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VASCULAR DIFFERENTIATION IN THE PEAR ROOT[1]

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INTRODUCTION

THE PRESENT PAPER deals with the development of the root of *Pyrus communis* L., with special attention to the vascular tissues. Though considerable information is available on root structure of herbaceous plants (Hayward, 1938; Esau, 1940),[3] only one rather complete account of tissue differentiation in a root of a woody species appears to exist in modern botanical literature (Hayward and Long, 1942). The need for such accounts in the teaching of plant anatomy, especially in agricultural institutions, is obvious.

The present problem was selected also because of the writer's interest in the differentiation of the phloem tissue in different organs of seed plants. Since many studies have been made on the phloem of roots of herbaceous plants (review by Esau, 1943), it seemed timely to add some data on the ontogeny of this tissue in a woody root.

MATERIALS AND METHODS

The root material used in preparing the permanent slides and the photomicrographs was obtained from trees grown in a culture solution by the Plant Nutrition division at Berkeley. The material was killed in a formalin-acetic-alcohol fixing fluid and imbedded in paraffin after ordinary dehydration and clearing in mixtures of ethyl alcohol and xylene.

The roots grown in the culture solution were compared with soil-grown roots from young trees 5 to 6 inches high grown from seeds of the Winter Nelis variety. The latter roots were examined in free-hand sections. No fundamental differences were found between those grown

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[3] See "Literature Cited" for complete data on citations mentioned in the text by author and date of publication.

in culture solution and those grown in soil.[4] All roots examined in the primary state were lateral, since the apices of the seedling taproots were not available. The apical meristem was studied only in the culture-solution material.

PRIMARY ORGANIZATION OF THE VASCULAR CYLINDER

The apex of the root shows the common separation into the primordial vascular cylinder (or stele), the immature cortex, and the rootcap (plate 1, *B*). In the apical-meristem region, however, only the stele is set off from the other regions with its own initials. The cortex, the epidermis, and the rootcap have a common origin.

The stelar initials form a uniseriate layer at the apex of the stele (*si* in plate 10). By periclinal divisions these initials give rise to the innermost part of the stele. Nearer the periphery of the initial layer the divisions are intermediate between the periclinal and the anticlinal, and they are entirely anticlinal in the outermost initial cells. The anticlinal divisions add cells to the pericycle. In plate 10 the pericycle (*p*) is evident as a layer of elongated cells immediately inside the white line on the sides of the stele. In this figure the pericycle can be followed as a uniseriate layer directly into the initial region. In other words, the pericycle of this root tip is individualized immediately behind the apical initials. The peripheral derivatives of the stelar initials may, however, undergo a periclinal division before the pericycle is delimited. In any case, the pericycle is histogenetically a part of the stele, and early becomes individualized.

The initial region giving rise to the cortex, the epidermis, and the rootcap, is composed of several layers of cells (*ci* in plate 10, about five layers of cells below the white line in the center of the figure). On the sides of this region anticlinal divisions contribute cells to the cortex. Acropetally the initial cells produce the core of the rootcap by periclinal divisions. The immediate products of these divisions also divide mainly periclinally, so that the youngest part of the rootcap core shows rather orderly-arranged longitudinal files of meristematic cells merging with the initials of the root apex (plate 10). The orderly files of cells remain evident also after the maturation of the rootcap core (plates 1, *B*, and 10). The peripheral portion of the rootcap is produced by periclinal and oblique divisions from the outermost lateral derivatives of the apical meristem. These derivatives are here interpreted as cortical cells and not as epidermis because the latter is set off from the cortex and the rootcap some distance from the apical meristem, after the divisions

[4] Dr. A. S. Foster furnished the killed and imbedded material of roots grown in culture solution, while Dr. L. D. Davis supplied the soil-grown material.

producing the rootcap cease. The peripheral rootcap cells are also aligned in longitudinal files at the source of their origin (plate 10), but this arrangement is somewhat disturbed during the further development of the cells (plate 1, *B*).

Judging by Schüepp's (1926) discussion of root-meristem organization, the pear-root apices described in the present paper belong to the type in which "the entire outer part of the cortex contributes toward the formation of the rootcap" and the stelar initials are independent of those producing the cortex, the epidermis, and the rootcap (Schüepp, 1926, p. 70, type III B). According to Schüepp, certain Rosaceae belong to this group.

The depth of the initial region and the subsequent periclinal divisions in the cortical meristem determine the final thickness of the cortex. Although some doubling up of the longitudinal cell layers occurs throughout the youngest region of the cortex, the addition of new cells through periclinal divisions in its innermost layer is more conspicuous. Plates 10 and 2, *A*, show the result of this meristematic activity. A succession of periclinal divisions in the innermost cortical layer form several rows of narrow cells, densely cytoplasmic. Farther away from the pericycle the cells are larger, their protoplasts less dense. Some anticlinal divisions also occur as the root increases in circumference. After completion of the periclinal divisions the innermost layer of cortical cells undergoes a differentiation as an endodermis (plate 3, *B*, *en*). Eventually the anticlinal divisions and the change in shape of the endodermal cells obscure their close histogenetic relation to the adjacent cortical layer (fig. 1; plate 3, *B*). Since the last periclinal divisions in the inner cortex may not pass all around the stele, the limit between the endodermis and the adjacent cortical layer may appear somewhat disorderly (fig. 1; plate 3, *B*).

The meristematic stele (the procambium) of the root shows a cytologic differentiation immediately behind the apical initials. The central region quickly develops conspicuous vacuoles, and the cells enlarge (plate 10). Comparatively few longitudinal divisions occur here. When the peripheral region is formed by the apical initials these, as was mentioned previously, divide obliquely; and the immediate derivatives undergo periclinal (longitudinal) divisions. Because of these divisions the periphery retains a meristematic appearance somewhat longer than the center of the stele (plate 10). Although nearest the apex the entire periphery of the stele is densely meristematic, some 200 microns higher the peripheral region becomes lobed through the increased vacuolation of certain portions of it. The densely cytoplasmic portion of the procambium becomes broken up into strands, whereas the more highly

vacuolated part assumes, in transverse sections, the appearance of a star (plate 2). Eventually the strands differentiate into the primary phloem, the vacuolated part of the stele into the primary xylem. Thus the xylem and phloem regions become delimited some 200 to 300 microns from the apex, and the metaxylem region is vacuolated before the protoxylem region. The longitudinal divisions that occur in the

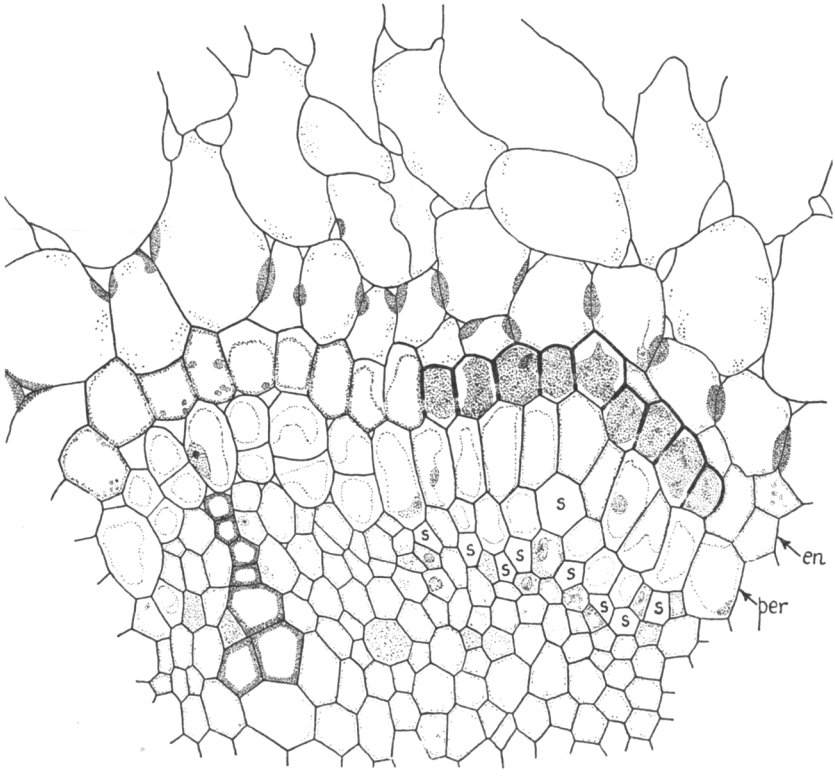

Fig. 1.—Transverse section through portion of root, illustrating the characteristics of the endodermis. The drawing was made from the same section as in plate 3, *B* (area within the rectangle). Details are: *en*, endodermis; *per*, pericycle; *s*, sieve tube. The faint areas in the endodermal walls indicate sections of the Casparian strips. Above the endodermis is the cortical layer with localized wall thickenings. (× 621.)

peripheral region of the stele last longest on the inner margins of the procambium strands that give rise to the phloem. Later the vascular cambium is initiated in this position (plate 4, *B*). The young pericyclic cells are as densely cytoplasmic as the future phloem cells, but larger (plate 2, *A*).

Densely staining inclusions, usually interpreted in the literature as being tannic in nature, appear in the xylem region, the endodermis, and

the cortex (plates 1, *B*, and 2, *A*). The early distribution of the tannic inclusions in the endodermis and in the adjacent cortical layers shows a peculiar relation to the stelar regions. Plate 2, *B*, for example, shows tannin throughout the endodermis and in certain groups of the adjacent cortical cells—groups located next to the regions of the stele that would later have differentiated into the protoxylem. In older stages of root development the tannic inclusions become dispersed throughout the cells instead of remaining confined to the peripheral cytoplasmic layer. This phenomenon is first noticeable in the parts of the endodermis next to the protophloem poles (plate 3, *B*, and fig. 1). Later all endodermal cells and scattered cells within the other root regions stain uniformly densely throughout the protoplasts, apparently because of the dispersed tannic inclusions (plates 3, *A*; 4; 5; 6, *B*; 7).

At levels located about 600 to 700 microns from the apical meristem the first sieve-tube elements differentiate, one in each phloem strand (plate 2, *B*). They mature at unequal levels at the different poles. In the root shown in plate 2, *B*, the section where the first of the five sieve tubes matured was 80 microns nearer the apex than the section where the fifth sieve tube was fully differentiated. The first sieve tubes appear next to the pericycle and are not associated with any cells that could be interpreted as companion cells (plate 6, *A*, sieve tube, *s*, in the center of the figure). Although, as was pointed out before, the pericycle is early individualized, periclinal divisions may occur in the outermost layer of the stele during the organization of the phloem, and a sieve-tube element may differentiate as a sister cell of a pericyclic cell (plate 6, *A*, sieve tube, *s*, in the center of the figure).

These first differentiated phloem elements merit the designation as sieve-tube elements because they have sieve plates on their more or less inclined terminal walls, lack nuclei, and show lightly stained mature protoplasts—all characteristics common to the protophloem sieve-tube elements of angiosperms. (See review by Esau, 1939.) The sieve-tube elements are about 70 microns long immediately upon maturation.

Additional sieve-tube elements differentiate at each pole laterally from the first sieve tubes. In plate 6, *A*, the first sieve tube of one of the phloem strands is in the center of the figure; the second appears to the right. The additional sieve tubes have companion cells but, like the first ones, appear next to the pericycle. When the xylem begins to differentiate, about two sieve tubes occur at each phloem pole. Then still more sieve-tube elements differentiate, some next to the pericycle, others in deeper layers of the procambium strand—that is, centripetally from the first sieve tubes (fig. 1). All these subsequent sieve tubes have companion cells.

Shortly before the xylem begins to differentiate, the entire stele becomes highly vacuolated even in the phloem and the pericycle regions (plate 6, *A*). The sieve tubes are therefore much less conspicuous in the more mature regions (plate 3, *B*) than nearer the apex, where they stand out as cells with lightly stained contents among the densely cytoplasmic procambial cells (plate 2, *B*).

Some 5 mm from the apex the deposition of the secondary walls is initiated in the first xylem elements. These cells differentiate next to the pericycle at the protoxylem poles that alternate with the protophloem poles. The relative position of the early xylem and phloem elements may be judged from figure 1 and plate 3, *B*, showing two views of the same section taken 2 cm from the apex of the root. The number of the protoxylem poles and, correspondingly, that of the protophloem poles varies, four (plates 3, *A*, and 5, *B*), five (plates 2, *B*; 4; and 5 *A*), and six (plate 3, *B*) having been observed in roots of larger, and two in roots of smaller diameters.

The distances from the apex to the first mature xylem and phloem elements were determined by the use of roots grown in culture solution. These distances are not necessarily comparable with those that would occur in roots grown in a different environment, but they vary also in roots grown under similar conditions (Esau, 1941). The differentiation of the sieve tubes in advance of the xylem elements appears, however, to be a usual phenomenon in roots. (See review by Esau, 1943.)

The first xylem elements have very narrow diameters (fig. 1) and in the culture-solution material show scalariform secondary thickenings. One or two elements at each pole are of this nature, the subsequent ones being reticulate and pitted. The later xylem elements have a greater diameter than the first (fig. 1). In soil-grown material the first elements were also scalariform or transitional between spiral and scalariform. Differences in the types of the secondary walls of the protoxylem can be expected in roots grown under different environmental conditions. As has been well established experimentally, the nature of the secondary walls is related to the degree of stretching—caused by the elongation of the entire organ—to which the elements are subjected during their differentiation and thereafter (Smith and Kersten, 1942). Whether the first xylem elements in the pear root are tracheids or vessels has not been ascertained; for convenience they are here called the *xylem elements* or *tracheary elements* (Foster, 1942, p. 80).

In the section shown in plate 3, *B*, about five to nine sieve tubes occurred at each protophloem pole, and about three to six mature tracheary elements. (In the section shown in figure 1 the two lowermost xylem elements were still immature.) At this stage of development the

endodermis shows Casparian strips. These structures, which are very inconspicuous, appear to be imbedded in the primary wall without forming a thickening on its surface. In sections stained with fast green and safranin they are evident as red wall areas contrasting with the green stain in the rest of the walls. As usual they occur on the radial and transverse walls near the inner tangential walls. The Casparian strips are somewhat more conspicuous in the endodermal cells located at the protophloem poles, probably because in these positions the endodermal walls are somewhat thicker than next to the protoxylem poles (fig. 1).

The cortical layer immediately outside the endodermis is characterized by prominent wall thickenings that resemble those of collenchyma cells (fig. 1; plates 3, *B;* 4; 5; and 7, *A*). These thickenings are not very bright in polarized light, are not lignified, and appear as bands in longitudinal views. Most of them occur on the radial walls, though some are located on parts of walls adjacent to the intercellular spaces (fig. 1; plates 4 and 7, *A*). Occasionally the thickenings also occur in the cortical layer second from the endodermis (fig. 1 and plate 7, *A*). Similar modifications of the inner cortical cells have been mentioned in the literature. Russow (1875, p. 72–73) referred to the similarly thickened cortical layer outside the endodermis as the *exodermis* and commented that the transverse sections of the thick walls resembled the Greek letter Phi. He reported such an exodermis in the roots of the Pomaceae, specifically mentioning *Pyrus,* and in certain other families of dicotyledons and gymnosperms. Guttenberg (1940, p. 121–22) calls this layer the *inner cortical sheath* and records its presence in the Rosaceae.

At the stage of root development illustrated in plate 3, *B,* and figure 1, the pericyclic cells show pronounced radial elongation and divide periclinally next to the protoxylem poles. As viewed in longitudinal sections the pericyclic cells appear short, in sharp contrast to the long cells of the adjacent vascular tissues. Plate 8, *A,* illustrates this difference in a root somewhat older than the one shown in plate 3, *B*.

On the basis of our present information regarding the stages in the differentiation of the primary vascular tissues (review by Esau, 1943), the terms *protophloem* and *protoxylem elements* are here applied to the phloem and xylem cells which mature in advance of the other vascular elements in the root and which by their position mark the pattern of differentiation followed by the primary vascular tissues. As is usual in roots, the phloem following the protophloem in time of appearance (that is, the metaphloem) and the subsequent primary xylem (the metaxylem) differentiate centripetally from the protophloem and protoxylem poles respectively. The phloem also spreads laterally from its

points of initiation, so that the protoxylem strands eventually appear as narrow strips of tissue crowded between the broad phloem strands (plate 4, *A*).

The demarcation between the protophloem and the metaphloem, and between the protoxylem and metaxylem is usually drawn somewhat arbitrarily (Esau, 1943). The first sieve-tube element at each pole in the pear root is the largest in diameter among the primary sieve tubes and lacks companion cells (plate 3, *B*, and fig. 1). These are probably rather common characteristics of the first sieve tubes of dicotyledonous roots (Esau, 1935, 1940, 1941). In time of appearance the first sieve tubes in the pear root are less sharply set off from the following sieve tubes than they are in tobacco-root tips studied by the present writer (Esau, 1941). In the pear root, as was mentioned earlier, one or two additional sieve-tube elements having rather narrow diameters and associated with companion cells differentiate at each pole before the first xylem elements begin to show a deposition of secondary walls.

Since there is no sure basis for delimiting the different parts of the primary vascular tissues (review by Esau, 1943), the first three or four elements at each pole (elements early crushed because of subsequent growth changes in the root) are here classified as protophloem and protoxylem elements. Conceivably, the distinctness with which the first vascular elements are set off from the subsequent ones in time of appearance is determined largely by the degree of elongation of the roots. Judging by the nature of the secondary walls of the protoxylem in the pear root (scalariform, rather than annular or spiral) and by the small amount of distortion that these walls show in sections of root with secondary growth, the roots used in this study must have been elongating only slightly, if at all, after the protoxylem matured. The lateral pressure of the adjacent living cells seems in this material to have been the principal cause of distortion of the protoxylem elements. Plate 5, *B*, indicates the encroachment of the adjacent cells upon the protoxylem, particularly at the protoxylem pole in the lower part of the figure. The crushing and the obliteration of the protophloem sieve tubes and their companion cells, if these are present, are rather conspicuous (plate 4, *B*, and 7).

By the definitions given above the sieve-tube elements in plate 6, *A*, are protophloem cells. The mature intact sieve-tube elements in plate 7, *A*, are metaphloem cells. The two immature sieve tubes at the lower left in plate 7, *A*, are the first secondary sieve tubes in this bundle. Certain cells of parenchymatous appearance in plate 7, *A*, are phloem-parenchyma cells, whereas others are much elongated elements and eventually differentiate as fibers. Plate 7, *B*, illustrates the early stage

in secondary-wall formation in the fibers of the protophloem, whereas plate 8, *B,* shows one of these fibers on the outer limit of the phloem in longitudinal view. Later, fibers differentiate in the metaphloem also. The primary-phloem fibers together with the fibers of the earliest secondary phloem form, in old roots, compact strands on the outer periphery of the vascular cylinder (plate 1, *A, fb*). The sieve tubes and companion cells are all obliterated in this region, while the parenchyma cells are much dilated, especially in the tangential direction. The parenchyma cells contain inclusions such as starch, tannin, and crystals; some of them become sclerified as stone cells. As the present writer has frequently emphasized (Esau, 1938, 1939, 1943), fibers that appear on the outer periphery of the vascular cylinder in stems commonly arise in the phloem. Lloyd (1911, p. 94) has given good evidence that the peripheral fibers of the root stele in *Parthenium* are phloem fibers.

The metaxylem comes to occupy the entire center of the stele (plates 1, *A;* 5; 6, *B;* and 8, *A*). Vessels, tracheids, and xylem parenchyma, all prominently pitted, occur in this region. Though the metaxylem is defined before the protoxylem in the meristematic stele, it matures rather slowly, so that its secondary-wall formation is not terminated before cambial activity sets in (plate 4, *B*).

SECONDARY GROWTH IN THE ROOT

As has been pointed out, the procambial divisions last longest on the inner margins of the phloem bundles. During the differentiation of the protophloem and protoxylem, the procambial cells in this position enlarge somewhat and vacuolate so that they merge imperceptibly with the immature phloem and xylem cells (plates 6, *A,* and 4, *A;* fig. 1). After the final delimitation (but not maturation) of the primary regions in the stele (plate 4, *A*) the divisions on the inner margins of the phloem bundles are resumed and now result in radial series of narrow cells (plate 4, *B*). These are divisions initiating the secondary growth of the vascular tissues.

As shown in plate 4, *B,* the first cambium occurs in isolated curved strips on the inner sides of the phloem bundles. This meristem, after producing some secondary xylem elements, becomes united into a continuous layer between the xylem and the phloem by the meristematic activity of the pericyclic cells located outside the protoxylem poles. Plates 4, *B,* and 5 show how markedly this early production of secondary xylem changes the outline of the cambium region in transverse sections. First it appears in the form of curved arcs, bulging toward the center of the root (plate 4, *B*); then the arcs are straightened out (plate 5, *A*). After this position is attained, periclinal divisions in the pericycle out-

side the protoxylem also form some cambium, and thereby this meristem becomes a continuous, more or less cylindrical layer of tissue around the entire circumference of the xylem. In plate 5, *B*, this stage had almost been reached. As previously indicated, the pericyclic cells divide periclinally at a very early stage in the primary development of the root (fig. 1). These divisions probably prepare the formation of the vascular cambium in this position.

In common with the vascular meristem of arborescent dicotyledons, the cambium of the pear root is composed of fusiform and ray initials. The pericyclic cells outside the protoxylem give rise to ray initials, so that vascular rays radiate from the protoxylem poles through the secondary vascular tissues (plate 1, *A*). In agreement with Barghoorn's (1940) observations on ray formation in roots, the rays formed at protoxylem poles in the pear root are the first multiseriate rays in the secondary xylem. The cambium arising in the procambium inside the primary-phloem strands also produces rays, but the earliest formed in this position are uniseriate.

Plate 1, *A*, shows a pear-root section with considerable secondary growth of the first season. The primary xylem, a five-pointed star, is imbedded in the secondary xylem. In the latter the wide pores (representing transverse views of vessels) and the rays are the conspicuous structural features detectable at this magnification. Plate 9, *B*, shows a section of the secondary xylem from plate 1, *A* (area delimited by a rectangle), in greater detail. Four rays are visible in this section, the one to the left being a multiseriate ray that arose in the pericycle outside the protoxylem. (Compare with plate 1, *A*.) The rays are parenchymatous and contain starch grains and tannin. In the longitudinal system the cells having the widest diameters (plate 9, *B*) are vessels. Some of the narrower cells are also tracheary elements; others are fibers and xylem-parenchyma cells. Starch grains and tannin occur in the latter.

The major part of the tissue located outside the cambium in plate 1, *A*, is phloem (*ph*). The rest is pericycle and periderm. The multiseriate and uniseriate parenchymatous phloem rays that are continuous with the xylem rays divide the secondary phloem into blocks of tissue composed of sieve tubes, companion cells, phloem parenchyma, and some fibers. A portion of the secondary phloem from plate 1, *A* (area delimited by a rectangle) is depicted at high magnification in plate 9, *A*. A multiseriate ray occurs to the left. In the lowermost part of this figure appears the cambium. Then follows the functioning part of the phloem with mature sieve tubes (*s*). Farther away from the cambium the sieve tubes and the companion cells are partly crushed among the enlarged parenchyma cells. This is the phloem part which, according to a common

concept, is no longer concerned with longitudinal conduction. The enlargement of the phloem parenchyma cells becomes particularly conspicuous towards the periphery of the stem, where a considerable tangential dilation occurs in all living cells of the phloem and pericycle.

The outer limits of the phloem may be determined by the position of the fibers which, as was described earlier, arise in the phloem, the earliest ones being in the protophloem (plate 7, *B*). The pericycle gives rise to the cork cambium. The formation of this meristem is preceded by an increase in thickness of the pericycle. As previously mentioned, the earliest tangential divisions in this region occur outside the protoxylem (fig. 1, plate 3, *B*). Later, such divisions spread all around the periphery of the stele (plates 5, *A*, and 7, *B*) and are repeated several times, so that the pericycle shows a marked increase in thickness (plates 5, *B*, and 8, *B*). In plate 5, *B*, the excessive width of the pericycle to the right of the stele results from growth phenomena associated with the development of branch roots. The latter are surrounded at their bases by collars of tissue resulting from a proliferation of pericyclic cells. In sectional views these collars resemble lenticels, provided the branch roots associated with them do not appear in the same view (plate 1, *A*, below). True lenticels have not been observed in the present material.

During the increase in the circumference of the stele through the cambial activity and the proliferation of the pericycle, the cortex together with the endodermis is crushed and sloughed off. Plate 3, *A*, shows the first splitting of the cortex. No cortex occurs in the section in plate 1, *A*.

The new pericycle cells are aligned in rather orderly radial rows (plates 5, *B*, and 8, *B*). The outer cells become tangentially stretched and radially compressed as the stele increases in circumference. After undergoing suberization they serve as a protective layer before the cork cambium and cork are formed in one of the deeper layers in the pericycle. In the material used in this study most of the sections showed only the first-formed periderm. Occasional roots showed isolated strips of cork cambium within the secondary phloem.

SUMMARY

The apical meristem of the root shows two sets of initials. One set, one layer deep, produces the stele with the pericycle; the other set, several layers deep, gives rise to the cortex, the epidermis, and the central core of the rootcap. The peripheral portion of the rootcap arises from the youngest cortical cells.

Within the stele the pericycle is individualized almost directly behind the apical initials. The phloem and the xylem regions are clearly

delimited before any vascular elements differentiate, the phloem region being composed of small, densely cytoplasmic cells, the xylem region of larger and more highly vacuolated cells.

The first protophloem sieve tubes mature in advance of the first protoxylem elements. The protophloem and the protoxylem appear next to the pericycle and alternate with each other. The number of the protophloem and protoxylem poles varies in roots of different diameters.

The differentiation of the metaphloem and metaxylem proceeds in the usual centripetal manner from the protophloem and protoxylem poles respectively.

The endodermis is a uniseriate layer with Casparian strips. The cortical layer next to the endodermis has localized thickenings on its walls.

The cambium arises in the manner characteristic of roots. It first appears on the inner side of the phloem bundles, then becomes continuous across the pericycle cells located outside the protoxylem. The secondary vascular tissues show the common characteristics of these tissues in woody dicotyledonous roots.

The pericycle, which is at first uniseriate, becomes multiseriate by tangential divisions. The outermost cells resulting from these divisions become cork cells, and beneath them arises a cork cambium. The cortex with its endodermis is sloughed off in connection with the secondary activity in the stele.

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PLATES

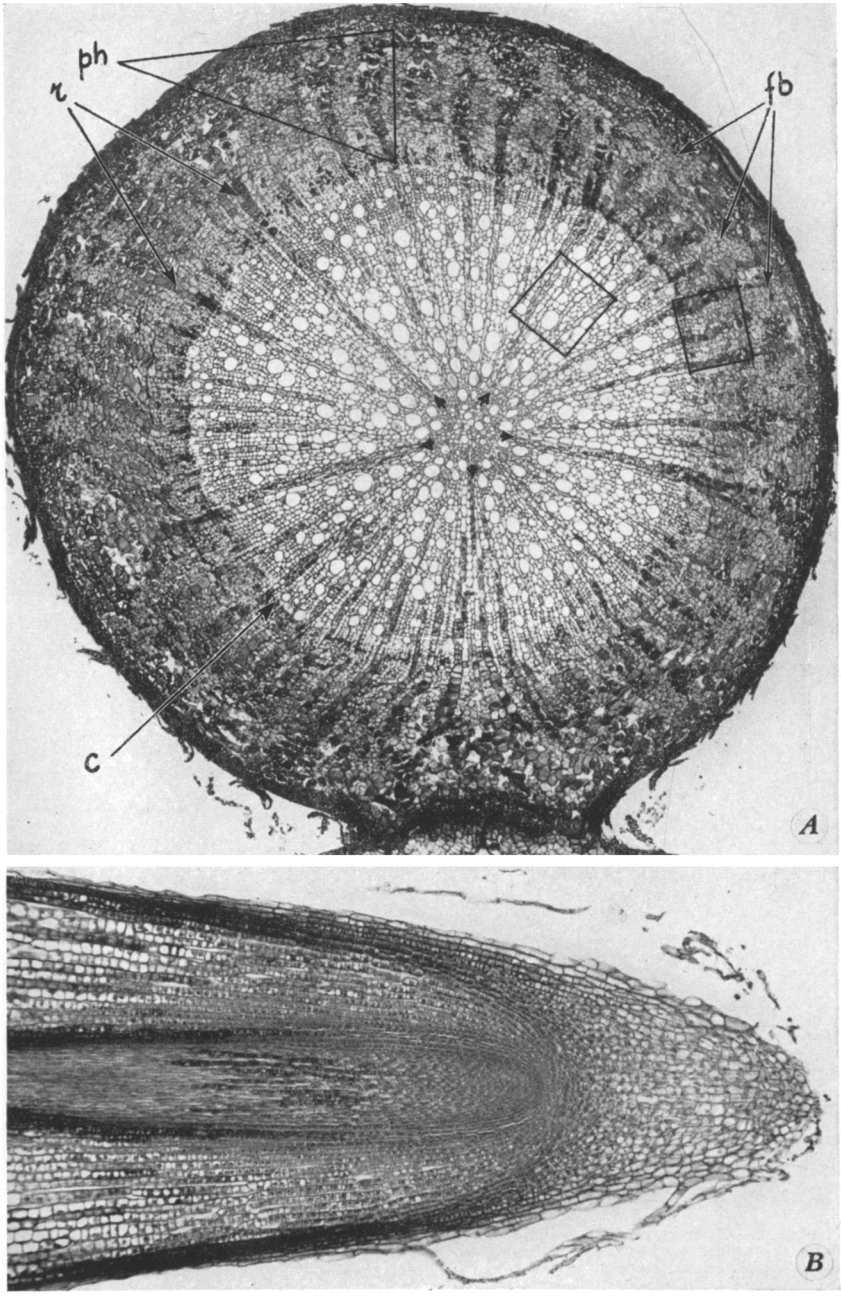

Plate 1.—*A*, Transverse section of a root with considerable secondary growth. Details are: *c*, cambium; *fb*, fibers; *ph*, phloem; *r*, rays. The rectangles delimit the areas of secondary phloem and secondary xylem depicted at high magnification in plate 9. The small arrowheads in the center indicate the five protoxylem poles. *B*, Longitudinal section of a root tip showing the apical meristem and the regions immediately derived from it. (*A*, × 50; *B*, × 90.)

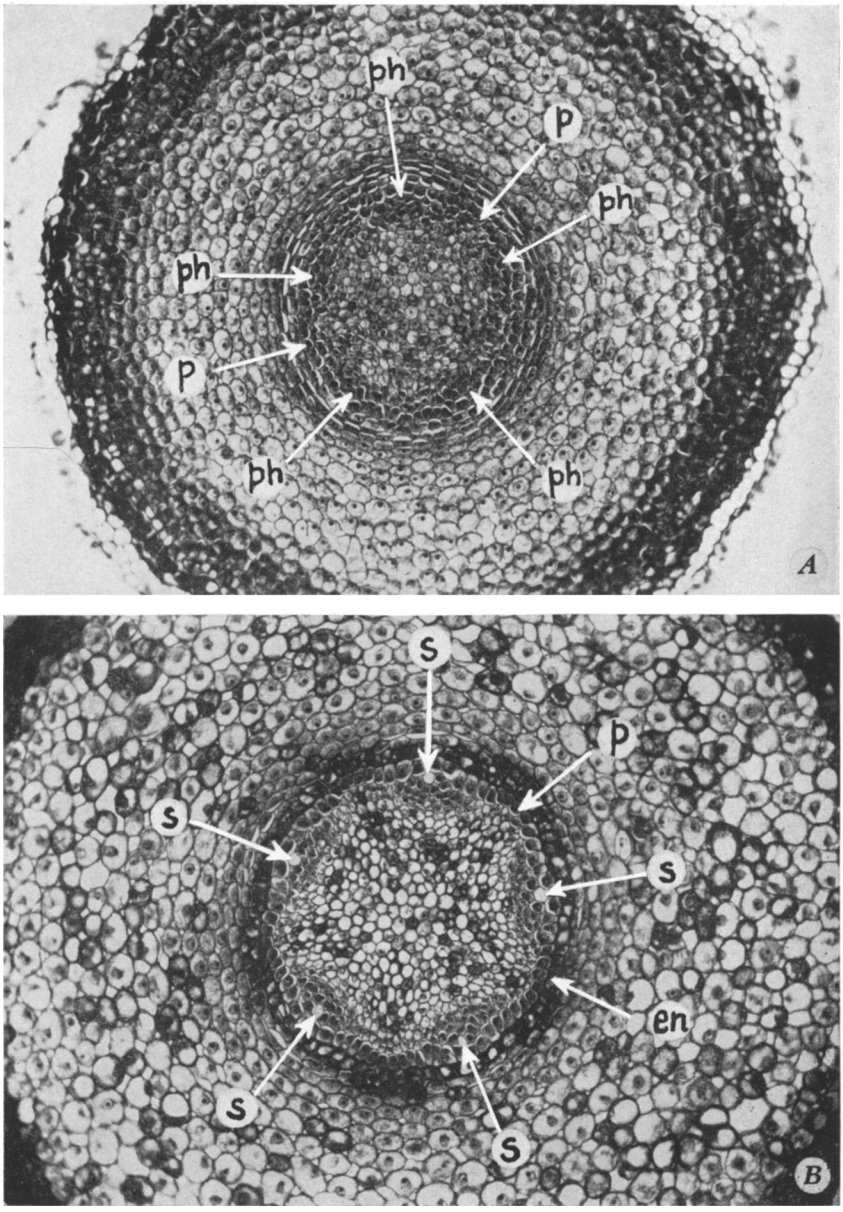

Plate 2.—Transverse sections of a root tip taken 280 microns (*A*) and 750 microns (*B*) from the apical meristem. Details are: *en*, endodermis; *p*, pericycle; *ph*, protophloem pole; *s*, sieve tube. (Both × 180.)

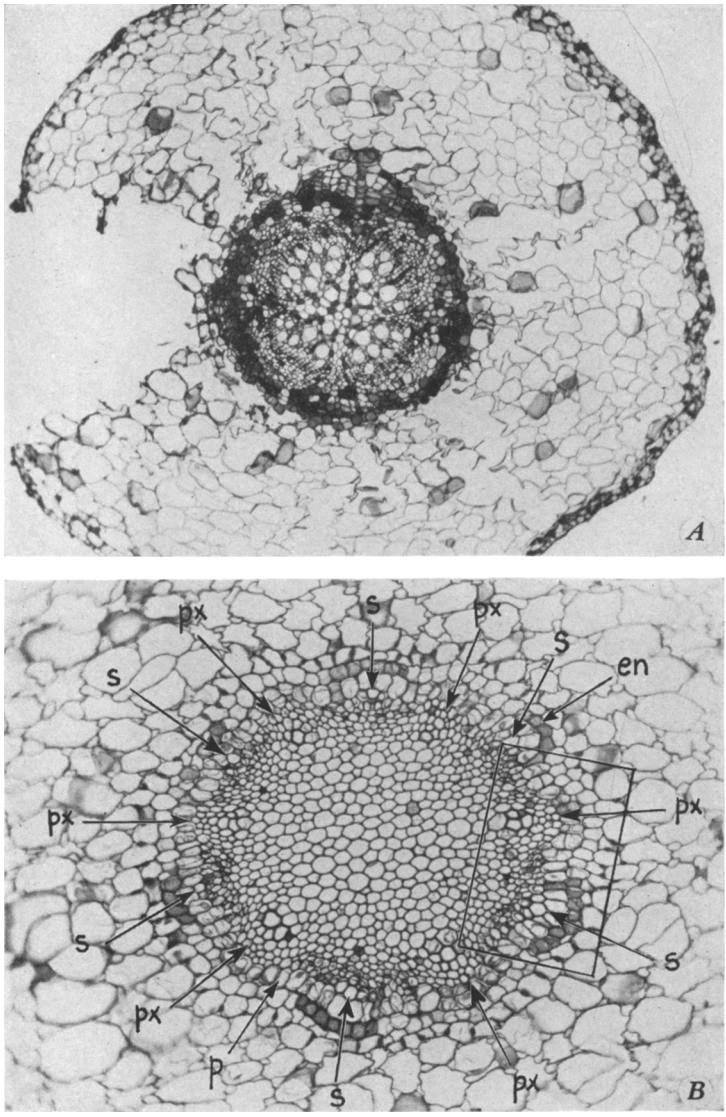

Plate 3.—*A*, Transverse section of root, showing splitting of cortex. The stage of development of the vascular tissues is comparable to that in plate 5, *B*. *B*, Transverse section of root taken about 2 cm from the apex. It illustrates an early stage of phloem and xylem differentiation. Details are: *en*, endodermis; *p*, pericycle; *px*, protoxylem; *s*, sieve tube. The rectangle delimits the area depicted at higher magnification in figure 1. (*A*, × 90; *B*, × 180.)

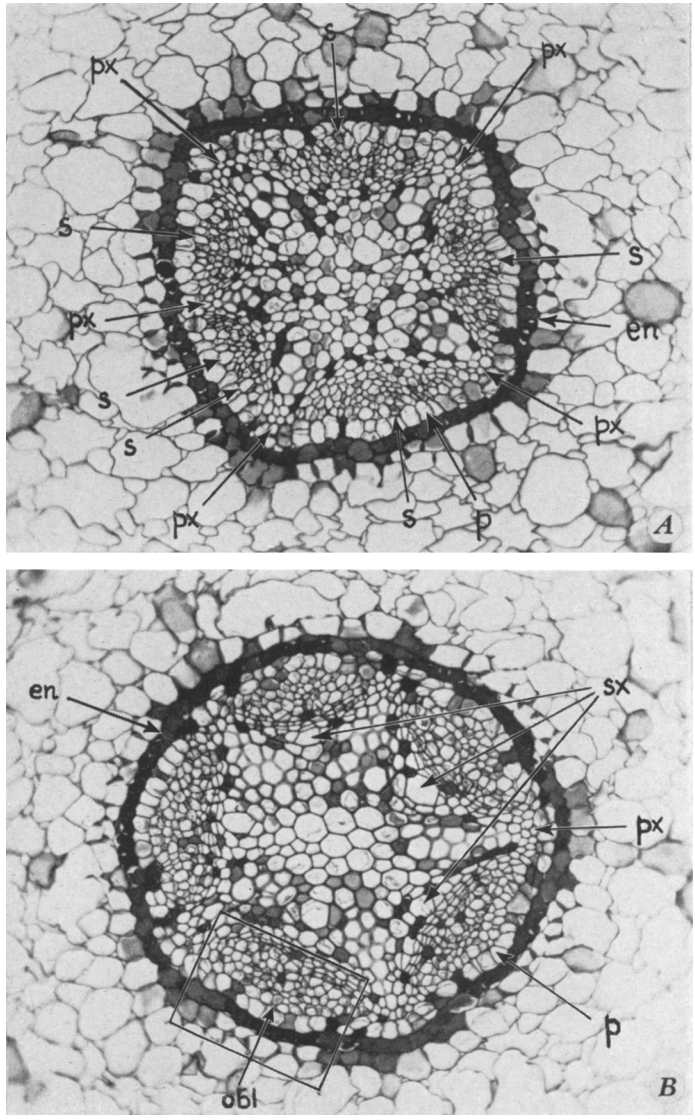

Plate 4.—Transverse sections taken about 4 cm (*A*) and 5 cm (*B*) from the apex of the root. *A* illustrates the stage just before the beginning of cambial activity. In *B* the first secondary xylem elements are present. Details are: *en*, endodermis; *obl*, obliteration of sieve tube; *p*, pericycle; *px*, protoxylem; *s*, sieve tube; *sx*, secondary xylem. The rectangle in *B* delimits the area shown at higher magnification in plate 7, *A*. (Both × 180.)

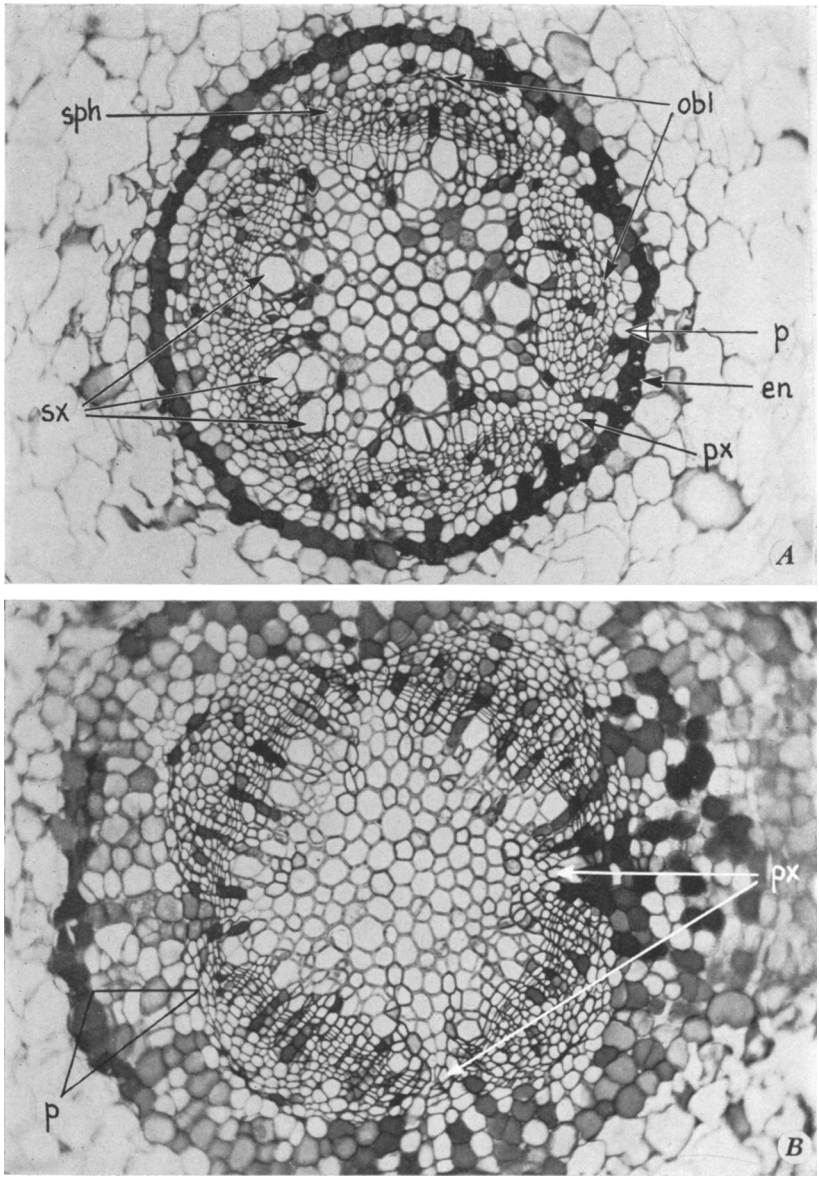

Plate 5.—Transverse sections taken about 7 cm (*A*) and 9 cm (*B*) from the apex of the root. *A* illustrates the stage just before the splitting of the cortex. In *B* the cortex was split. Five protoxylem poles occur in *A*, four in *B*. Details are: *en*, endodermis; *obl*, obliteration of sieve tube; *p*, pericycle; *px*, protoxylem; *sph*, secondary phloem; *sx*, secondary xylem. (Both × 180.)

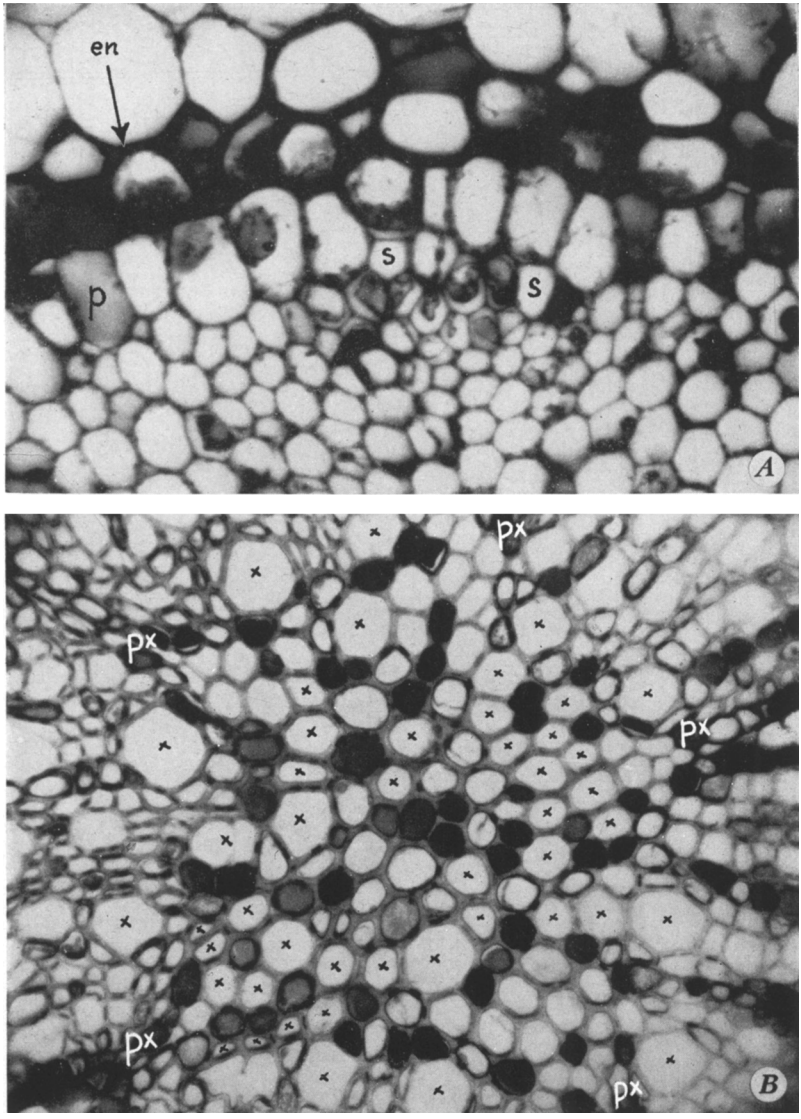

Plate 6.—*A*, Transverse section through a protophloem pole with two sieve tubes (*s*) taken 1,720 microns from the apical meristem. *B*, High-power view of the primary-xylem region from a section somewhat older than that shown in plate 5, *B*. Details are as follows: *en*, endodermis; *p*, pericycle; *px*, protoxylem; *s*, sieve tube. In *B* the tracheary elements have been indicated by small crosses. (*A*, × 810; *B*, × 360.)

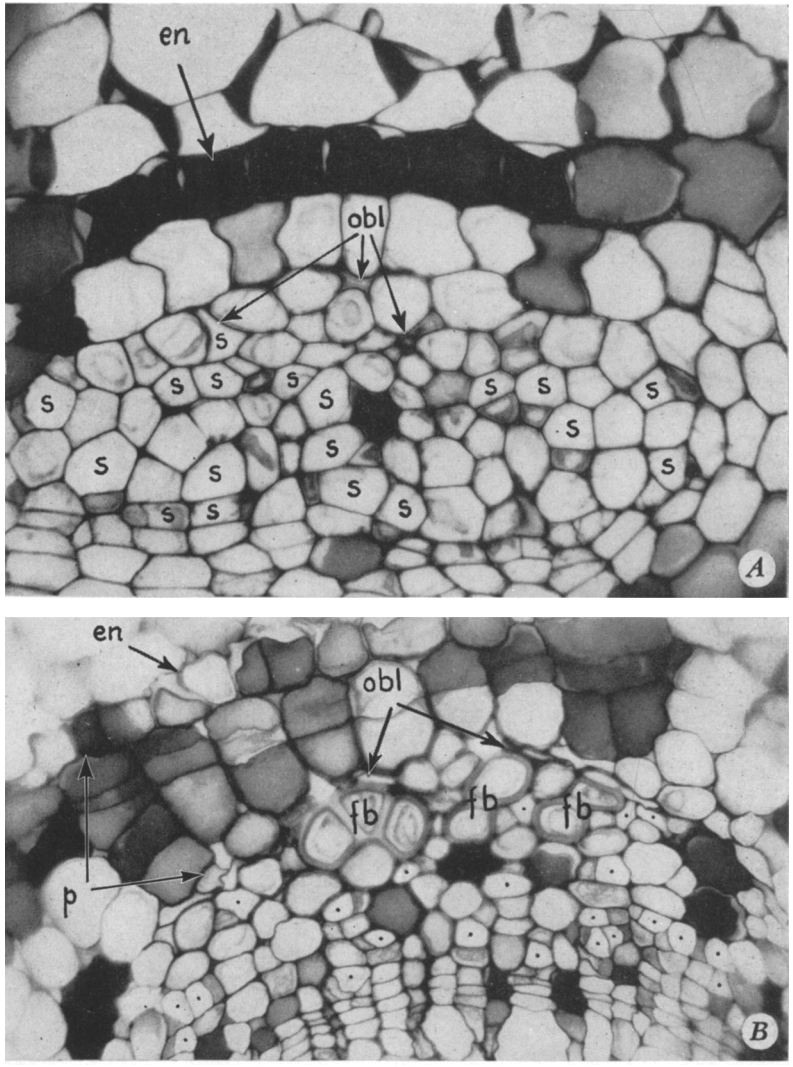

Plate 7.—*A*, High-power view of portion of transverse section figured in plate 4, *B* (area within the rectangle). It shows the primary phloem, the endodermis, and the inner cortical sheath above the endodermis. *B*, High-power view of portion of transverse section figured in plate 3, *A*. It shows the primary phloem during the early stage of fiber development and the first secondary phloem near the cambium. Details are: *en*, endodermis; *fb*, fiber; *obl*, obliteration of sieve tubes; *p*, pericycle; *s*, sieve tube. The sieve tubes in *B* are marked by dots. (*A*, × 810; *B*, × 540.)

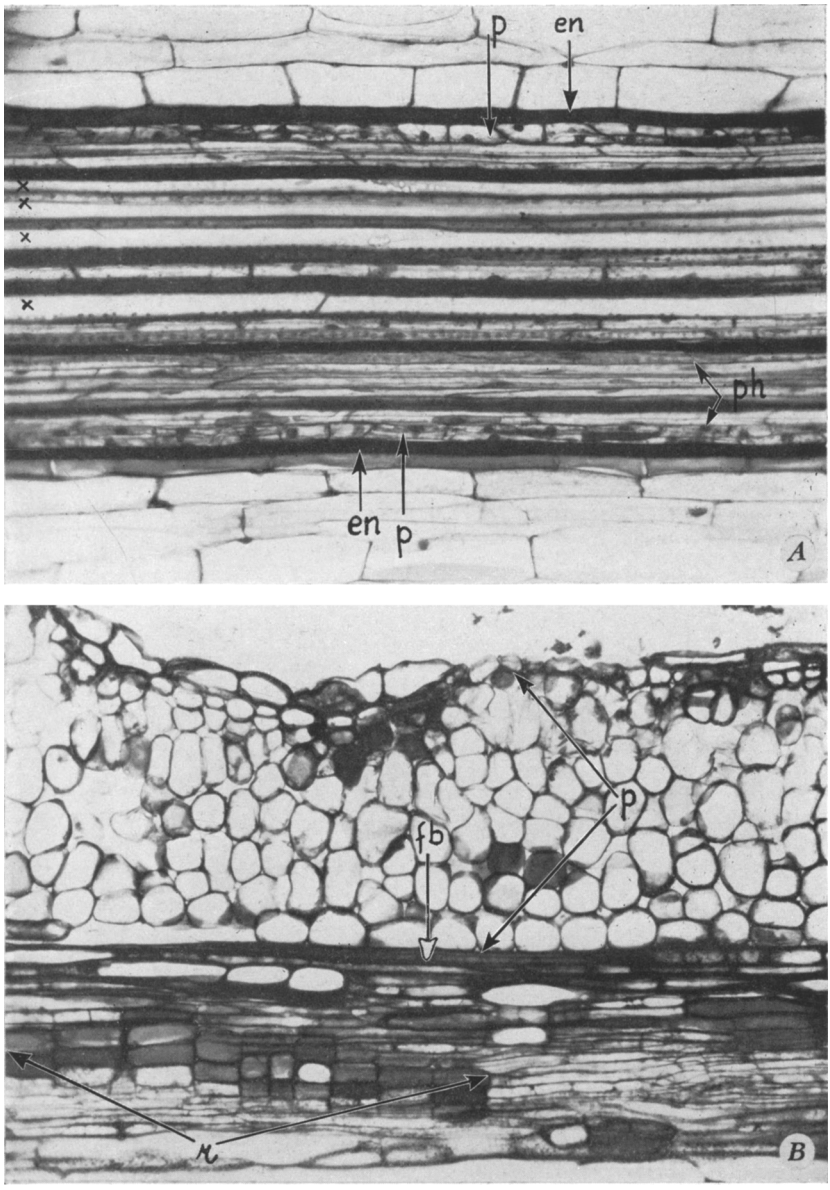

Plate 8.—*A*, Radial longitudinal section of root at the end of primary growth as in transverse view in plate 5, *A*. The cells marked with small crosses are pitted tracheary elements. *B*, Radial longitudinal section of a root sampled after the proliferation of the pericycle as in transverse section in plate 5, *B*. Details are: *en*, endodermis; *fb*, fiber in the phloem; *p*, pericycle; *ph*, phloem; *r*, ray. (Both × 180.)

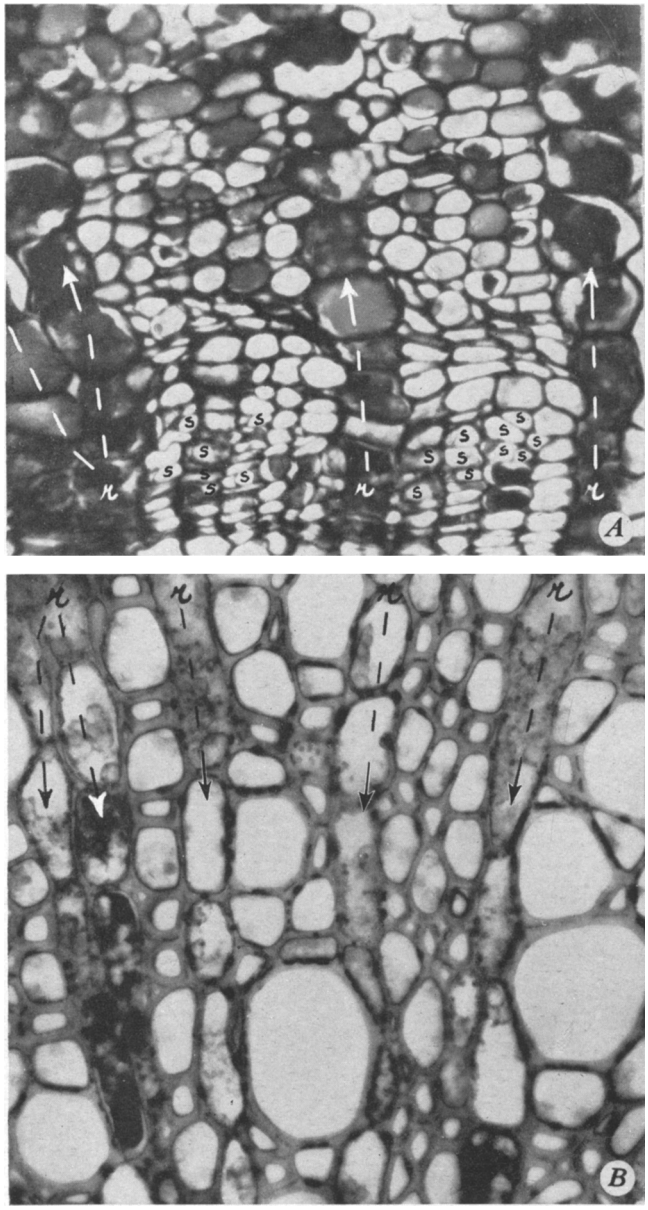

Plate 9.—Portions of transverse sections of secondary phloem (*A*) and secondary xylem (*B*) from the same section as in plate 1, *A* (areas delimited by rectangles). The letter *s* in *A* indicates the sieve tubes in the mature phloem. Above this region is the old phloem with partly crushed sieve tubes and prominent parenchyma cells. The letter *r* indicates the rays in both figures. (Both × 360.)

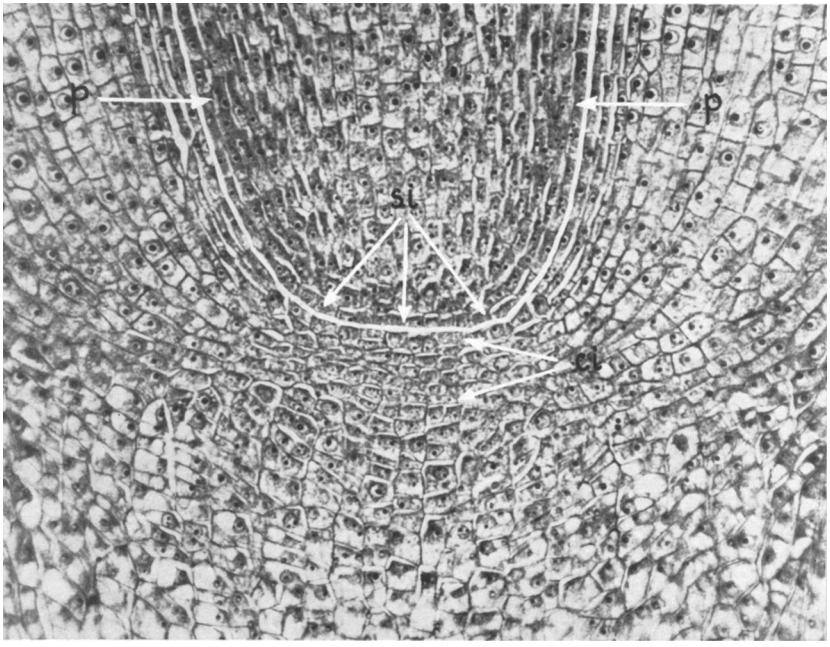

Plate 10.—Median longitudinal section of root tip through the apical-meristem region. The limits of the stele are indicated by a white line. Details are: *ci*, cortical initials; *p*, pericycle; *si*, stelar initials. (× 300.)