

## TISSUE DIFFERENTIATION IN THE ROOTS OF SOME FERNS<sup>(1)</sup>

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**Abstract:** The sequences of differentiation and maturation of eight different species of ferns (including both eusporangiate and leptosporangiate) are investigated in this report. With the exception of *Botrychium* and the giant roots of *Angiopteris* all other roots are protostelic. The numbers of the protoxylem strands range from two to seven. The larger the root diameter, the more the protoxylem poles occur. The endodermis is characterized by a Casparian strip in the roots of *Ceratopteris*, *Angiopteris* and *Botrychium* or is darkly stained in the roots of *Adiantum*, *Osmunda*, *Pteris* and *Marsilea*. The relationship between the origin of lateral roots and the stele can be summarized as follow: If the pericycle consists of more than one layer of cells, the lateral root initiates from this tissue, e. g., as in *Osmunda* and *Angiopteris*; whereas if the pericycle has only one layer of cells, the lateral root is endodermal in origin, e. g., *Adiantum*, *Ceratopteris*, *Marsilea* and *Pteris*. In roots having diarch or triarch protoxylem, the lateral roots originate opposite the protoxylem, but lateral roots originate between the xylem and the phloem in roots having tetrarch or heptarch protoxylem. The occurrence of sclerenchyma in the cortex is due to genetic factors rather than physiological ones.

### INTRODUCTION

It has long been known that some studies support the observations in which the progressive acropetal differentiation of the sieve elements mature closer to the root apex than do the xylem elements in angiosperms (Esau, 1943, 1965a, 1965b; Popham, 1955; Peterson, 1967; Riopel and Steeves, 1964). Recently Chiang (1971) found that the maturation sequence of vascular elements in an aquatic fern—*Ceratopteris* agreed with this view. Nevertheless, the root of *Ophioglossum petiolatum* showed a different pattern, in which the tracheary elements mature before the sieve elements (Chen and Chiang, 1972).

The vascular cylinder in the roots of the lower vascular plants shows less variation in its morphology than angiosperms. They usually have an entire protostele with rather few protoxylem points (except in the giant roots such as members of the Marattiales). But it seems to the authors that fern roots probably show more variation in their differentiation and maturation pattern than that found in the roots of angiosperms.

The lateral root primordia in flowering plants have been described as pericyclic, both pericyclic and endodermal or originating from more than these two tissues whereas the lateral roots in most pteridophytes originate from the endodermis (Chiang, 1970; Chiang, 1971; Cutter, 1971; Esau, 1961, 1965a; Seago, 1973), but in some ferns, it develops from the tissues other than the endodermis (Ogura, 1938). Though the position of the lateral roots in relation to the xylem or phloem of the

(1) This work was supported by a grant of Biological Research Center, Academia Sinica.

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parent root in angiosperms has also been described (Esau, 1965), little is known regarding the orientation of lateral root in the pteridophytes (Chiang and Gifford, 1971).

The primary objectives of the present study are to carefully observe the sequences of differentiation and maturation of vascular elements and their associated tissues in the roots of vascular cryptogams including both eusporangiate and leptosporangiate ferns and to determine whether any type of regularity with regard to maturation sequence of root tissues and the origin of lateral roots can be found in the plants investigated. The detail processes of tissue differentiation in the fern roots of *Ceratopteris thalictroides* (Chiang, 1971) and *Ophioglossum petiolatum* (Chen and Chiang, 1972) have been studied. In the present report the authors are not examining the tissue differentiation for each species in minute detail, but merely intend to point out the sequence of development of several conspicuous tissues of the central stele such as phloem, protoxylem, metaxylem, endodermis as well as its associated cortical cells.

### MATERIALS AND METHODS

The materials used in the present investigation and their source and growth habit are listed in Table 1.

Table 1. The source of plants studied together with their habit

	Source	Growth habit
<i>Adiantum capillus-veneris</i>	NTU green house	terrestrial in damp soil
<i>Angiopteris lycopodiifolia</i>	Shih-Ting (石碇), Taipei	terrestrial
<i>Botrychium lunaria</i>	Chin-Ping Shan(金平山), Taipei	terrestrial in damp soil
<i>Ceratopteris pteridoides</i>	NTU green house	aquatic, rooting in mud
<i>C. thalictroides</i>	NTU green house	aquatic, rooting in mud
<i>Marsilea crenata</i>	NTU green house	aquatic, rooting in mud
<i>Osmunda japonica</i>	Shih-Ting (石碇), Taipei	terrestrial
<i>Pteris multifida</i>	NTU green house	terrestrial

All the materials were fixed in FAA immediately after collection. Three to seven specimens of each species were sectioned for study. After being washed in 50% ethanol, the specimens were dehydrated through a tertiary-butanol series and embedded in tissueemat. Serial transverse and longitudinal sections were cut at the thickness of 8  $\mu$  and stained with either safranin and fast-green (Jensen, 1962), or by tannic acid and iron alum with safranin and orange G (Sharman, 1943).

### RESULTS

#### General Structure of the Vascular Stele

(1) *Adiantum*, *Pteris*, *Ceratopteris* and *Marsilea*. The radial direction of xylem maturation in *Adiantum*, *Pteris*, *Ceratopteris* and *Marsilea* is exarch and diarch. The tracheary elements in the mature roots are simply arranged. Two to three or four identically large metaxylem elements always occupy almost the entire center (Figs. 1a, 1b, 1c). So that the sieve elements lie along both sides of the enlarged metaxylem

elements. Phloem consists of one to two cell layers (always one in *Adiantum*, *Pteris* and *Marsilea*). A constantly one cell layered pericycle is present inside the uniseriate endodermis. Pericyclic cells are characteristically large in the developing root (Figs. 3a, 3b), but become more or less identical or even smaller than their neighbouring cells in fully developed roots (Figs. 1a, 1b, 1c). They are parenchymatous in all the stages observed.

(2) *Osmunda*. The xylem in *Osmunda* is either diarch or triarch (Figs. 1d, 2). In both diarch and triarch roots, xylem consists of a rather large number of metaxylem elements. Parenchymatous pericyclic cells are conspicuously larger than their neighbouring cells and are always in one or two cell layers. The endodermal cells as well as some of their adjacent cortical cells are deeply stained. The boundary between the cortical cells and endodermal layer is not clear because of the darkly stained substance in them and the similarity of their size (Figs. 1d, 2f).

(3) *Botrychium*. Diarch, triarch and tetrarch xylem are found in this investigation. Both triarch and tetrarch conditions have been seen in a single root. It possesses triarch xylem in the region near the root tip and becomes tetrarch farther from the tip (Fig. 1f). The medullation of the center of the root appears in all the roots examined. In the other words, pith is present in all stages of these roots. Metaxylem elements are numerous. The number of cells in the pericyclic layer ranges from one to three but is usually two.

(4) *Angiopteris*. The xylem ranges from tetrarch to heptarch (Figs. 1e, 3c). The roots which have more than four xylem poles are always medullated whereas in the tetrarch root the central part is always occupied by metaxylem (or with only one or two parenchyma cells) (Fig. 1e). The arrangement of tracheary elements is narrow and simple, only one to two rows of cells extend from the protoxylem to metaxylem. The phloem region is wider having many cells (Fig. 1e).

### Endodermis

The endodermal cells represent the inner boundary of the cortex. The endodermal cells in the root of *Adiantum* are small, uniseriate and only consist of six cells (Fig. 1b). They are intimately surrounded by a layer of cortical cells which are exceptionally large and also six in number. The endodermis in *Pteris* and *Marsilea* is also uniseriate but made up of more than ten cells. The endodermal cells in these three genera have no typical Casparian strip. The entire cell contents are darkly stained in the region where all the tracheary elements have secondary thickenings (Figs. 1a, 1b). The structure of this darkly stained material has not been clarified.

The Casparian strips in the endodermal cells of *Ceratopteris*, *Botrychium* and *Angiopteris* are very conspicuous (Figs. 1d, 1e; Chiang, 1971, Fig. 7a). It appears on the radial and transverse walls of the endodermal cells. These strips of *Ceratopteris* occupy rather small areas on the cell walls whereas in *Botrychium* and *Angiopteris* they cover a wider part of the anticlinal walls. The endodermal cells in *Ceratopteris* are usually smaller than the cortical cells and almost the same size as the pericyclic cells which lie next to them. But the endodermal cells of *Botrychium* and *Angiopteris* are conspicuous, being larger than the cortical cells lying on the outside or the stellar cells (tracheary elements, phloem cells, pericyclic cells etc.) lying within.

The endodermal cell as well as some of its adjacent cortical cells are darkly stained in *Osmunda* (Figs. 1d, 2). The boundary between the cortical cells and the endodermal layer is not clear because of the presence of this darkly stained substance and because of their similarity in size.

### Cortex

*Angiopteris* and *Botrychium* bear rather fleshy roots. They do not have a wiry-like nature as those of other terrestrial ferns, such as *Pteris*, *Adiantum* and *Osmunda*. No sclerenchyma has been found in the cortex of *Angiopteris* and *Botrychium*. The diameters of some roots in *Angiopteris* are very large and are up to 6 mm. But they are parenchymatous except for their vascular tissue. Sclerenchyma is constantly present in the roots of all other species investigated. The cortical sclerenchyma in *Pteris* and *Marsilea* is characteristically thick-walled (Figs. 1c, 1e), whereas that in the roots of *Ceratopteris*, *Adiantum* and *Osmunda* is rather thin-walled (Figs. 1a, 2b). The sclerification of cortical cells in the radial direction is always constant in the roots of a given species. It is centripetal in *Osmunda*, but is centrifugal in the other species (Table 3).

Table 2. Structural variation in the roots of different species

	number of protoxylem strands	medullation of stele	cell layers in pericycle	characteristic of endodermis	lateral root origin	position of lateral root origin
<i>Adiantum capillus-veneris</i>	2	—	1	dark stained	endodermis	xylem <sup>(2)</sup> between xylem and phloem
<i>Angiopteris lygodifolia</i>	4-7	±	1-3	C-strip	pericycle	between xylem and phloem
<i>Botrychium lunaria</i>	2-4	+	1-3	C-strip	pericycle <sup>(1)</sup>	xylem and phloem <sup>(2)</sup>
<i>Ceratopteris pteridoides</i>	2	—	1	C-strip	endodermis	xylem
<i>C. thalictroides</i>	2	—	1	C-strip	endodermis	xylem
<i>Marsilea crenata</i>	2	—	1	dark stained	endodermis	xylem
<i>Osmunda japonica</i>	2-3	—	1-2	dark stained	pericycle	xylem
<i>Pteris multifida</i>	2	—	1	dark stained	endodermis	xylem

(1) lack direct evidence

(2) opposite protoxylem pole

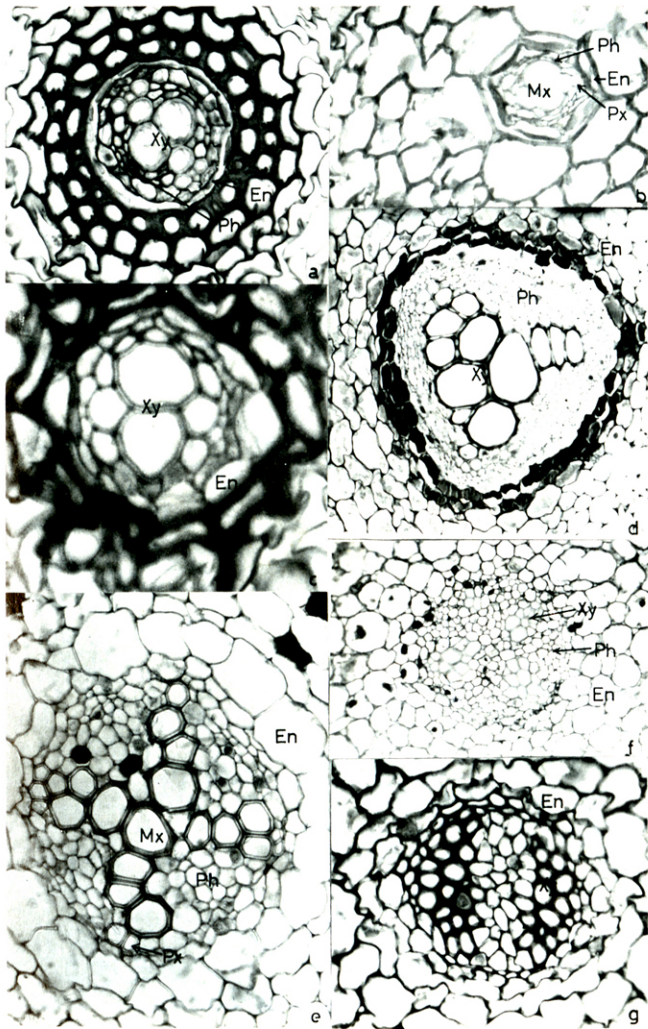
(3) in tetrarch root, no lateral roots bearing diarch or triarch roots have been seen

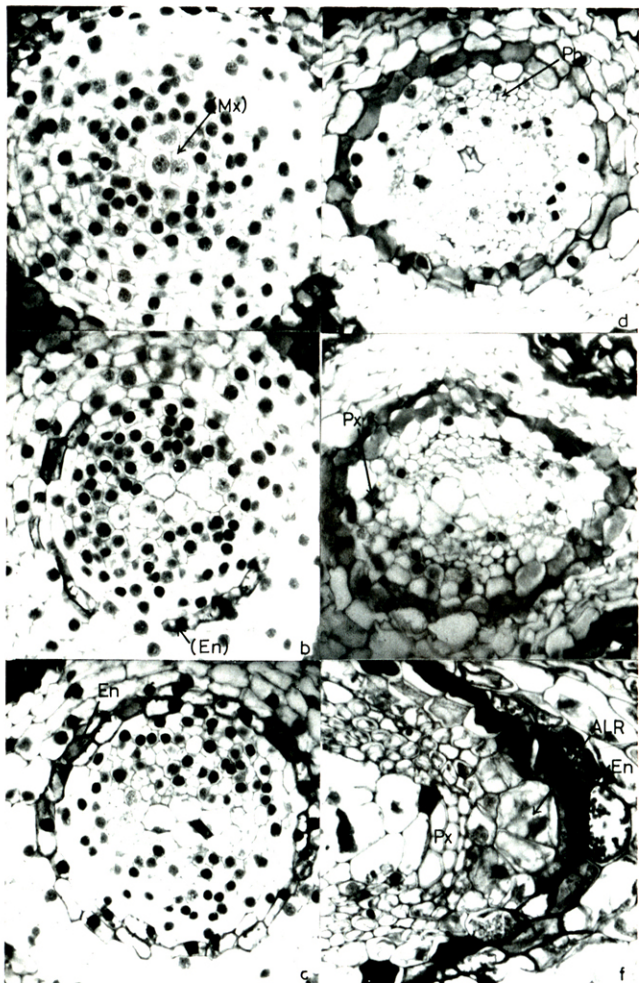
### Sequence of Tissue Maturation

The apical meristems of all roots examined have a single apical cell. Apparently all the tissues of these ferns (both eusporangiate and leptosporangiate) arise from the tissues or cells formed from this apical cell. More than six roots of each species were examined in the study of the differentiation and maturation of root tissues. All the roots of a single species show a similar sequence of differentiation and

Fig. 1. Transverse sections of mature roots. a. *Pteris*, showing diarch protoxylem with linearly arranged phloem and centrifugal sclerenchyma in the inner portion of the cortex. ( $\times 350$ ); b. *Adiantum*, showing diarch protoxylem, linearly arranged phloem and darkly stained endodermis. ( $\times 350$ ); c. *Marsilea*, showing diarch protoxylem. ( $\times 1000$ ); d. *Osmunda*, showing triarch protoxylem, phloem and darkly stained endodermis. ( $\times 175$ ); e. *Angiopteris*, showing tetrarch protoxylem and endodermis with conspicuous Casparian strip. ( $\times 375$ ); f. and g. *Botrychium*, showing medullated stele and endodermis with Casparian strip. (f.  $\times 175$ ; g.  $\times 350$ ).

Key to labelling: ALR, Apical cell of lateral root; (En) Immature endodermis; En, Endodermis; LI, Lateral root initial; LR, lateral root; (Mx), Immature metaxylem; Mx, Metaxylem; Ph, Phloem; Px, Protoxylem; (Xy), Immature xylem; Xy, Xylem.





maturation of the tissues. A detailed investigation was carried out on one species, *Osmunda japonica*, which has a diarch xylem. The sequence of differentiation and maturation of the root tissues in *Osmunda* is as follows: metaxylem initials appear first by the enlargement and vacuolation of the cells (Fig. 2a), the endodermal cells can be recognized with the thickening of the cell walls (Fig. 2b), thick-walled endodermal cells form a complete circle (Fig. 2c), phloem elements mature, protoxylem forms secondary walls (Figs. 2d, 2e), and finally the metaxylem elements mature.

The developing sequence in an aquatic fern has already been studied in *Ceratopteris* (Chiang, 1970; Chiang, 1971), and that of the other species dealt with in this investigation is shown in Table 3. The numerical numbers given after each species indicates the sequence of the maturation of the different root tissues. As shown in Table 3, the phloem elements mature first of all the tissues except in *O. japonica*. The protoxylem matures next after the phloem and metaxylem mature last. The endodermis matures by the development of a Casparian strip (such as in *Angiopteris*, *Ceratopteris* and *Botrychium*) or by the formation of darkly stained substances inside the cells (such as in *Adiantum*, *Pteris*, *Marsilea* and *Osmunda*). The formation of the endodermal cells takes place either before or after the maturation of protoxylem. In terrestrial species the endodermis always forms before the development of the secondary walls in the protoxylem, and the metaxylem elements mature after the sclerification of the cortical cells outside the stele. In *Angiopteris* and *Botrychium*, no sclereids have been found in the cortex. The sclerification of cortical cells occurs very early in developing roots of some ferns especially the terrestrial ones (Table 3). Sclerification of cortical cells takes place opposite where the first phloem cells

Table 3. The sequence of tissue development in roots

	phloem	protoxylem	endodermis	metaxylem	cortex sclerification
<i>Adiantum capillus-veneris</i>	1	4	3	5	2(centrifugal)
<i>Angiopteris lygodifolia</i> (small root with tetrarch)	1	3	2 (by enlargement of cells)	4	?
<i>Botrychium lunaria</i>	1	3	2	4	?
<i>Ceratopteris pteridoides</i>	1	2	3	4	5(centrifugal)
<i>C. thalictroides</i>	1	2	3	4	5(centrifugal)
<i>Marsilea crenata</i>	1	2	4	5	3(centrifugal)
<i>Osmunda japonica</i>	3	4	2	5	1(centripetal)
<i>Pteris multifida</i>	1	4	3	5	2(centrifugal)

Fig. 2. Transverse sections of the root of *Osmunda* showing the developmental sequence of the different tissues (all  $\times 350$ )

- immature metaxylem identified
- individual endodermal cell differentiated
- endodermis matured
- first phloem element matured
- first protoxylem matured
- the apical cell of a lateral root initiated opposite the protoxylem from one of the pericyclic cells

appear in roots of *Adiantum* and *Pteris*. The sclerified cortical cells in *Marsilea* and *Osmunda* are seen before the maturation of both endodermis and metaxylem but after the maturation of endodermis and metaxylem in *Ceratopteris*.

### Lateral Root Formation

The lateral roots are constantly initiated from a single endodermal cell of the parent roots in *Pteris*, *Adiantum*, *Ceratopteris thalictroides*, *C. pteridoides* and *Marsilea*. They arise very close to the apical cells of their parent roots where most of the root tissues have not yet matured. The lateral root initial in *C. thalictroides*, *C. pteridoides* and *Marsilea* originates in the region where either matured cells or identifiable tissues can be seen (Fig. 3b; Chiang, 1971, Fig. 6a). In other words, all the root tissues are still meristematic. In *Pteris* and *Adiantum* lateral roots initiate after the maturation of the phloem and before the maturation of other tissues in the stele of their parent root, such as protoxylem and metaxylem. The lateral roots arise constantly opposite to the protoxylem. The first division of lateral root initial in the endodermis undergoes either periclinal or anticlinal division. The first new cell wall formed in the lateral root initial is oblique between periclinal and anticlinal direction. During the initiation and development of a lateral root, it undergoes orderly cell divisions, and establishes all the root tissues including the apical meristem. It finally results in the formation of a lateral root which gradually penetrates the tissues outside the endodermis of the parent root. The developing pattern of root tissues in lateral roots of *Adiantum*, *Pteris* and *Marsilea* is quite similar to that of *Ceratopteris* (Chiang, 1971).

The lateral root initial in *Osmunda* originates in the pericycle. The numbers of protoxylem strands range from two to three and the lateral roots develop at the poles opposite the protoxylem strands (Figs. 2f, 3d). A single pericyclic cell opposite a protoxylem pole undergoes an oblique cell division to form a lateral root (Fig. 2f). No lateral root initial located very close to the apical cell of the parent root has been found. They originate at regions where the protoxylem and phloem are mature, but the secondary thickening of cell wall in the metaxylem has not yet matured.

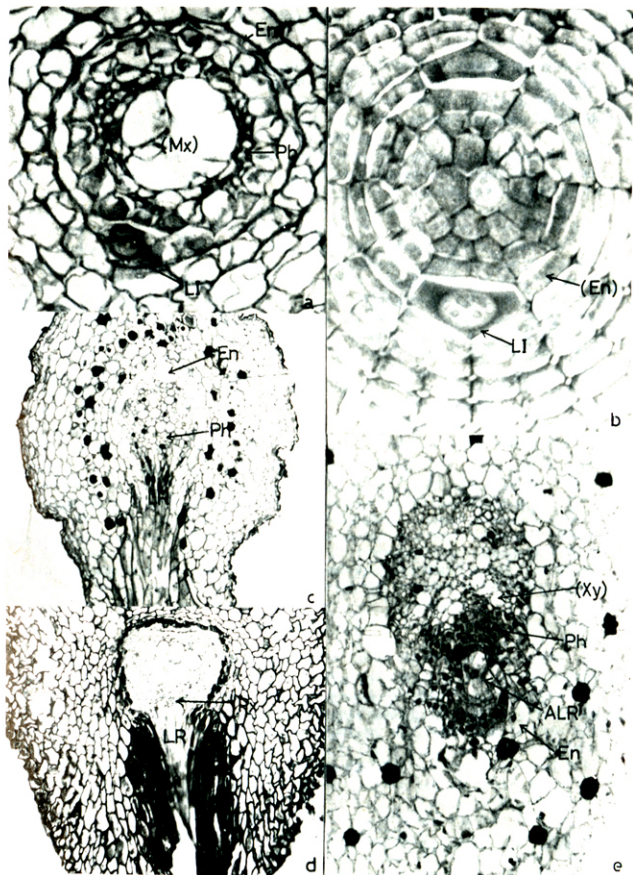
The earliest stage of the lateral initials in *Angiopteris* was not found in the present investigation. We were not able to identify the first division of lateral root initials from the sections obtained. Nevertheless, we have found a section which shows a small group of meristematic cells of a lateral root primordium, they were located inside the endodermis of its parent root, in which the endodermal cells of the parent root still maintain their complete arrangement, and the phloem elements of the parent root can still be identified by their cellular shape (Fig. 3e). Apparently the lateral root of *Angiopteris* forms inside the endodermis. It is pericyclic in origin.

The orientation of a lateral root in its parent root differs from that in the spe-

Fig. 3. Transverse sections of roots of different species of ferns showing the origin and orientation of the lateral roots

- Pteris*, the lateral root initial originates from the endodermal cell opposite the protoxylem ( $\times 410$ )
- Marsilea*, the lateral root initiates from the immature endodermal cell ( $\times 900$ )
- Angiopteris* with tetrarch protoxylem, the lateral root originates between the xylem and the phloem ( $\times 88$ )
- Osmunda*, the lateral root originates opposite the protoxylem pole ( $\times 88$ )
- Angiopteris* with heptarch protoxylem, the lateral root originates from the pericyclic cell and between the xylem and the phloem ( $\times 175$ )





cies mentioned above. The lateral roots of *Angiopteris* initiate from between the protoxylem and phloem groups (Figs. 3c, 3e, 4c, 4d).

The lateral roots of *Botrychium* are seen in roots which have tetrarch xylem. No early stages of lateral roots were found in the sections examined. The only section we have in our present investigation is of a stage which shows the orientation of the lateral root in relation to the xylem and phloem, but not the original initial in the tissue of the parent root. The lateral root of *Botrychium* forms between the xylem and the phloem.

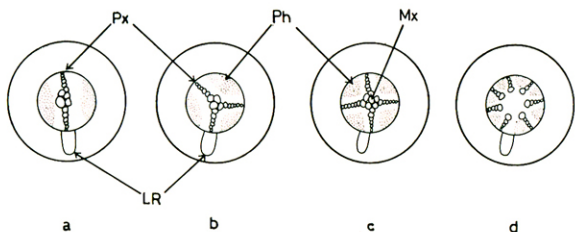


Fig. 4. Diagrams showing the arrangement of primary vascular tissues and orientation of lateral root and illustrating the relationship between them

- The lateral root originates opposite the protoxylem pole in diarch roots, e.g., *Adiantum*, *Ceratopteris*, *Marsilea*, *Osmunda* and *Pteris*.
- The lateral root originates opposite the protoxylem pole in triarch root, e. g., *Osmunda*.
- and d. The lateral root originates between the xylem and the phloem in tetrarch and heptarch root, e. g., *Botrychium* and *Angiopteris*.

## DISCUSSION

The roots in most of the vascular cryptogams are known to be protostelic. In this study the root diameter in all the materials is almost identical in the same species except for *Angiopteris*. *Angiopteris* bears roots ranging from very thin to thick ones. No medullated roots have been seen in all the roots observed except in the roots of *Botrychium* and the roots of most *Angiopteris*. Both protostelic and medullated roots occur in a single species of *Angiopteris* whereas all are medullated in *Botrychium*. Bierhorst (1971) stated that parenchyma is occasionally present in the center, but he did not mention the relationship between the diameter and the medullation of the roots.

Another category which concerns the diameter of the root is the numbers of the protoxylem points. This relationship is clear in the roots of *Angiopteris*, *Botrychium* and *Osmunda*. The larger the root diameter the more protoxylem points occur. So that the increase in the root diameter results in the increase of protoxylem poles as well as the medullation in the center. The marattialean roots follow both the increase of protoxylem points and medullation. The lower filicalean ones change in their number of protoxylem poles, since the possession of a pith in the

roots of this group have not been found (Bower, 1932; Foster and Gifford, 1959; Bierhorst, 1971).

The occurrence of sclerenchyma in the cortex is genetical rather than physiological. The sclerification of ground tissue is very common in the filicalean members even in the group where the plant body is filmy (DeVol, 1970) and aquatic (Table 3). In the present study it is found that the appearance of ground sclerenchyma and endodermal cells in the terrestrial members is always earlier than that in aquatic ones (Table 2). The maturation of metaxylem is commonly very late in all species. Many workers consider that the endodermis plays an important role in absorption as well as the conduction of the water. In our data, it is known that the endodermis in aquatic *Marsilea* and terrestrial *Osmunda* appear later than the sclerification of ground tissue. It is shown that the environment factor or growing habit of plants plays an important role in the differentiation and maturation of vascular elements, the endodermis and the sclerification of the cortical cells. The formation of endodermal cells and sclereids in the cortex is more influenced by its growing habit.

Ogura (1938) has mentioned that the lateral roots originate mainly from the endodermis but Bierhorst (1971) stated they are mainly pericyclic in origin. Both endodermal and pericyclic origins are found in the materials dealt with in the present study, but they are never formed from both in a single lateral root as in some angiosperms (Chiang, 1973; Cutter, 1971; Esau, 1961; Seago, 1973). It is certain that in most of the roots listed in this report the lateral root originates from a single endodermal or a single pericyclic cell. The present study shows that the lateral root initiates at the endodermis of the parent root which bears a one layered pericycle (Table 2). On the contrary, it forms from the pericyclic cell of parent roots which possess a pericycle with more than two cell layers. The orientation of the lateral roots in the parent root undergoes certain regularity. As in *Dennstaedtia punctilobula* (Conard, 1908) and diarch roots of some other ferns (Campbell, 1918), the lateral roots arise regularly from the places corresponding to the ends of xylem plate in the diarch stele in the present investigation (Fig. 4a). Guttenberg (1940) and Knobloch (1954) summarized the spacing of lateral roots with reference to the xylem and phloem poles of the parent root. The spacing of the lateral root in ferns which have diarch xylem differs from that in the angiosperms which possess diarch xylem. If the parent root is triarch, it is similar with that in angiosperms, but differs in the root with tetrarch xylem. In the roots which have four protoxylem points, the lateral roots of ferns arise from between the xylem and the phloem, but arise from the xylem pole in angiosperms. If the parent root has more than four xylem poles, the laterals also originate between the xylem and the phloem in ferns whereas in angiosperms these initiate from the phloem pole.

#### LITERATURE CITED

- 蔡淑華, 1973. 植物解剖學. 世界書局. 臺北. 臺灣.
- BIERHORST, D. W., 1971. Morphology of Vascular Plants. Macmillan Co., New York.
- BOWER, F. O., 1932. The Ferns. Vol. III. Univ. Press. Cambridge.
- CAMPBELL, D. H., 1895. The Structure and Development of the Mosses and Ferns. Macmillan Co., New York.
- CHIEN, Y. S., & Y. L. CHIANG, 1972. A study on the root of *Ophioglossum petiolatum*. *Taiwania*, **17**: 92-106.
- CHIANG, S. H. T., 1971. Sequence of tissue differentiation in the root of *Ceratopteris thalictroides*. *Taiwania*, **16**: 31-47.

- \_\_\_\_\_, & E. M. Jr. Gifford, 1971. Development of the root of *Ceratopteris thalictroides* with special reference to apical segmentation. *J. Indian Bot. Soc.* **50A**: 96-106.
- CHIANG, Y. L., 1970. Macro-and microscopic structure of the root of *Ceratopteris pteridoides*. *Taiwania*, **15**: 31-50
- CONARD, H. S., 1908. The structure and life-history of the hay-scented fern. Carnegie Inst. of Washington Pub. No. 94. Washington D. C.
- CUTTER, E. G., 1971. Plant Anatomy: Experiment and Interpretation. Part 2, Organs. Edward Arnold Ltd., London.
- DEVOL, C. E., 1970. The Pteridophyta of Taiwan-6 Hymenophyllaceae: Hymenophyllum. *Taiwania*, **15**: 271-300.
- ESAU, K., 1943. Origin and development of primary vascular tissues in seed plants. *Bot. Rev.*, **9**: 125-206.
- \_\_\_\_\_, 1961. Anatomy of Seed Plants. John Wiley & Sons Inc., New York & London.
- \_\_\_\_\_, 1965a. Plant Anatomy 2nd ed. John Wiley & Sons Inc., New York.
- \_\_\_\_\_, 1965b. Vascular Differentiation in Plants. Holt, Rinehart & Winston, Inc., New York.
- FOSTER, A. S., & E. M. Jr. GIFFORD, 1959. Comparative Morphology of Vascular Plants. Freeman & Company. San Francisco & London.
- GUTTENBERG, H. VON, 1940. Der primäre Bau der Angiospermenwurzel. In: K. Linsbauer. Handbuch der Pflanzenanatomie. Band 8. Lief. 39.
- JENSEN, W. A., 1962. Botanical Histochemistry. Freeman & Company. San Francisco & London.
- KNOBLOCH, I. W., 1954. Developmental anatomy of chicory-the root. *Phytomorphology*, **4**: 47-54.
- OGURA, Y., 1938. Anatomie der Vegetationsorgane der Pteridophyten. In Linsbauer. Handbuch der Pflanzenanatomie. Band 7. Gebrüder Borntraeger.
- PETERSON, R. L., 1967. Differentiation and maturation of primary tissues in white mustard root tips. *Can. J. Bot.*, **45**: 319-331.
- POPHAM, R. A., 1955. Levels of tissue differentiation in primary roots of *Pisum sativa*. *Am. J. Bot.*, **42**: 529-540.
- RIOPEL, J. L., & T. A. STEEVES, 1964. Studies on the root of *Musa acuminata* cv. Gros Michel. I. The anatomy and development of main roots. *Ann. Bot.*, N. S. **28**: 475-490.
- SEAGO, J. L., 1973. Developmental anatomy in roots of *Ipomoea purpurea*. II. Initiation and development of secondary roots. *Am. J. Bot.*, **60**: 607-618.
- SHARMAN, B. C., 1943. Tannic acid and iron with orange G in studies of the shoot apex. *Stain Tech.*, **18**: 105-111.