On the Gaps in the Stele of some Polypodiaceae.

By

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Since the end of the last century, the problem of the stele has been discussed by many authors, especially with regard to Pteridophytes, and various nomenclatures about the stele were introduced. Among them Solenostele and Dictyosteile may be adopted here, as was done by TANSLEY\(^1\), for the stele with single tubular form.

Solenostele was defined by GWYNNE-VAUGHAN\(^2\) as "a single hollow cylinder with phloem and phloecterma on either side, the complete continuity of which is interrupted only by the departure of leaf-traces; the gap thus produced being closed up in the internode above before the departure of the next leaf-traces." Dictyosteile was defined by BREBNER\(^3\) in the following manner: "a vascular tube with large overlapping leaf-gaps, so that the whole structure becomes a network of vascular strands or meristeles. The meristeles are concentric. This is closely allied to the preceding (Solenostele), the difference being due to the approximation and overlapping of the leaf-gaps."

The distinction between these two stelar forms depends on the presence or absence of overlapping leaf-gaps, but there are other types of steles, in which gaps other than leaf-gaps are present. They were called by TANSLEY\(^4\) as 'perforated' and 'dissected' steles. If

4) TANSLEY, l. c. '07, p. 192.
we discuss the case with leaf-gaps, putting aside the type with perforation or dissection for a moment, it may be considered that the dictyostele is derived from the solenostele by the overlapping of foliar gaps. As to the process of the overlapping GWYNNE-VAUGHAN\(^1\) says, "it appears that two different factors may be concerned in bringing about this overlapping of the leaf-gaps. In the first place it is evident that if the leaf-gaps remain open long enough after the departure of the leaf-traces, they will evidently overlap; again, the same result will also be obtained if the leaves be crowded sufficiently close together, although the leaf-gaps may close up comparatively rapidly."

In a word, he considered two factors—the prolongation of foliar gaps and the shortness of internodes. These factors were also adopted by TANSLEY\(^2\) as correct. If this view is correct, the intermediate types between the two stelar forms may be found. In fact, there are many such intermediate or transitional types.\(^3\)

Next, the form and the relation of rhizomes and leaves in Polypodiaceae will be considered. There are two extreme forms of rhizomes, one creeping and the other erect. In general, leaves in the former are arranged loosely on the rhizome, while in the latter the arrangement of leaves is so crowded that the rhizome forms, with petiolar bases, a bulb-like mass. The distinction between these two forms, however, is not absolute, because they are not only connected by many intermediate ones, but also are variable in the different parts of one and the same individual. In this respect, DIELS\(^4\) says that, "das kriechende Rhizom......besitzt Internodien von verschiedener Länge, ventral angefügte Wurzel und dorsal meist zweizeilig, sehr selten einzeilig angeordnete Blätter. Das aufsteigende oder aufrechte Rhizom zeigt meist stark gestauchte Internodien und dichte spiralig gestellte Blätter." Accordingly, gaps may be said to overlap in the erect rhizome with crowded leaves, but this is very doubtful in the case of the creeping one with loosely arranged leaves. On this point, GWYNNE-VAUGHAN\(^5\) says, on the solenostelic ferns, that "all these (solenostelic) ferns have a creeping, more or less dorsiventral rhizome.

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1) GWYNNE-VAUGHAN, l.c. '03, p. 694.
2) TANSLEY, l.c. p. 187.
3) GWYNNE-VAUGHAN, l.c. '03.
5) GWYNNE-VAUGHAN, l.c. '03, p. 691.
with leaves arranged in two rows on the upper surface.” Tansley\(^1\) also says, in ferns in general, that “it may be remembered that in the radial type the relative position of two meristeles changes as the phyllotaxic spirals passed through, whereas in the dorsiventral type it is constant.” These show us that in the creeping rhizome leaves arrange themselves in two rows on the upper side of the rhizome, while in the erect one they are arranged radially all round the rhizome. Such creeping rhizomes are actually met with in few cases—Microlepia pilosella, M. marginata, M. Wilfordi—but, most of the creeping rhizomes have, so far as my anatomical investigations have proved spiral foliar arrangement such as \(\frac{1}{2}\) etc., just as in the case of erect one, though the relation is very indistinct in external appearance. This is in accordance with the observation by Conwentz.\(^2\)

I have once investigated the construction of the stele in Dryopteris sophoroides, which has a horizontal rhizome with rather long internodes, even as long as 10 cm., and found that the stele is a perfect dictyostelic type. Then the question occurred to me about the two factors as the causes or conditions of the formation of dictyostely. So I have examined various rhizomes of Japanese Polypodiaceae and it was found that their steles were constructed almost in dictyostelic type. Such cases were figured by Chandler\(^3\) in some sporelings of ferns, though he did not touch this problem. They showed also the individual constancy in the stelar construction.

Materials and Methods.

Rhizomes of various species of Polypodiaceae, which are common in the vicinity of Tokyo, were investigated. They differed from one another externally as well as internally. Anatomically, they show some different stelar types, such as solenostele, dictyosteole, transitional type between the two, Lindsaya-type,\(^4\) perforated and polycyclic types, of which the first three will be described here. The following species were investigated:

1) Tansley, l.c. ’07, p. 191.
5) The nomenclature of Polypodiaceae is different according to various authors; I have followed that of J. Matsumura’s Shokubutsu-meii (Tokyo, 1916). Some synonyms and Japanese names were added.
Adiantum monochlamys Eat.; A. aethiopicum Th. (hakone-shida)
A. pedatum L. (kujaku-shida)
Asplenium incisum Th.; A. trichomanes Th. (tora-no-o-shida)
Athyrium niponicum Hance.; Asplenium niponicum Mett. (inu-warabi)
A. yokoscence Chr.; Asplenium yokoscence F. et S. (hebi-no-negoa) Coniogramme fraxinea Diels.; Gymnogramme javanica Bl.;
G. fraxineum Don. (iwagane-zemmai)
Diplazium Conilii Mak.; Asplenium Conilii S. et F. (hosobashikeshida)
D. japonicum Brd.; Asplenium japonicum Th. (shikeshida)
D. lanceum Pr.; Asplenium lanceum Th. (hera-shida)
D. Wichurae Diels.; Asplenium Wichurae Mett. (nokogiri-shida)
Dryopteris africana Car.; Polypodium africanum Desv.; Nephrodium Totta Diels. (mizo shida)
D. decursivo-pinnata Kze.; Polypodium decursivo-pinnatum Hall.; Nephrodium decursivo-pinnatum Bak. (gejigeji-shida)
D. gracilescens Kze. var. abbreviatum Kod.; Aspidium gracilescens Bl.; Nephrodium glanduligerum Mak. (hashigo-shida)
D. japonica Chr.; Nephrodium japonicum Bak.; Aspidium japonicum Mak. (harigane-warabi)
D. setigera Kze.; Cheilanthes setigera Bl.; Aspidium oligophlebium Chr. (hime-warabi)
D. sophoroides Kze.; Polypodium sophoroides Th.; Nephrodium sophoroides Desv. (ho-shida)
Matteuccia orientalis Trev.; Struchiopteris orientalis Ik. (inugansoku)
Microlepia marginata Chr.; Davallia marginalis Bak.; Dicksonia marginalis Sw. (fumoto-shida)
M. pilosella Moore.; M. hirsuta Pr.; Davallia hirsuta Sw. (inu-shida)
M. Wilfordi Moore.; Davallia Wilfordi Bak. (ören-shida)
Onoclea sensibilis L. (kōya-warabi)
Plagiogyria adnata Bedd.; Lomaria adnata Bl. (kiji-no-o-shida)
Polystichum aculeatum Sch. var. japonicum Chr.; Aspidium aculeatum Doell. var. japonicum F. et S. (inode)
P. aristatum Pr.; Aspidium aristatum Sw. (kana-warabi)
P. falcatum Diels. var. Fortunei Bak.; Aspidium Fortunei Sm. (yabu-sotetsu)
P. lepidocaulon Sm.; Aspidium lepidocaulon Ik. (oridzuru-shida)
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P. Standishii CHR.; Aspidium viridescens Miq. (ryōmen-shida)
P. varium PR.; Aspidium varium Sw. (itachi-shida)
Woodwardia radicans Sw., var. orientalis Sw.; W. orientalis Sw.
( ko-mochi-shida)

All these materials were examined in fresh condition. From the series of free-hand sections a solid model of the stele was constructed in order to find the relation of foliar traces and gaps. For the sake of clearness in demonstration, however, the stelar model was developed diagramatically in such a way that the left side of the figure corresponds the upper side or the part near the apex of the rhizome.

Though the determination of phyllotaxy from the external appearance is difficult, it may be done comparatively easily from the arrangement of foliar gaps. Frequently there will be cases with twisted rhizomes, but in the present descriptions and diagramatic figures they are described and figured, for the sake of clearness, as if they were not twisted. Though the anatomical structure of meri-stele was also studied, it was omitted here, for it is not the object of the present paper to describe it in detail.

Observations.

Microlepia pilosella (HK.) Moore. Slender creeping rhizome with pretty long internodes. The structure was described by Gwynne-Vaughan\(^1\) as Davallia hirsuta. The result of the present research agrees with his observation. Insertion part of a leaf-trace is parallel to the axis of the rhizome, and a gap is situated lateral to the trace. Leaves are arranged actually in two alternating rows on the upper side of the creeping rhizome. The stele is typically solenostelic, because gaps do not overlap.

Microlepia Wiefordi Moore. The external and internal construction is quite similar to the preceding species, and it is not necessary to describe further.

Microlepia marginata (Hoëtt.) CHR. Though the configuration is far larger and the branching occurs very often, the construction is equivalent to the preceding. Gwynne-Vaughan\(^1\) also described correctly as Davallia marginalis.

Adiantum pedatum L. Creeping rhizome with pretty crowded leaves, rarely with long internodes. Each foliar trace and gap are

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1) Gwynne-Vaughan, i.e. '03.
of typical form. The latter has a definite length so that it occasionally overlaps each other in shorter internodes, thus indicating a transitional type. Foliar arrangement can be estimated from that of gaps, which are arranged in $\frac{1}{3}$ counterclockwise manner.\(^5\)

*Adiantum monochlamys* EAT. External and internal construction is similar to the preceding, but in this species the overlapping of gaps is so frequent that it appears often like a dictyostelic type.

*Athyrium nipponicum* (Mett.) HANCE. Creeping rhizome with foliar arrangement in $\frac{1}{3}$ clockwise manner. A model of the stele constructed from the serial sections (Fig. 1, A) and a figure developed from it (Fig. 1, B) illustrates the construction of the stele. According to these features it may be seen that there are three horizontal rows of very long gaps, and also that a foliar trace departs from the bottom of a gap (Fig. 2, A; marked with $\bigcirc$) though it divides immediately after the departure. It is clear that foliar traces and gaps arrange themselves in $\frac{1}{3}$ clockwise manner. Then, the relation of two consecutive gaps in one and the same row will be considered. The end of a gap approaches the next one, so that two gaps are separated by a short transverse commissure. This relation is invariable throughout the rhizome regardless of internodal length. In such a way three or four gaps overlap in every cross section, so that the stele is divided always into two or three meristeles. Exceptionally a gap may be discrepant with the next (Fig. 1). Such a case will be illustrated later in other species.

*Athyrium yokoscence* (Fr. et Sav.) CHR. Oblique rhizome with leaves closely arranged in $\frac{1}{3}$ counterclockwise manner. This arrangement affects the construction of the stele, which is quite different from the preceding species (Fig. 2, B). Behavior of foliar traces is

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1) Direction of spiral foliar arrangement viewed from the apex.
also same with the latter in the diagram the departing point is marked with $\bigcirc$).

_Diplazium Wichurae_ (Mett.) Diels. Creeping rhizome with closely or loosely arranged leaves. Foliar arrangement is $\frac{1}{3}$ clockwise, and the stelar construction is the same with that of _Athyrium nipponicum_, the only difference being in that two foliar traces depart from both sides of a gap independently at the part pretty behind the next gap (Fig. 2, A; marked with $\times$).

_Dryopteris decursivo-pinnata_ (Halle) Kze. Almost erect rhizome with very crowded leaves. This has $\frac{1}{3}$ counterclockwise phylloaxy, and two foliar traces depart from a gap in the part pretty behind the next gap (Fig. 2, B; marked with $\times$), so that the stelar construction is quite contrariwise to the abovementioned species.

_Coniogramme fraxinea_ (Don.) Diels. Large creeping rhizome with long internodes. The construction of the stele is similar to the preceding, only differing in that, the departing parts of leaf-traces are situated somewhat anterior to those in the preceding species (Fig. 2, B; marked with $\Delta$).

_Polystichum lepidocaulon_ (Hk.) Sm. Creeping rhizome usually with crowded leaves, showing $\frac{1}{3}$ clockwise arrangement. Though the construction of the stele is similar to that of _Athyrium nipponicum_, foliar traces in every gap is three, one departing from the bottom of the gap, two from the part as _Diplazium Wichurae_ (Fig. 2, A; marked with $\bigcirc$ & $\times$).

_Polystichum aculeatum_ (L.) Sch. var. japonicum Chr. Oblique rhizome with very crowded leaves. Construction of the stele is similar to the preceding. Among three traces two are situated slightly anterior to the case of the above mentioned species. (Fig. 2, A; marked with $\bigcirc$ & $\Delta$).

_Dryopteris africana_ (Desv.) Chr. Creeping rhizome with leaves
arranged closely or loosely in $\frac{1}{3}$ clockwise manner. The stelar construction is different from the preceding. Though the gaps are arranged in three rows, two neighbouring gaps in one and the same row are discrepant. Consequently, the strand separating the two gaps becomes oblique; the orientation of the strand being constantly counterclockwise, that is, running across from below the right to above the left in the diagram (Fig. 3, A). This tendency was observed in *Athyrium nipponicum* in exceptional cases, but it occurs definitely in this species. The number of meristeles in a cross section is three or four. Foliar traces, two in number depart from the margin of a gap toward the end of the commissual strand in the next row (Fig. 3, A; marked with $\times$).

*Dryopteris japonica* (Bak.) Chr. Creeping rhizome with loosely arranged leaves. The construction of the stele and foliar traces are as in the foregoing species.

*Dryopteris gracilescens* (Bl.) Kze. var. *abbreviatum* Koid. Oblique rhizome with crowded leaves. Stelar construction is as in the above mentioned species.

*Diplazium lanceum* (Th.) Pa. Slender creeping rhizome with long internodes. Stelar construction is similar to the preceding, only differing in that the departing points of traces are slightly posterior (Fig. 3, A; marked with $\Delta$).

*Dryopteris sophoroides* (Th.) Kze. Typical creeping rhizome with very long internodes, even as long as 10 cm. The stelar construction, however, is quite the same with the preceding species, only differing in that the two traces depart nearly at the end of the gap (Fig. 3, A; marked with $\circ$).

*Diplazium japonicum* (Th.) Bedd. Creeping rhizome with leaves arranged loosely in $\frac{1}{4}$ counterclockwise manner. The stelar construction is quite contrariwise to the precedings, the oblique commissure running across clockwise or from above the right to below the left.
in the diagram (Fig. 3, B). Foliar traces, two in number, depart from the end of the commissural strand in the next row (Fig. 3, B; marked with \( \times \)).

*Diplazium Conihi* (Fr. et Sav.) MAK. Slender rhizome like the above mentioned species. The stelar construction is also similar to the latter.

*Onoclea sensibilis* L. Creeping rhizome with long internodes. The stelar construction is similar to the preceding.

*Dryopteris setigera* (Bl.) Kze. Almost creeping rhizome with crowded leaves. The stelar construction is the same with that of the preceding species, but two traces depart slightly posterior (Fig. 3, B; marked with \( \Delta \)).

*Asplenium incisum* Th. Internal as well as external structure is similar to the preceding.

*Polystichum falcatum* (L.) DIELS. var. *Fortunei* BAK. Oblique rhizome with radially arranged leaves. The construction of the stele is like that of *Dryopteris africana*, but foliar traces which depart from a gap are three, one from the bottom, the others from the middle part of the gap.

*Polystichum aristatum* (Forst.) Pr. Creeping rhizome with long internodes. The stele is constructed as in the preceding, but the number of foliar traces in each gap is mostly seven, one departing from the bottom, the others from the margin of the gap. The last pair is always larger than the others.

*Plagiogyria adnata* (Bl.) Bedd. Nearly erect rhizome with radially arranged leaves. The internal construction of the stele shows that foliar gaps are arranged in \( \frac{3}{5} \) counterclockwise manner. Accordingly, the stelar structure is quite different from the above stated species. Stelar gaps are situated in five rows and in each row two neighbouring gaps are separated by a transverse commissure. A gap overlaps with gaps of different rows, so that usually three or four meristelles are seen in a cross section. A foliar trace departs from the bottom of the gap. (Fig. 4, B; marked with \( \circ \)).

*Woodwardia radicans* (L.) Sw. var. *orientalis* Sw. Oblique or erect rhizome with mostly radial foliar arrangement. The stelar construction is quite the same with the preceding, only differing in that two traces depart from the middle part of both sides of a gap. (Fig. 4, B; marked with \( \times \)).

*Matteuccia orientalis* (Hk.) Trev. Erect rhizome with radially arranged leaves. The stelar construction is quite contrariwise to
the preceding species, because leaves are arranged in $\frac{2}{5}$ clockwise manner. Foliar traces, two in number, depart from both sides of a gap (Fig. 4, A; marked with $\times$).

*Polystichum variium* (L.) Pr. Oblique or erect rhizome with leaves arranged very closely in $\frac{2}{5}$ clockwise manner. The stelar construction is quite similar to that of the above mentioned species. The number of foliar traces is five to seven, one departing from the bottom, the others from both sides of a gap. The last pair is always larger than the others (Fig. 4, A; marked with $\circ$).

*Polystichum Standishii* (Moore) Chr. Erect rhizome with $\frac{2}{5}$ counterclockwise foliar arrangement. The stelar structure is quite contrariwise to the preceding. Foliar traces are from five to seven in number.

**General Considerations and Conclusions.**

The gaps of the stele above described, have the relation to foliar traces. The foliar traces depart from the margin of gaps as one, two, three or more separate strands according to different species. In his paper advocating his view of the absence of foliar gaps in Lycopsida, Jeffrey\(^1\) characterized the foliar gap in the following manner: "the foliar gap may be distinguished from the other gaps in the wall of the fibrovascular hollow cylinder by the fact that it occurs immediately above a leaf trace. A true foliar gap, moreover, is always related to put a single leaf-trace. If several traces appear in relation to a stelar gap and especially if they are related to the side of the gaps, it may be concluded at once that no true foliar gap is present." Following this restriction the gaps of Polypodiaceous

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stele above described should not be regarded as the true foliar gaps; and if it be so, would it not be a contradiction to put Polypodiaceae among Pteridopsida? The typical foliar gaps following his definition are present in some species of Adiantum, and also according to Gwynne-Vaughan in Loxsoma. There are some cases where a trace divides as soon as it departs from the gap (as in Athyrium), and if this tendency becomes more prominent two traces will leave the stele separately from both sides of a gap (as in Diplazium, etc.); and the cases when three or more traces depart separately from a gap may result. Such a case was observed in sporelings of Marattiaceae. The primordial leaves in this family have only a single foliar trace, while the following ones have a trace divided into two at the upper part, though it remains single at the base; and in some subsequent leaves two traces leave separately from a gap, and at last the particular type of traces develops gradually. Thus, it will be natural to consider that the gaps above described as belonging to the true foliar gaps, and also that the Polypodiaceous steles having such gaps are the typical dictyostele.

In some younger part of the rhizome with dictyostele, we may find the solenostelic condition (such as in Athyrium nipponicum, Diplazium japonicum). Considering these facts and the occurrence of the transitional types between two stelar forms, it seems natural to conclude, as many authors have done, that the dictyostely may be derived from a solenostely. But, two conditions or factors mentioned before on the formation or appearance of the dictyostely, do not hold true in this respect, because even in the rhizomes with long internodes dictyostelic condition is generally present irrespective of the length of internodes. The dictyostely of Polypodiaceae, therefore, at least in the species I have investigated, can be ascribed to the constant relation of foliar gaps and commissure between them, and not to the length of internodes.

Summary.

1. In some creeping rhizomes of Polypodiaceae, leaves are arranged in two rows on the dorsal side of the rhizome. This is,

1) Gwynne-Vaughan, I. c.
however, to be seen in comparatively rare cases, such as *Microlepia pilosella*, *M. Wilfordi* and *M. marginata*.

2. In most creeping as well as erect rhizomes of Polypodiaceae, leaves are arranged all round the rhizome, though the external appearance may not reveal this condition in the creeping rhizome.

3. The arrangement of foliar gaps of the stele in the rhizome is generally constant in every species, though in some cases there are slight variations.

4. The number and the position of departure of foliar traces are generally constant in each species. The former varies according to species from one to seven or more, at the point of departure from the gap.

5. The stele in some species shows solenostelic construction; e.g. *Microlepia pilosella*, *M. Wilfordi*, *M. marginata*.

6. Some species have the stele of transitional type between the solenostelic and the dictyostelic; e. g. *Adiantum pedatum*, *A. monochlamys*.

7. Rhizomes of most species of Polypodiaceae have dictyostelic stele. They may be classified as follows.

A. Rhizomes with \(\frac{1}{3}\) phyllotaxy.

I. Those with transverse commissures or with two and three meristele in a cross section of the stele.

a. A leaf with a single foliar trace.
   
   a. Clockwise phyllotaxy......*Athyrium nipponicum*.
   b. Counterclockwise phyllotaxy......*Athyrium yokoscence*.

b. A leaf with two foliar traces.
   
   a. Clockwise phyllotaxy......*Diplazium Wichurae*.
   b. Counterclockwise phyllotaxy......*Dryopteris decursivo-pinnata*, *Coniogramme fraxinea*.

c. A leaf with three foliar traces.
   
   a. Clockwise phyllotaxy......*Plystichum lepidocaulon*, *P. aestivalis var. japonicum*.

II. Those with oblique commissures or with three and four meristéles in a cross section of the stele.

a. A leaf with two foliar traces.
   
   a. Clockwise phyllotaxy......*Dryopteris africana*, *D. sophoroide*, *D. japonica*, *D. gracilescens var. abbreviatum*, *Diplazium lanceum*.
   b. Counterclockwise phyllotaxy......*Diplazium japonicum*, *D. Conilii*, *Dryopteris setigera*, *Asplenium incisum*, *Onoclea sensibilis*.
b. A leaf with three foliar traces.
   a. Clockwise phyllotaxy.......Polystichum falcatum var. Fortunei.

c. A leaf with several foliar traces.
   a. Clockwise phyllotaxy.......Polystichum aristatum.

B. Rhizomes with \( \frac{2}{3} \) phyllotaxy.
   a. A leaf with a single foliar trace.
      \( \beta \). Counterclockwise phyllotaxy.......Plagiogyria adnata.
   b. A leaf with two foliar traces.
      a. Clockwise phyllotaxy.......Matteuccia orientalis.
      \( \beta \). Counterclockwise phyllotaxy.......Woodwardia radicans var. orientalis.
   c. A leaf with several foliar traces.
      a. Clockwise phyllotaxy.......Polystichum varium.
      \( \beta \). Counterclockwise phyllotaxy.......Polystichum Standishii.

8. The length of the gap directly varies with that of the internode, that is to say, both are closely related to each other, so that the relation of the two consecutive gaps in one and the same row and the commissure between them is constant. The result is that the dictyostely and solenostely in Polypodiaceae are determined irrespective of the length of the internode in contradiction to what has been hitherto assumed by some authors, but chiefly by the length of the gap in the respective species.

The writer intends to carry out a further study with other species of Polypodiaceae.

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