

A DEVELOPMENTAL STUDY OF ROOTS OF PRESUMED SEED FERN ORIGIN FROM THE UPPER PENNSYLVANIAN OF ILLINOIS

ROBERT L. DENNIS

Department of Botany, University of Iowa, Iowa City

ABSTRACT.—A coal ball petrification of Upper Pennsylvanian age has been found containing extensive remains of roots of a new type including two root apical meristems and a bud-like meristem. Ontogenetic sequences of root development are described and illustrated. The root meristems have large, multicellular, initial zones producing root cap and meristematic tissues which subsequently give rise to differentiating cells of the protoderm, ground meristem, and procambium. Serial sections of the roots illustrate a development of the vascular cambium much like that found in the roots of extant, dicotyledonous plants. A comparison of the present specimens with similar root types from the Pennsylvanian is made. In general features of organization the material described in this account appears most like roots of medullosan seed ferns.

The present study describes some exceptionally well preserved roots of probable seed fern origin. Included in the study is a description of root apices and early ontogeny of the primary and secondary bodies. No previous reports of comparable material have described the ontogeny of the root or any apical meristematic regions. The few available descriptions of roots found in coal balls and having only primary tissues, such as that of Hoskins (1931), do not describe ontogenetic development. The present description is based on a coal ball petrification from the Berryville locality in which

there occurred three axes that had the apical meristems present. Two of these axes are typical roots which lie adjacent to one another and are attached to a portion of a branching root system (Fig. 14). One root apex having a triarch stele has been sectioned transversely (Figs. 7-13). The other root having a pentarch stele was of sufficient length so that the apical initial zone could be studied from longitudinal sections and the basal portion studied from transverse sections (Figs. 1-6). The third axis is a problematical bud-like organ with vascularized "scale-leaves" (Figs. 15-23). The bud-like structure is attached to an axis which has typical root anatomy and lies adjacent to the better preserved system. There is, however, no cellular connection to the better preserved roots. The bud-bearing axis can be identified with the root system for reasons discussed later in the text.

MATERIAL AND TECHNIQUE

The location from which the specimen was collected is near the town of Berryville, Illinois (Section 7, T 2 N, R 13 W, Sumner Quadrangle, Lawrence County, Illinois). The most recent stratigraphic position and age published is that of Taylor (1965) which identifies the coal balls as coming from the Calhoun Coal, Mattoon Formation, McLeansboro Group. The age is Upper Pennsylvanian.

Serial sections for the study were made by employing the cellulose peel technique as described by Joy, Willis, and Lacey (1956). The coal ball bears the designation U. Ia. C. B. 315.

DESCRIPTION

Organization of the Root Apex. In longitudinal section the growing tip of the root has a cellular arrangement that is typical of a multicellular apical meristem as opposed to that commonly found in meristems having a single apical cell (Fig. 1). At the extreme apex of the root the pattern of cell arrangement lacks specific organization into zones or histogens. The promeristem of the root apex consists of two poorly defined zones of small, isodiametric cells of relatively uniform appearance (Fig. 1, indicated by PI). Two areas of promeristem at the root tip suggest that the root was in the early stages of undergoing a dichotomy. In the upper portion of Figure 1, a peripheral ground meristem zone is present (indicated by GM) which surrounds a central area of procambium (indicated by PC). As one proceeds toward the tip of the root, axial rows of cells converge on each of the two initial zones which are separated by a zone of larger cells, presumably representing ground meristem. These axial rows of meristematic cells are not traceable to specific initials because the cells of the initial zone are non-aligned. The alignment of cells occurring back of the initial zone indicates the later occurrence of periclinal divisions in cells produced from the promeristem initials. In general, such a row of cells extends only a short distance before irregularity disrupts the sequence. These aligned meristematic cells give rise to the differentiated cells of the protoderm, the ground meristem, and the procambium. The root cap results from divisions of the promeristem initials.

The apical meristem studied in transverse section shows promeristem cells (Fig. 7, indicated by PI) that are apparently differentiating into a root cap through increased size and elongation. The root cap is bluntly cone-shaped (Figs. 7 and 8, indicated by RC).

Cells of the protoderm occur on the flanks of the initial area in the specimen studied in transverse sections. These cells are contiguous with those of the root cap and form a recognizable small-celled protoderm one cell

layer in thickness (Fig. 8, indicated by PD). Stages in epidermal differentiation are precluded by the poor preservation of the apical meristem sectioned longitudinally. The outer portion of this specimen consists of dark-colored, poorly preserved remains of the root cap and protoderm (Fig. 1).

Cells of the ground meristem appear as typical parenchyma cells except that they are aligned vertically in short rows, and apparently represent daughter cells produced by successive anticlinal divisions. These cells are characterized by their large diameters, isodiametric to slightly vertically elongate shape, and compact disposition within the tissue (Fig. 1).

In transverse sections of the root apex, the first evidence of vascular tissue differentiation consists of the appearance of a central procambial core made up of extremely narrow cells. It is of interest to note that the first indication of vascular tissue differentiation occurs in the center of the procambium in a region that is ultimately destined to form the central portion of the metaxylem of the stele. The procambial cells retain narrow diameters, whereas cells in the developing cortex increase markedly in diameter (Fig. 8).

In the region of initial differentiation of vascular tissue procambial cells enter a phase of elongation during which they do not increase greatly in diameter. This elongation phase occurs simultaneously with the initiation of secondary wall thickenings which consist of narrow, simple, scalariform bars.

Phloem can be distinguished in these roots as relatively large cells with dark walls. The first indication of the presence of phloem in the region behind the promeristem occurs at the periphery of the provascular tissue (Fig. 2). Two of the five phloem groups in Figure 2 are more prominent than the other three, however, this may be the result of crushing of the tissue. By comparing the two largest phloem areas in Figures 3 and 4, one can determine that phloem development is centripetal.

The initial appearance of protoxylem consists of several (five in the instance illustrated) clusters of small-diametered cells located midway between the phloem positions on the periphery of the provascular cylinder. These areas are identified (Figs. 5 and 6, indicated by PX) by the relatively narrow diameters of the cells, topographic posi-

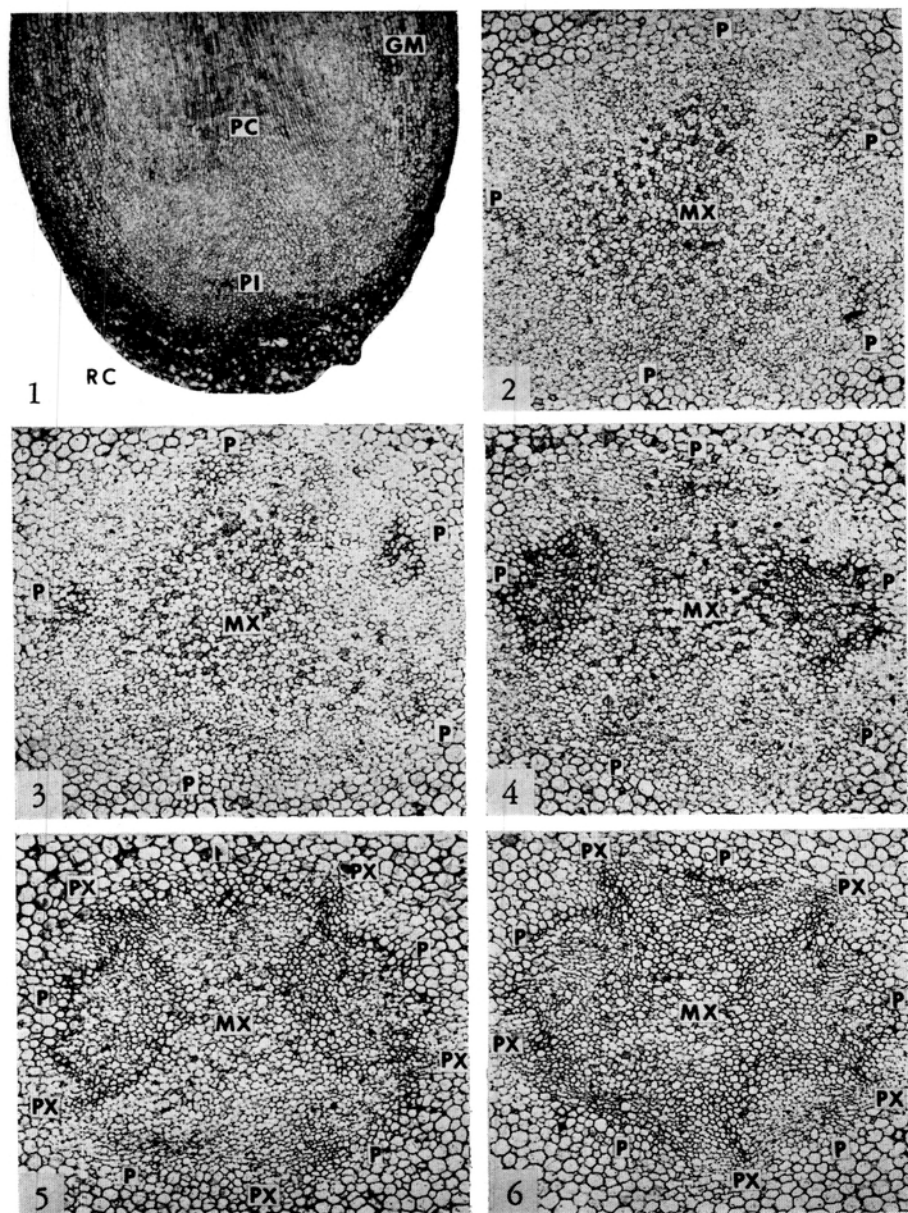


PLATE I

FIGURE 1. Median longitudinal section of apex of a root having a pentarch stele. Promeristem initials are indicated by PI, procambium by PC, ground meristem by GM, and root cap by RC. U. Ia. c. b. 315 B₂(Bottom) #4, section 14. X 18.

FIGURES 2-6. Representative transverse sections of a pentarch root illustrating successive stages in the maturation of the primary stellar tissues. Figure 2. A level just behind the growing tip where areas of phloem first become apparent. U. Ia. c. b. 315 B₂(Bottom) #225. Figure 3. A level at which the characteristic dark-walled cells of the phloem are more obvious. U. Ia. c. b. 315 B₂(Bottom) #210. Figure 4. A level illustrating the progressive centripetal maturation of phloem in two of the better preserved phloem regions. U. Ia. c. b. 315 B₂(Bottom) #170. Figure 5. A level at which the regions of protoxylem first become obviously apparent. U. Ia. c. b. 315 B₂(Bottom) #130. Figure 6. A level showing the mature primary condition of the stele. U. Ia. c. b. 315 B₂(Bottom) #51. In these figures primary phloem is indicated by P, metaxylem by MX, protoxylem by PX. All figures X 39.

tion, and relatively thick walls which have apparently resulted from more rapid secondary wall deposition. Protoxylem cells do not undergo any marked increase in diameter beyond this level in the root, whereas metaxylem tracheids continue to increase in diameter. It is this ontogenetic sequence that produces the characteristic configuration of the primary stele, which may be pentarch as seen in Figure 6, or triarch as seen in Figure 9.

The Mature Primary Condition. The disposition of the primary tissues resulting from the organization of the apical meristem is typical of that found in several types of seed fern roots. The central part of the stele consists of metaxylem tracheids with occasional strands of parenchyma. No pith is present. Metaxylem tracheids measure 33μ in diameter and are characterized by simple scalariform thickenings on the walls (Fig. 26). In a few instances, these pits appear to be bordered as in Figure 25.

An examination of all the roots shows the primary xylem to be triarch (Fig. 9), tetrarch (Figs. 14 and 24), or pentarch (Fig. 6). Protoxylem and metaxylem cells intergrade with regard to diameter so that the transition between these tissues is gradual. Protoxylem tracheids may be identified by their position, smaller diameter, and presence of widely spaced secondary thickenings on the walls.

Two types of cells have been distinguished in the primary phloem. Typical protophloem elements possess thin walls, tapering ends, and diameters of about 43μ (Fig. 26, indicated by PP). A centripetally developed zone about three to twelve cells wide apparently represents sieve cells of the metaphloem. These cells possess extremely dark walls and are axially elongate. Cells of this type measure about 60μ in diameter and are indicated by MP in Figure 26.

At levels in the root which apparently represent the mature primary condition, no evidence of a pericycle was observed. The cortex consists of a homogeneous parenchyma composed of isodiametric cells which apparently lack intercellular spaces. The epidermis is typically not preserved, however, at some levels remnants of this tissue were identified.

Secondary Development. Initial stages of secondary tissue development are present in the roots. A complete sequence is presented for a triarch root in Figures 10-13. This includes stages from the first appearance of secondary tracheids to a condition in which radial rows with numerous tracheids exists. The cambium arises in the zone between the metaxylem and the phloem in areas about midway between the protoxylem points. The initial stage of cambial production is shown in Figure 10 at the indication C. The production of secondary tissue occurs in this specimen a short distance behind the level of differentiation of the primary vascular tissues. The most prominent portion of the secondary vascular tissue consists of radially oriented rows of secondary tracheids which develop between the protoxylem points (Figs. 10-13). Initially, the cambium is difficult to distinguish, however, as secondary development continues, it becomes more evident (compare Figs. 10 and 11 with Figs. 12 and 13). As already noted, the cambium initially develops midway between the protoxylem points and subsequently develops laterally toward the protoxylem areas. No cambium develops opposite the protoxylem areas, and consequently, a continuous ring of cambium is never produced in the roots. Parenchyma cells occupy the areas opposite the protoxylem points and effectively divide the secondary wood into segments that correspond in number to the protoxylem points. The vascular

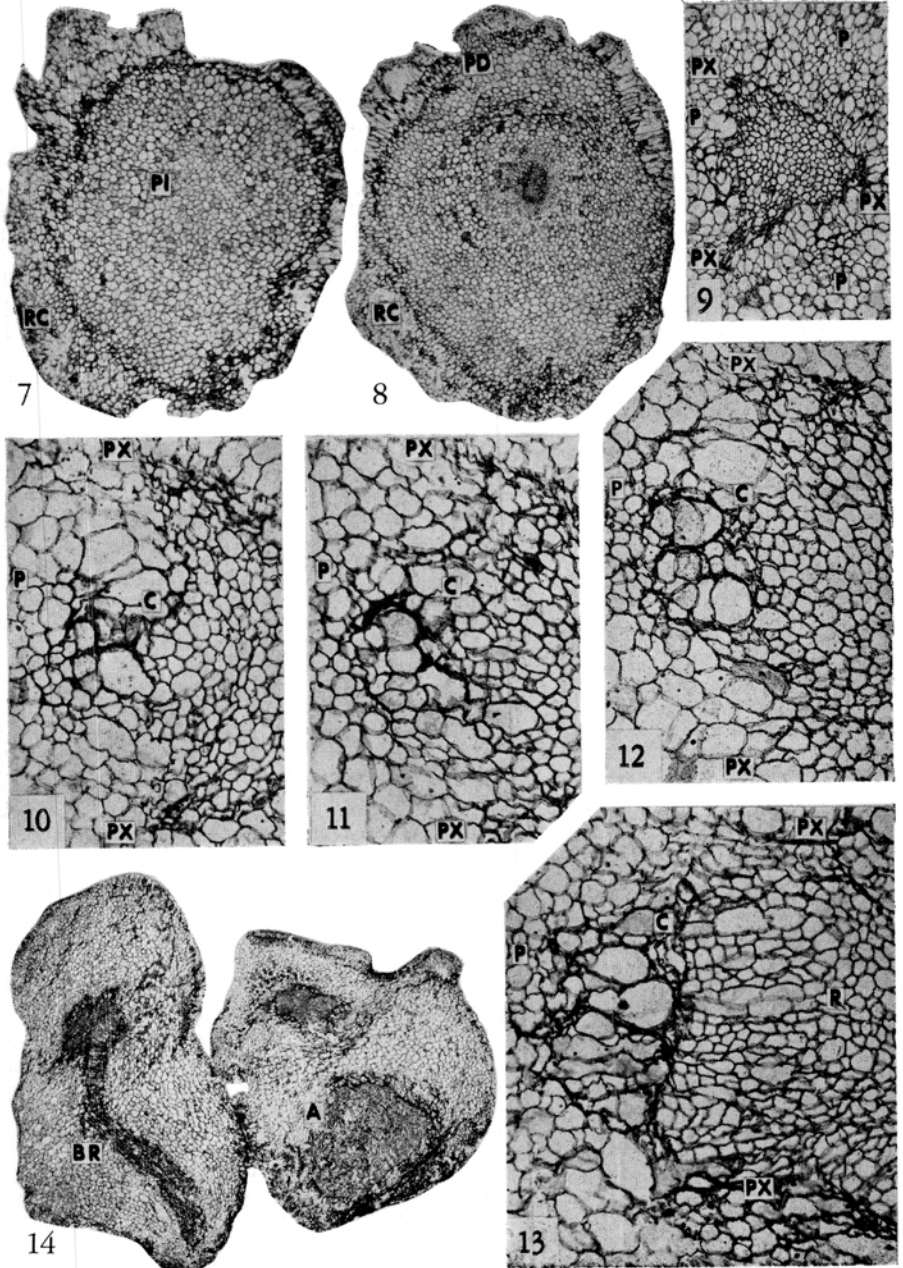


PLATE II

FIGURE 7. Transverse section of the root cap and promeristem initial zone of a root having a triarch stele. Promeristem initials indicated by PI., root cap by RC. U. Ia. c. b. 315 B₂(Bottom) #71. X 18.

FIGURE 8. Transverse section of the root cap, protoderm, and procambial region of the same root as that shown in Figure 7. Root cap indicated by RC, protoderm by PD. U. Ia. c. b. 315 B₂(Bottom) #50. X 12.

FIGURE 9. Mature primary condition of the triarch stele of the same root as that shown in Figures 7 and 8. Protoxylem areas indicated by PX, primary phloem areas by P. U. Ia. c. b. 315 B₂(Bottom) #39. X 49.

FIGURES 10-13. Transverse sections at progressively lower levels of the portion of the stele toward the left in Figure 9. The figures illustrate successive stages in cambial development and production of secondary vascular tissues. Figure 10. A level showing the region in which the vascular cambium is initiated. U. Ia. c. b. 315 B₂(Bottom) #35. Figure 11. A level illustrating an early stage in secondary xylem production. U. Ia. c. b. 315 B₂(Bottom) #26. Figure 12. A level illustrating an increased amount of secondary xylem and the crushed cells of the vascular cambium. U. Ia. c. b. 315 B₂(Bottom) #21. Figure 13. A level illustrating radial files of tracheids and vascular rays of the secondary xylem zone. U. Ia. c. b. 315 C(Top) #5. In the figures protoxylem areas are indicated by PX, phloem by P, vascular cambial zones by C, wood or vascular ray by R. All figures X 83.

FIGURE 14. Transverse section of a portion of the root system illustrating several tetrarch roots. A branch root is indicated by BR. A branch root with anomalous stelar tissues is indicated by A. U. Ia. c. b. 315 C(Top) #10. X 6.

cambium produced comparatively little secondary phloem; in some instances radially aligned rows of three to six large sieve cells have been found (Fig. 24 at indication P). Pitting of the secondary tracheids does not differ from that of the metaxylem elements and is of the uniseriate scalariform type. Rays are relatively infrequent and are usually uniseriate or biseriate (Fig. 13 indicated by R.) Steles of a few representative roots with abundant secondary tissues are shown in Figures 14 and 24.

Branching of the roots is very common. Branch roots arise opposite a protoxylem point of the parent root (Fig. 14 indicated by BR). Apparently, the branch roots did not arise endogenously as occurs in a typical seed plant because no evidence of a separate cortex to the branch roots could be found. In one instance anomalous structure has been found in one of the branch roots (Fig. 14 at the indication A) which contains tracheids that twist around one another at all angles. The aberrant tracheidal mass is in turn surrounded by phloem and cortex. Periderm has not been observed.

A *Bud-bearing Axis*. One axis has been discovered which terminates in a bud-like apex. Behind this apical region, where mature tissues are present, the axis enlarges and is typically root-like in morphology. Figures 15-21 illustrate progressively lower levels of the bud-like portion of the axis. The transition from the bud-like area to that at which typical root structure is present occurs in a poorly preserved portion of the specimen which has been sectioned very obliquely so that structural details of

the transitional phase cannot be determined. Figure 22 shows the base of the bud-like area in attachment to the root portion of the specimen, while Figure 23 illustrates the lowest level of the specimen at which typical root structure is present.

The most striking feature of the apical portion of the bud is the presence of an armor of small, scale-like, lateral appendages which cover the growing tip of the axis (Figs. 15-18). These lateral appendages exhibit several features which are characteristic of leaves, but their exact morphological nature is not certain. For the sake of convenience, these lateral appendages will be referred to as scale-leaves in the following portions of the text. The scale-leaf primordia are apparently produced from superficial tissues of the apical meristem as are typical leaf primordia. At a level such as that shown in Figure 17, the scale-leaves appear to be arranged in a spiral pattern. The cells forming the apical meristem possess thin walls, a homogeneous appearance, and are much smaller than those of the surrounding scale-leaves. Since the meristem was studied only from cross sections, it was not possible to determine whether there was a single apical initial or a group of initials in the promeristem region.

Although, superficially, the scale-leaves appear to be borne in a fairly uniform spiral arrangement, no consistent phyllotaxy can be determined. In all, the bud-like portion bears twenty-four scale-leaves which range up to 3 mm in width. Epidermal cells of the scale-leaves are poorly preserved. Rela-

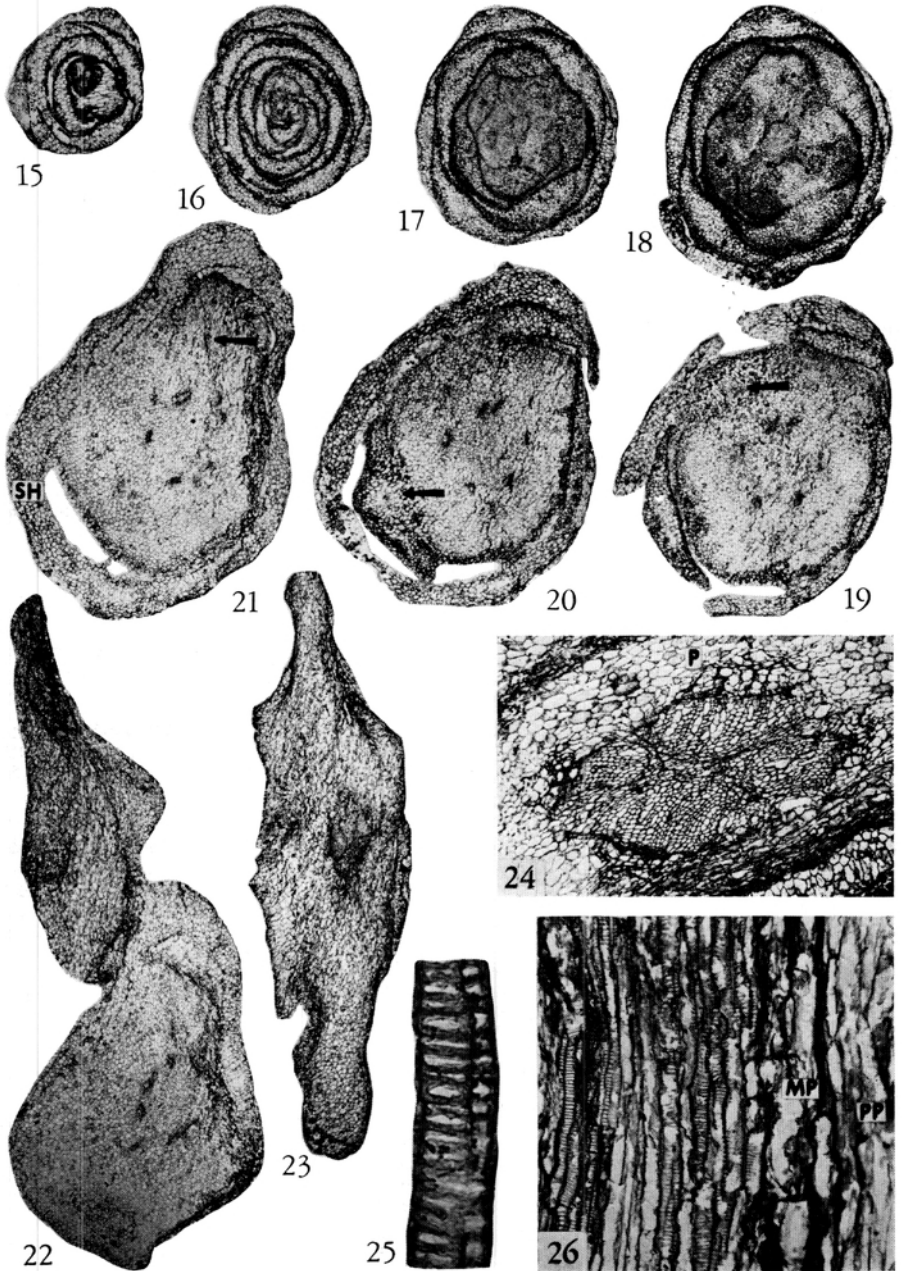


PLATE III

FIGURES 15-21. Representative series of transverse sections at progressively lower levels through a bud-like portion of the axis. Figure 15. Most distal level

illustrating the overlapping scale-leaves which overtop the axis. U. Ia. c. b. 315 B₂(Bottom) #32. Figure 16. A level at the very summit of the growing point where a few cells of promeristem are surrounded by a broad zone of scale-leaves. U. Ia. c. b. 315 B₂(Bottom) #18. Figure 17. A level through the promeristem region showing scale-leaf primordia and the bases of more mature scale-leaves. U. Ia. c. b. 315 B₂(Bottom) #1. Figure 18. A level showing a central region of presumed procambial tissue, vascular traces in the bases of several scale-leaves, and the distal-most part of the sheath. U. Ia. c. b. 315 B₂(Bottom) #4a. Figure 19. A level showing the lower portions of a series of vascular strands to scale-leaves arranged in a ring. Arrow indicates a vascular strand in the base of a scale-leaf. Several fragmentary areas of sheath partially surround the axis and scale-leaves. U. Ia. c. b. 315 C(Top) #1. Figure 20. A level where the sheath forms a continuous zone around the axis, and the bases of the two lowermost scale-leaves are present. Arrow indicates a vascular strand in the base of a scale-leaf. U. Ia. c. b. 315 C(Top) #16. Figure 21. A level showing the tissues of the sheath continuous with those of the axis and the base of the lowest scale-leaf. The arrow indicates a vascular trace entering the base of the lowest scale-leaf. U. Ia. c. b. 315 C(Top) #39. All figures X 9.

FIGURE 22. Transverse section through the base of the bud-like portion shown in Figures 15 through 22 where it is in attachment to the portion of the specimen with root anatomy. U. Ia. c. b. 315 C(Top) #56. X 8.

FIGURE 23. Oblique transverse section through the portion of the specimen shown in Figures 15-22 where typical root anatomy is present. U. Ia. c. b. 315 C(Top) #88. X 7.

FIGURE 24. Transverse section of a representative tetrarch stele with secondary vascular tissues. An area of primary and secondary phloem is indicated by P. U. Ia. c. b. 315 B₁(Bottom) #8. X 14.

FIGURE 25. Longitudinal view of a metaxylem tracheid showing uniseriate, scalariform, wall thickenings. The junction of two walls is shown. U. Ia. c. b. 315 C(Top) #45. X 330.

FIGURE 26. Longitudinal section of a portion of a stele showing the primary vascular tissues. The tissues are, from right to left; protophloem indicated by PP, metaphloem indicated by MP, and xylem. U. Ia. c. b. 315 B₁(Bottom) #18. X 75

tively large diameter parenchyma cells form the ground tissue of the scale-leaves. In the central portion of the lamina of the scale-leaves this zone is about eight cells wide and tapers to one cell row at each lateral edge. A single vascular trace enters the base of each of the more mature scale-leaves (Figs. 19-21). Leaf traces are present only in the basal regions and do not extend into the free laminate portion. The scale-leaves are broadly attached to the parent axis.

The first indication of the production of a scale-leaf is the departure of a trace from the stele of the parent axis. This trace angles outward slowly traversing the cortical zone until it occupies a position about twelve cell layers beneath the epidermis. An outward bulging of the epidermal tissue of the main axis delimits the base of the scale-leaf. Complete separation takes place along this line by the progressive devel-

opment of two equal, lateral invaginations. Unlike the remaining scale-leaves of the specimen, the lowest scale-leaf is not symmetrical at its base and has a free lamina extending along only one of its sides. Distally, each scale-leaf decreases in thickness, becomes laminate or flattened, and gradually tapers. The terminal portions of the scale-leaves tightly enclose and overarch the growing tip of the parent axis (Figs. 15 and 16).

The major features of the vascular system of the bud-like portion of the specimen are as follows. Ten vascular strands to scale-leaves have been traced back toward their points of origin from the vascular system of the main axis. The vascular trace of each scale-leaf arches inward across the cortex and fuses with a vascular trace from a lower scale-leaf. At lower levels these fused vascular strands come to assume positions somewhat equidistant from each

other forming a ring around the center of the main axis. The fusion of vascular strands continues until the trace from the lowest scale-leaf joins the system. This latter event occurs at a level where the specimen is sectioned very obliquely and preservation is poor. At this level, however, there appears to be four main vascular strands. At this same level, the bud-like portion of the specimen is attached to a root-like region whose long axis lies nearly at right angles to the bud-like portion (Fig. 22). The preservation of the root portion of the specimen improves sufficiently to determine that it has a tetrarch stele exhibiting the same structure as the roots previously described (Fig. 23). Due to the preservation of the specimen, it is impossible to determine whether the bud-like portion represents a lateral of the root-like part or is merely a continuation of the axis.

A curious feature of the specimen is the presence of a sheath of large-celled parenchyma which covers the lower portion of the bud. At its lowest level the sheath is continuous and encloses the bases of the lowest scale-leaves (Fig. 21, indicated by SH). Toward the apex the sheath becomes broken into fragments and is sloughed away completely so that the scale-leaves make up the outer part of the upper region of the bud.

DISCUSSION

Several accounts on the structure of roots having a similar stelar anatomy to those described here have been published. These have been, for the most part, roots attached to, or in association with, stems of the seed fern genus *Medullosa*. Although similar in structure, the roots described in this paper differ in several respects from those previously described.

Although the roots of *M. anglica* as described by Scott (1899) show numerous points of similarity to those described here, several important structural details representing distinct differences deserve consideration. Roots of *M. anglica* possess

protoxylem elements with spiral secondary wall thickenings, metaxylem tracheids with numerous rows of crowded bordered pits, secondary tracheids with rows of crowded bordered pits present only on the radial walls, and primary xylem in a triarch configuration. Periderm development apparently occurred early in ontogeny in the roots of *M. anglica*. These features of the roots of *M. anglica* were substantiated by Arber (1903) who also described the phloem.

Roots thought to be borne by species of *Medullosa*, described by Hoskins (1931), differed from those of *M. anglica* in that some of the older roots lacked periderm. In addition, note, the primary xylem was found to be triarch, tetarch, or pentarch.

Steidtmann (1944) described roots in attachment to stems of *M. noei* which showed a similar range in the number of protoxylem points. In addition, the roots of *M. noei* were described as having spiral thickenings on the walls of the protoxylem tracheids and bordered pitting on the walls of the metaxylem tracheids. The pits of the secondary tracheids in both stem and roots is multi-seriately arranged and bordered. As in *M. anglica*, roots of *M. noei* were found to have periderm at relatively early stages in root development.

In contrast to *M. Anglica* and *M. noei*, roots described in this study have simple scalariform thickening on both metaxylem and secondary tracheids. Protoxylem tracheids also have simple scalariform thickenings. Periderm has not been observed in any of the roots, however, these roots, in respect to the amount of secondary vascular tissues pres-

ent, correspond to developmental stages described for *M. anglica* and *M. noei*. Roots of *M. noei* and those described here have a similar range in the number of protoxylem areas. This feature is clearly one that cannot be relied upon in distinguishing taxa since the specific number of protoxylem points present in a given order of root is known to vary greatly in a single root system of numerous kinds of living vascular plants.

Roots of such monostelic genera of seed ferns as *Lyginopteris* and *Heterangium* differ markedly from those described in this paper and cannot be easily confused with them.

The preponderance of evidence suggests that the roots described here are most similar to those of *Medullosa*. They are clearly distinct, however, from all previously described roots assigned to that genus. Because of the great amount of variability demonstrated and small number of specimens available for examination, no new name is being assigned.

A significant feature of the material is the exceptionally complete sequence of early developmental stages present. Such stages of root development are extremely rare in the fossil record although they are known to occur (Daugherty 1963).

One of the most curious features of the material is the structure that has been referred to as a bud. This structure clearly represents either a lateral appendage or a continuation of an axis that was a root. Whether this bud represents an early stage in shoot development or merely some atypical portion of the root system cannot be determined. The presence of the lateral appendages referred

to as scale-leaves seems to suggest that the bud represents an early stage in shoot development. Ontogenetically, these scale-leaves developed from superficial tissues at the apical meristem and are vascularized. These features are characteristic of true leaves. In contrast to these leaf-like features, no consistent phyllotactic pattern could be determined. Moreover, vascularization does not extend into the free portions of the appendages. These latter features are more typical of epidermal appendages. The occurrence of leaves on a root is not known to occur in any extant or fossil vascular plant of which the author is aware.

ACKNOWLEDGMENT

The author is indebted to Dr. Donald A. Eggert, Department of Botany, University of Iowa, for his able guidance and assistance during the preparation of the manuscript. This research was supported in part by National Science Foundation grants GB-1540 and GB-4126.

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Manuscript received August 3, 1967.