-bundle becomes closed up again behind it. Fig. 12 shows this state of affairs, which would seem to indicate that the trace has gone off without leaving a break in the xylem. The gap is thus a very short one. Through it, however, the fundamental tissue inside the bundle, or 'pith', becomes continuous with that outside the bundle, or ' cortex'. This cannot be seen at any one height, however, for the groundtissue between the arms of the pinna-trace is cut off by the closing stele from its connexion with the 'pith' before it becomes continuous with the 'cortex' by the complete separation from the leaf-bundle of the vascular tissue of the free end of the trace. At a certain level, therefore, there is apparently an island of fundamental tissue completely surrounded by vascular elements.

The rachis of a leaf of a very young plant of *O. regalis* was also examined. Though as yet very small, and composed of but few cells, the

leaf-bundle shows two well-marked gaps opposite the traces departing to the pinnae.

In O. cinnamomea the very small vascular supply of the pinna leaves the foliar bundle in a curious fashion. The arch first bends outward near its ends, as in O. regalis. In this case, however, the trace, consisting of the xylem-arch with its included phloem and stelar parenchyma, is constricted off, and the gap behind it closed, before the xylem of the two bundles separates. Fig. 13 shows the condition of affairs before the gap has entirely disappeared. The trace to the pinna now breaks away from the leaf-bundle, and when seen at this height apparently causes no interruption in the xylem of the leaf-stele. The fundamental tissues on the inside and on the outside of the main bundle do not become continuous at this point as they do in O. regalis, a gap being formed in the xylem-ring only, just as in the stem, without breaking through the entire cylinder. This gap is an oblique perforation in the wall, and the interruption in the ring of wood can be seen at no one level.

In O. Claytoniana the condition of affairs is somewhat more simple. The sides of the arch bend out as before, but in this case the trace breaks away quickly, and both its ends become free at about the same time. A gap is formed in the xylem only, the rest of the stelar tissue being merely constricted opposite the point of departure of the trace (Fig. 14). The xylem gap in this case is much longer than in the other two species, and does not close up for a considerable distance.

In *Todea barbara*, the rachis is much stouter than in the filmy members of the genus, and the foliar bundle is consequently large. The trace of the pinna arises near the sides of the arch, as before, and, as in *O. regalis*, becomes free at its adaxial or lower end much sooner than at its upper one. Since the gap does not speedily close, however, the internal and external fundamental tissue become freely continuous through it. Fig. 15 shows the stage in the departure of the trace before it becomes entirely free. The break in the vascular tissue of the leaf-stele is not repaired till long after the separation of the pinna from the rachis.

The leaves of the other three species of *Todea* are characterized by their so-called 'filmy' habit. The lamina is very thin, and possesses neither intercellular spaces nor stomata. The vascular supply to the leaf is consequently much reduced.

In *T. hymenophylloides* the strand departing to the pinna leaves a wellmarked gap in the leaf-stele through which the 'pith' and 'cortex' become continuous (Fig. 16). This gap, like the one in *T. barbara*, remains open for a considerable distance up the rachis.

In the case of *T. Frazeri*, a clear break in the xylem is caused by the outgoing trace of the pinna, but the continuity of the vascular ring is not quite interrupted. A deep constriction occurs in it, however, along which

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the internal and external endoderms almost meet (Fig. 17). The state of affairs here is somewhat intermediate between that found in O. Claytoniana and that in T. hymenophylloides.

In the last species, T. superba, the trace to the pinna is very small. Opposite to its point of departure, a gap is formed in the leaf-stele around the ends of which the internal and external endoderms become continuous. This gap is not wide enough, however, to permit the connexion through it of the 'pith' with the 'cortex', the two rows of endodermal cells lying side by side, as shown in Fig. 18.

In all the species examined, therefore, gaps in the leaf-stele at the point of departure of the vascular supply of a pinna were observed, though in *O. regalis* and *O. cinnamomea* they are very short, and at certain heights apparently absent.

There seems to be a general relation between the size of the trace to the pinna and the character of the gap which it subtends in the leaf-bundle. The pinnae of O. regalis are fewer, and consequently larger than those of the other two species in the genus, and the gaps subtended by their traces are consequently much wider. T. barbara and T. hymenophylloides, also, whose pinnae are rather large in proportion to the leaf, possess more prominent 'pinna-gaps' than does T. superba, where the primary divisions of the frond are much smaller. A leaf of Dicksonia antarctica was looked at in this connexion. Near the middle of the leaf the pinnae are large, but diminish in size towards the base till they become very small. It was found on examination that the traces to the large pinnae left wide gaps, through which the inner and the outer fundamental tissue became freely continuous, while in the case of the small pinnae the gap was minute and affected the xylem only, not breaking through the whole stele.

The evidence from the leaf-trace, therefore, distinctly confirms that derived from fossil forms and from the structure of the young plant, in pointing towards the primitive existence of the foliar gap in the Osmundaceae.

#### CONCLUSIONS.

The ancestry of the Osmundaceae, as we have above remarked, is much a matter of doubt. From such fossil evidence as we possess, however, that bears on the matter, and from what we have observed in the structure of the young plant and of the leaf, both very tenacious of primitive characters, it seems reasonably certain that in all those ancient members of the family which possessed a true parenchymatous pith, the leaf-trace, as it departed from the stele, always formed a gap in the xylem, and very probably, as indicated by the structure of *Osmundites Skidegatensis*, in the whole vascular ring. The evidence also seems to point towards the correctness of Jeffrey's and Faull's view of the Osmundaceae as a reduction series, for the occurrence, in so many cases where it can hardly be explained

on physiological grounds, of the strong tendency for a foliar bundle to cause a gap in the stele from whence it arises, seems most easily attributable to the persistence, in a reduced condition, of an ancestral feature. The Osmundaceae, therefore, must apparently be included in Jeffrey's phylum Pteropsida. They give strong support to the general principle proposed by him that in all the members of this great group, the departure from a tubular stele of a vascular strand, no matter how much reduced, which supplies a foliar organ, causes a break in the continuity of the xylem of the stele.

#### SUMMARY.

1. In the mature stem of the six species of the Osmundaceae which were studied, a foliar gap, or break in the continuity of the stelar ring of xylem, was formed at the departure of the leaf-trace from the cylinder. A number of cases were observed, however, in all the species but one, where the gap did not become complete for some time after the departure of the leaf-trace, which thus at first seemed to go off in a gapless manner. In no case which could be thoroughly investigated by complete serial sections, was there found to be the real absence of a foliar gap.

2. None of the fossil Osmundaceae, so far as we know them, which possessed a true parenchymatous pith, present a clear instance of the departure of a leaf-trace which does not cause a break in the xylem-ring. In *Osmundites Dunlopi*, which seems at first sight to be an exception to this statement, we probably have a form with very short and narrow gaps, which have been largely obliterated in the process of fossilization.

3. In all the young plants of the Osmundaceae which have been investigated by the writer and others, foliar gaps have been observed from the very youngest condition, with the barely possible exception of the very early stages in *Todea hymenophylloides*. Our evidence in this species, however, is as yet insufficient.

4. In the seven species studied, the departure of the trace to the pinna, or primary division of the frond, was always found to leave a gap in the arch-shaped leaf-bundle. In three species this gap affected only the xylem, but in the remaining four a complete break in the vascular tissue was made. In only three of the latter, however, was the gap wide enough to permit of the connexion through it of the fundamental tissue on the inside with that on the outside of the leaf-bundle. The width and character of the gap in all instances seemed to depend largely on the relative sizes of the pinna-trace and the main bundle.

5. From such fossil evidence as is available, therefore, and from the structure of the young plant and of the foliar strands, both of which are known to be conservative of ancestral characters, it seems quite clear that the presence of foliar gaps is a primitive feature in the Osmundaceae.

6. The Osmundaceae are therefore very properly placed in Jeffrey's phylum Pteropsida, the members of which are primitively phyllosiphonic.

I am under obligations to Mr.A. J. Eames and to Professor Jeffrey for their kindness in supplying material, and wish to express to the latter my sincere thanks for advice during the course of the work.

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### DESCRIPTION OF PLATES XI AND XII.

Illustrating Mr. Sinnott's paper on Leaf-gaps in Osmundaceae.

Fig. 1. Osmunda cinnamomea. Leaf-trace leaving the cylinder, apparently without making a complete gap.  $\times$  40.

Fig. 2. O. cinnamomea. The same trace as in Fig. 1 a little higher up in the stem, showing the well-marked gap subtended by it.  $\times 40$ .

Fig. 3. O. regalis. Leaf-trace departing from the cylinder in an apparently gapless fashion.  $\times$  40. Fig. 4. O. regalis. The narrow gap eventually subtended by the trace shown in Fig. 3.  $\times$  200.

Fig. 5. Todea superba. Leaf-trace departing without making a complete gap. x 60.

Fig. 6. T. superba. The same trace as in Fig. 5, showing the well-marked gap which finally appears. x 40.

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Fig. 7. T. hymenophylloides. Apparently gapless condition at the departure of a leaf-trace. × 40.

Fig. 8. T. hymenophylloides. The narrow gap which eventually appears opposite the trace shown in Fig. 7. x 200.

Fig. 9. Osmunda regalis. Section of a young plant, showing two departing traces and their subtended gaps. x 60.

Fig. 10. Todea hymenophylloides. Section through the slender base of a stem, showing two traces in the early stages of departure, and three foliar gaps.  $\times$  40.

Fig. 11. Osmunda regalis. Showing the gap formed in the leaf-bundle by the trace departing to the pinna.  $\times$  40.

Fig. 12. O. regalis. Condition of affairs slightly higher up than in Fig. 11, showing the apparent absence of a gap at the departure of a trace to a pinna.  $\times$  40.

Fig. 13. O. cinnamomea. Trace to the pinna being constricted off from the leaf-bundle.  $\times$  60. Fig. 14. O. Claytoniana. 'Pinna-gap,' affecting only the xylem of the leaf-bundle.  $\times$  40.

Fig. 15. Todea barbara. Early stage in the departure of the trace to the pinna, showing complete break in the leaf-stele.  $\times$  40.

Fig. 16. T. hymenophylloides. Leaf-bundle, showing two 'pinna-gaps' and the trace subtending one of them.  $\times$  40.

Fig. 17. T. Frazeri. Leaf-bundle with two 'pinna-gaps' which do not quite break through the stele.  $\times$  40.

Fig. 18. T. superba. Leaf-bundle, with two traces departing to the pinnae, showing the complete gaps in the leaf-stele.  $\times$  40.



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