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COMPARATIVE HISTOGENESIS OF VEGETATIVE AND FLORAL APICES IN AMYGDALUS COMMUNIS, WITH SPECIAL REFERENCE TO THE CARPEL

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DEVELOPMENTAL ANATOMY OF THE FLESHY STORAGE ORGAN OF DAUCUS CAROTA[1]

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THE PRESENT STUDY of the anatomy of the fleshy, edible storage organ of the carrot plant (*Daucus carota* L.) describes, in different stages of development, the tissues making up this organ and interprets its gross morphological features in terms of histological details.

This investigation was completed when a paper by Havis (1939)[3] on the anatomy of the hypocotyl and root of the carrot appeared in press. Since Havis' article gives fewer ontogenetic details and emphasizes other points than the present study, a publication of the latter constitutes no duplication of material.

MATERIAL AND METHODS

Seedlings obtained by germinating carrot seed upon moistened moss in desiccators served for the study of the earliest stages. Larger plants were grown in a sandy soil in a greenhouse. The seed was of the variety Imperator.

The material, killed in a chrom-acetic-formalin solution (Rawlins, 1933), was imbedded in paraffin after being dehydrated with ethyl and butyl alcohols. The microtome sections were stained with the combination of tannic acid and iron chloride recommended by Foster (1934). Certain seedlings cleared in lactic acid were particularly useful in studying the transition region.

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[3] See "Literature Cited" for complete data on citations, which are referred to in the text by author and date of publication.

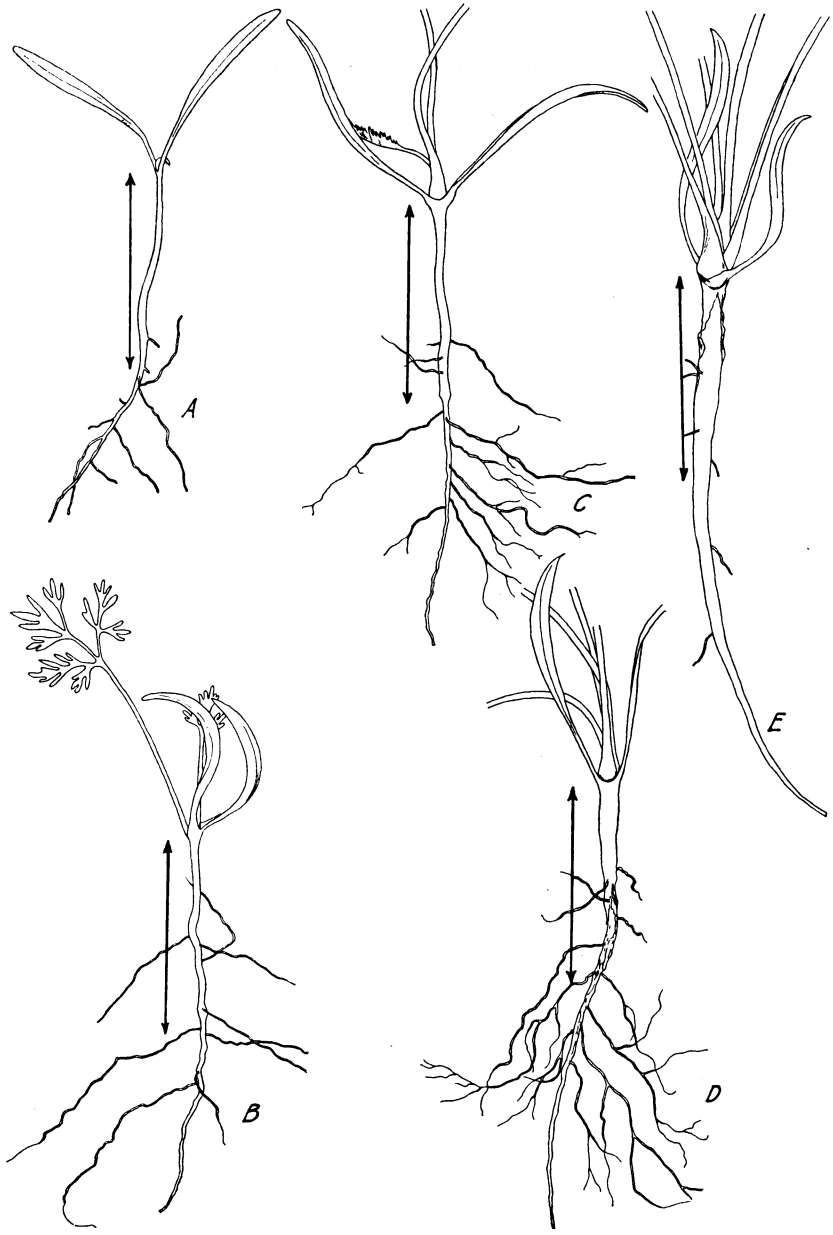

Fig. 1.—Carrot plants in successive stages of development collected the following number of days after the seed had been sown: *A*, 11; *B*, 18; *C*, 25; *D*, 32; *E*, 39. The seedlings were up in four days. The larger foliage leaves have been removed in *C–E;* the lateral roots in *E;* the thin portion of the taproot in all plants. *D* shows the beginning of rupture of the cortex. In *E*, the root region has no cortex; the hypocotyl shows fragments of it. The arrows indicate the approximate length of the hypocotyl, which had ceased to elongate in these plants. (All × 1.)

Figures 3; 4; 5, *A–D;* 8, *A, C,* and *D;* 9; and 12, *A;* and plates 1 and 2 were prepared from sections of the seedlings that were grown in desiccators. For all other illustrations in the paper, the greenhouse plants were used.

EXTERNAL MORPHOLOGY

Before the foliage leaves appear, the young carrot plant shows a rather clear demarcation between the taproot and the hypocotyl. The latter bears no lateral roots at first and is thicker than the root. The epidermis of the root has root hairs, structures that do not appear on the hypocotyl. Sometimes the change in thickness from the hypocotyl to the root is very abrupt (fig. 1, *C*). Above, the hypocotyl gradually merges with the cotyledons whose bases are united (fig. 1, *C*, and plate 7, *A*.) When the axis bearing the rosette of leaves develops from the plumule enclosed between the cotyledons, the bases of the latter are greatly stretched (plate 7, *B*).

The lateral roots are arranged in four longitudinal rows. They appear first at the base of the root—that is, just below the hypocotyl—and then develop toward the root apex. Later they also arise on the hypocotyl, first at its base (fig. 1, *A*), then acropetally toward the cotyledons (figs. 1, *B–E,* and 2). The lateral roots remain thin.

With the development of the lateral roots and with the increase in thickness of the hypocotyl and the taproot, the external distinction between the two regions is gradually effaced until they merge into one elongated tapering structure (figs. 1, *E,* and 2). In the mature state the hypocotyl makes up about 1 inch of the upper part of the fleshy organ, although its length varies somewhat with the depth of planting of the seed and certain other environmental conditions. The lower part of the storage organ is derived from the taproot (figs. 1 and 2).

The increase in thickness of the root and the hypocotyl results in the loss of the cortex. The rupture of this layer occurs first at the base of the root, then advances toward the apex of the root and acropetally in the hypocotyl (fig. 1, *D* and *E*). Thus the deterioration of the cortex proceeds in the same direction as the development of the lateral roots. In older storage organs the cortex is entirely absent (fig. 2, *B–D*) and the surface is covered with a periderm which bears horizontal grooves at the base of each lateral root (fig. 2, *D*).

The characteristic orange color appears after the loss of the cortex, approximately at the stage shown in figure 1, *E*. It is evident first in the root portion of the storage organ and later becomes evident in the hypocotyl.

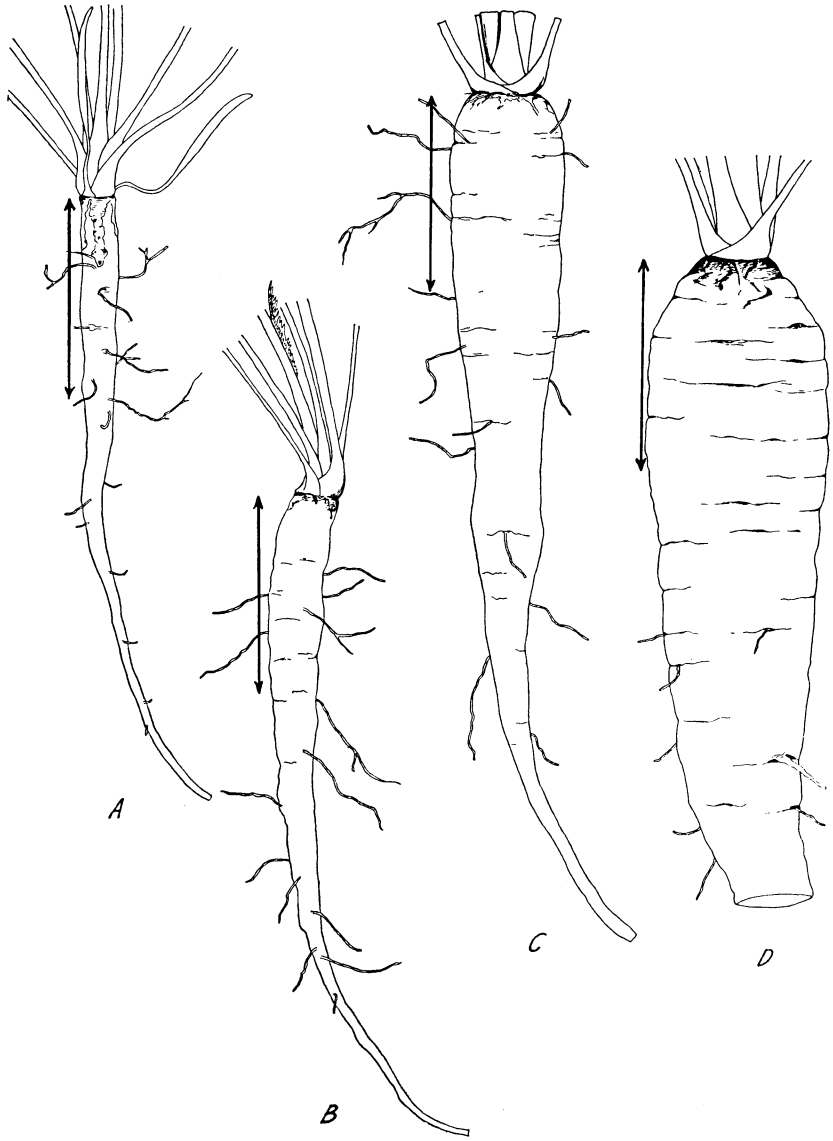

Fig. 2.—Carrot plants in successive stages of development, showing increase in size of the fleshy hypocotyl and root. The plants were collected the following number of days after the seed had been sown: *A*, 46; *B*, 53; *C*, 60; *D*, 67. The lateral roots, the thin portion of the taproot, and the leaves have been removed in all plants. The cotyledons and fragments of the cortex of the hypocotyl are present in *A*. In the other plants the cotyledons and the cortex are absent. The arrows indicate the approximate length of the hypocotyl. (All × 1.)

ONTOGENY OF THE PRIMARY ROOT

The root tip of the seedling is composed of four regions: the meristematic stele, the meristematic cortex, the meristematic epidermis, and the rootcap (fig. 3, *A*, *B*, and *F*). Though a detailed study of the apical meristems was not intended in this investigation, an examination of several root tips of seedlings has indicated that the apex lacks a clear-cut differentiation into the initials of the stele, the cortex, and the epidermis. The cells at the apex of the central cylinder appear to be continuous with the longitudinal rows of the rootcap cells (fig. 3, *A*), as if the stele and the central portion of the rootcap were derived from the same initials. Transverse sections give a similar picture. The dividing cell in the stele in figure 3, *F*, is apparently cutting off one cell toward the stele, the other (fig. 3, *E*) toward the rootcap. Judging from the presence of starch grains, the section in figure 3, *E*, is part of the rootcap. The cortex and the epidermis have a common origin with the peripheral portion of the rootcap. Nearer the center of the cap certain initials give rise to cortical and rootcap cells by alternating anticlinal and obliquely periclinal divisions. On the periphery the rootcap cells are formed by periclinal divisions in the epidermis (fig. 3, *A*).

The rootcap characteristically contains starch grains (fig. 3, *C* and *D*), which become evident immediately adjacent to the apical initials (fig. 3, *E*). The dead peripheral rootcap cells, on the other hand, lack starch and have somewhat thick walls (fig. 3, *C*).

The cortex is increased in thickness, usually from two to four or five cells, by periclinal divisions of the innermost layer of cells (figs. 3, *A*, *B*, and *F*, and 4, *C*, *E*). The first of these divisions occurs just behind the apical initials (fig. 3, *A* and *F*). After the last division the layer next to the stele differentiates into an endodermis (fig. 5, *B*). The Casparian strips appear in the endodermal cells after the differentiation of the first sieve tubes and shortly before the maturation of the first vessels. The strips, which are rather narrow, occur on the radial and the transverse walls near the inner tangential wall.

Whereas the youngest cortical cells are approximately isodiametric (fig. 3, *F*), the older ones are tangentially elongated (figs. 4, *E*, and 5, *A*; plates 1 and 2, *A*). At first the epidermal cells show radial elongation (fig. 5, *A*, and plate 1); later their tangential diameters increase somewhat (plate 2). (The poor fixation usually obtained in the elongating region of the root has caused the distortion of the cell shape in plate 2, *B*.)

The cortical intercellular spaces first appear between the second and the third layers from the epidermis (plate 1). Later they spread inward

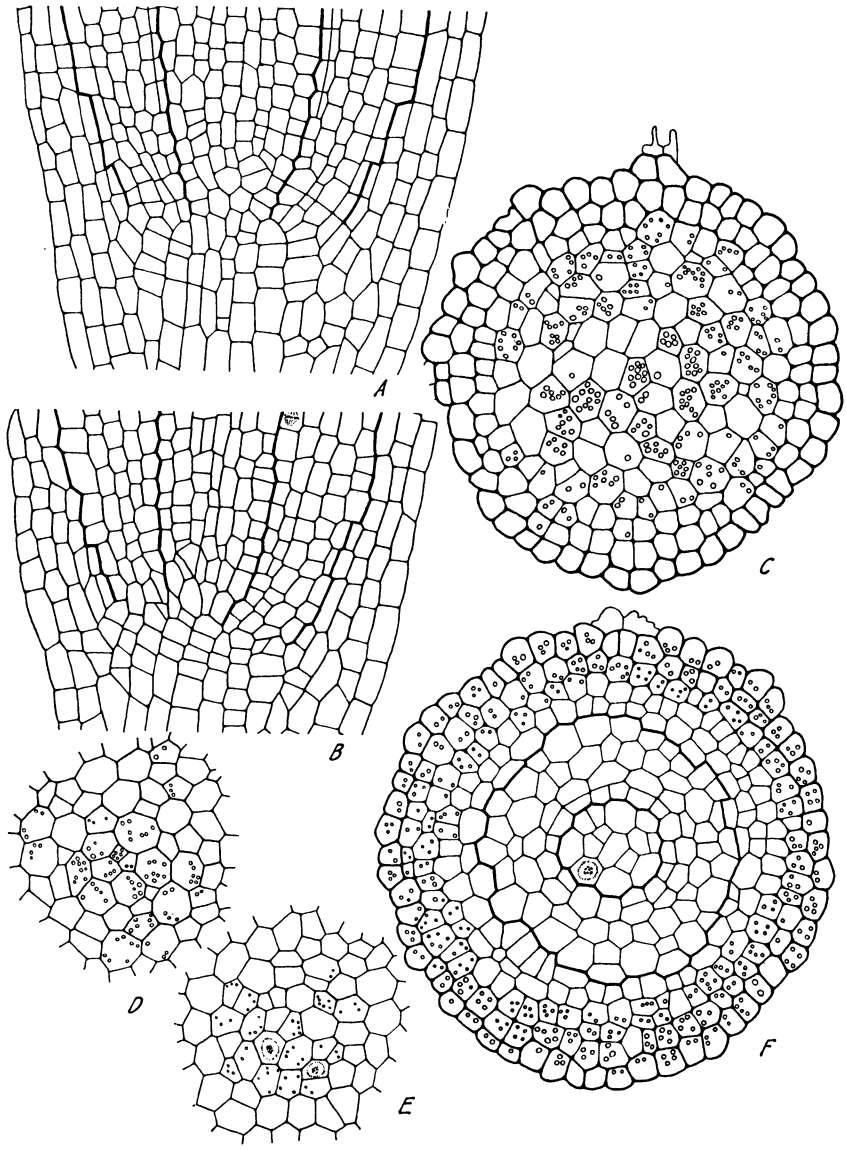

Fig. 3.—Structure of the root apex of a seedling. *A* and *B*, Longitudinal sections showing the region of apical initials. *A* is the median section; *B* is 10 microns away from *A*. The heavy lines indicate the limits of the central cylinder and the cortex jointly with the epidermis. Rootcap cells appear right and left and below in each drawing. *C–F*, Successive transverse sections of the root apex. *D* and *E* show only the central portions of the sections. *C–E* represent the rootcap region; *F*, the region of apical initials. The small circles in *C–F* represent starch grains. The heavy lines in *F* delimit the stele, the cortex, jointly with the epidermis, and the rootcap. (All × 372.)

(plate 2) and outward in the cortex, but do not develop between the epidermal and the subepidermal layers (fig. 5, *B*, and plate 3, *A*).

The stele is clearly set off from the cortex just behind the terminal

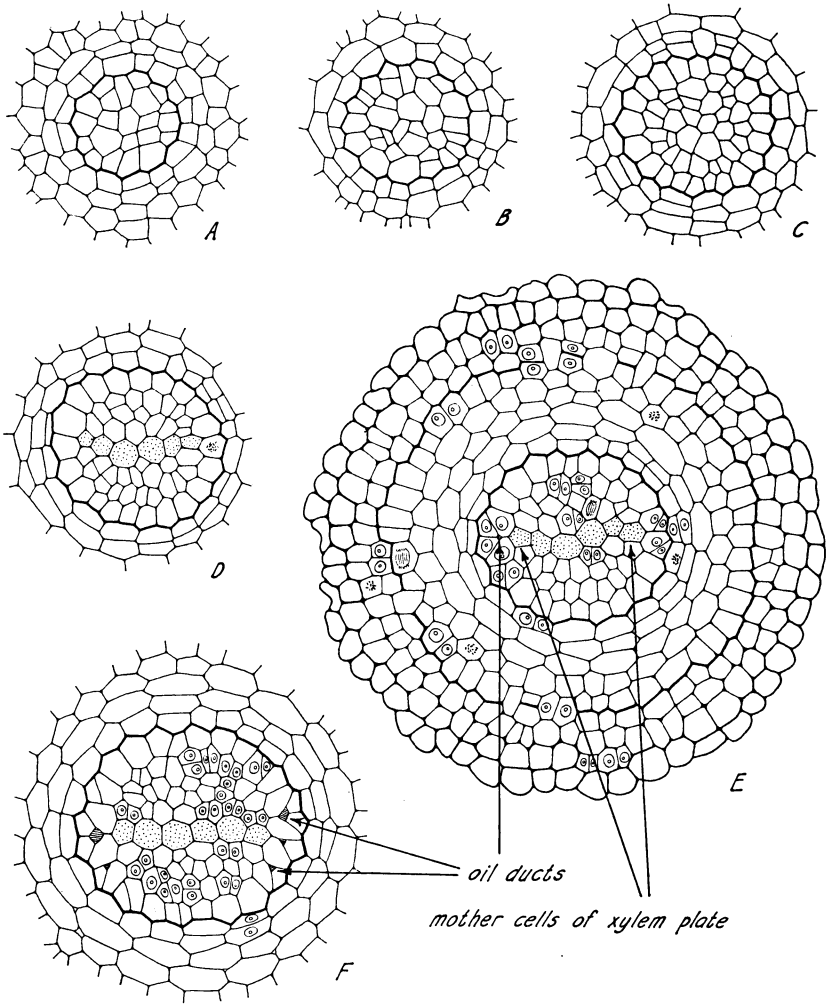

Fig. 4.—Successive transverse sections of root apex continuing the series shown in figure 3, *C–F*. *A–D*, and *F* show only the central portions of the sections. The oil ducts in *E* and *F* are in the pericycle. The heavy lines indicate the limits of the stele and of the cortex jointly with the epidermis. (All × 372.)

meristem (fig. 3, *A* and *F*). Within the stele the first region to become individualized is the pericycle (fig. 4, *C*). In longitudinal sections this layer may appear to be entirely independent; but in transverse sections

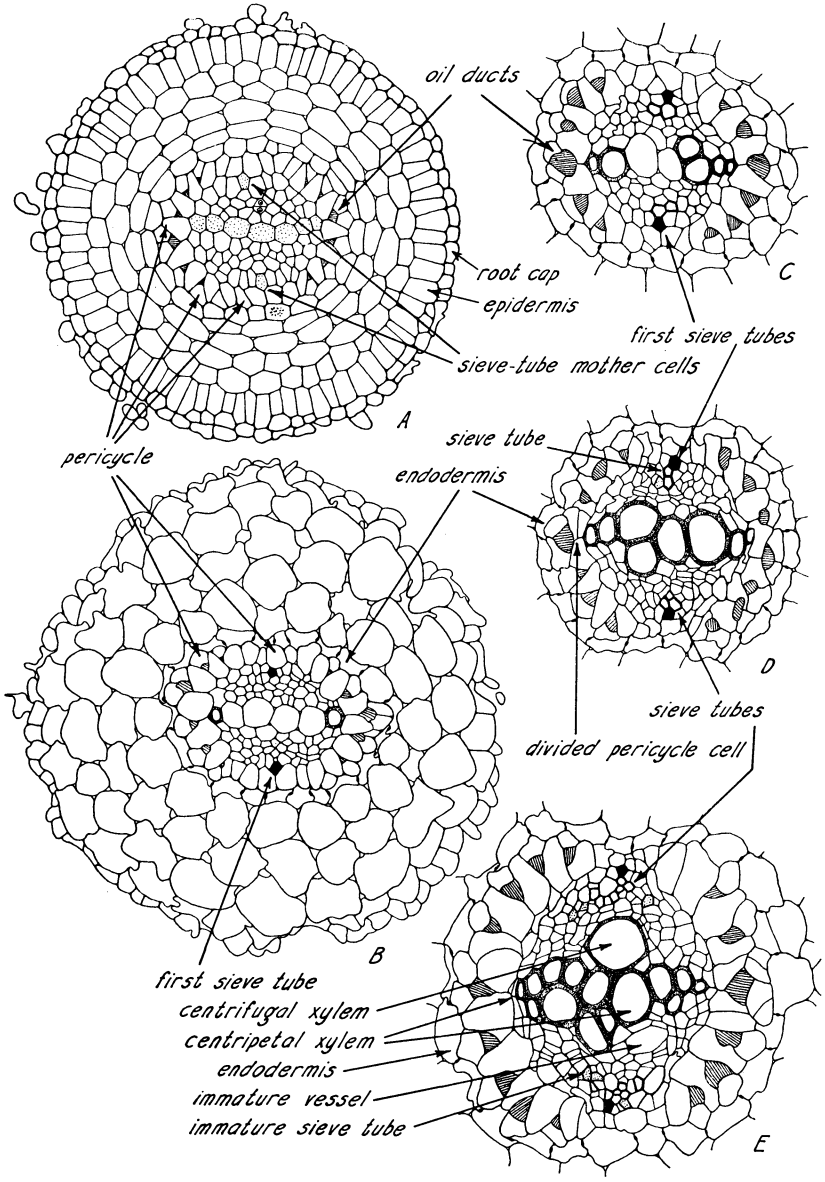

Fig. 5.—Transverse sections of young taproots in different stages of development. *C–E* depict only the central portions of the sections. *A–C* complete the series of transverse sections shown in figures 3 and 4. *D* and *E* were taken from older plants, the one used in *E* being comparable with the plant in figure 1, *A*. Some of the immature vascular elements are indicated by stippling; the pericyclic oil ducts by hatching. The first two sieve tubes are shown in black. (All × 256.)

it is not clearly outlined at first (figs. 3, *F*, and 4, *A*, *B*). It becomes distinct about 20 microns from the apex of the root (fig. 4, *C*). Twenty microns farther the pericycle undergoes a series of oblique longitudinal divisions (fig. 4, *E*). The resulting cells form a characteristic pattern, with intercellular spaces—the pericyclic oil ducts—appearing at the junction of the oblique and the radial walls (figs. 4, *E* and *F*, 5, *A* and *B*; and plates 1, 2, and 3). Oil ducts traverse the pericycle horizontally as well as vertically (plate 9, *A*) and continue into the cotyledons (plate 8).

After the delimitation of the pericycle, the cells in the interior of the stele continue to divide (fig. 4, *C*). About 30 microns from the apex, a median row of cells becomes conspicuous because of the enlargement and vacuolation of its components. These are the vessel mother cells of the future xylem plate (fig. 4, *D*, and plate 1, *A*). Enlargement and vacuolation begin in the middle of the plate, then spread toward the cells next to the pericycle (plates 1 and 2). The outermost cells of the plate are, however, the first to mature into xylem elements (fig. 5, *B*). They do not attain as large a size as the cells in the center. Usually the xylem plate is complete from pericycle to pericycle as soon as it becomes evident. It does not, however, remain a one-celled row, since other laterally adjacent cells also enlarge, vacuolate, and later differentiate into xylem elements (fig. 5, *C* and *D*).

The cells enclosed between the primordial xylem plate and the pericycle on both sides of the plate continue to divide in all planes (fig. 4, *E* and *F*). About 200 microns from the apex of the root, the mother cells of the first two sieve tubes are perceptible in the median peripheral positions in these two areas (fig. 5, *A*, and plate 1, *A*); and the organization of the stele is definitely established. This region now contains a primordial diarch xylem plate reaching from pericycle to pericycle; two sieve-tube mother cells located opposite each other and next to the pericycle, in a plane at an angle of 90° to the xylem plate; and a pericycle, which is one-layered opposite the future protophloem but double-layered elsewhere. The pericycle has oil ducts arranged in two arcs, each with the central duct usually located opposite one of the future protoxylem points.

Below the region where the vascular elements mature, the longitudinal cell divisions are more numerous in the stele than in the cortex. The cells of the latter become, therefore, considerably larger, in transverse sections, than the stelar components. Within the stele itself the pericycle and the xylem cells attain larger transverse diameters than the cells in the phloem region (fig. 5, *A* and *B*, and plates 1 and 2).

The two sieve-tube mother cells are the first among the vascular ele-

ments to reach maturity. They elongate and lose their nuclei (fig. 12, *A*); their cytoplasm vacuolates and becomes definitely parietal. About 300 microns from the apex of the root the two protophloem sieve tubes are fully differentiated. Although these elements have plastids, their contents are otherwise as clear as those of the pericyclic oil ducts (fig. 12, *A*, and plate 1, *B*). Their transverse walls bear sieve plates, and the longitudinal ones show thickening layers—the *nacré walls.* (See review by Esau, 1939.) As the elements further elongate, these walls become thinner. In figure 12, *A*, only two cells show the nacré walls; the other mature elements have rather thin ones.

Since their mother cells rarely divide by longitudinal walls, the two protophloem sieve tubes have usually no companion cells. The series of cells shown in figure 12, *A*, could be followed almost to the apex of the root; but among the twenty-four cells in the series, only one was divided longitudinally. At higher levels several more sieve tubes, also lacking companion cells, differentiate centripetally with respect to the first two phloem elements (fig. 5, *C* and *D*). Shortly before the end of the primary growth, sieve tubes with companion cells appear.

The first two protoxylem elements mature after the first two sieve tubes. In the same seedlings where the first phloem cells have matured about 300 microns from the terminal meristem, the vessels begin to develop secondary walls at the 1-mm level and are fully differentiated 2 millimeters from the apex—slightly below the root-hair region. Like the first sieve tubes, the first xylem elements lie next to the pericycle (fig. 5, *B*). The points in a cross section of a stele at which xylem and phloem elements first mature are sometimes conveniently called the *protoxylem* and the *protophloem* poles, respectively.

The subsequent xylem elements develop centripetally with respect to the first two (fig. 5, *C, D,* and plate 3, *B*). After the differentiation of the centripetal xylem, a few more elements appear centrifugally in relation to the diarch xylem plate (fig. 5, *E*). These are not yet derived from the cambium but lie in line with the future secondary vessels. As is usual with the primary xylem of roots, the diarch plate consists of annular, spiral, scalariform, and reticulate vessels.

The first xylem having annular and spiral elements and lying near the pericycle is commonly called the *protoxylem;* the elements appearing later and in the center of the xylem plate, the *metaxylem.* The primary centrifugal xylem is also regarded as metaxylem. In conformity with the xylem, the phloem appearing first and nearest the pericycle is termed *protophloem.* It is followed by the *metaphloem* differentiating centripetally with respect to the protophloem.

With the development of the centrifugal xylem, the primary growth of the root is completed. Figure 5, *E*, depicts the structure of the stele and the endodermis at the beginning of the secondary growth. The cells between the xylem and the phloem show the first tangential cambial divisions. The pericycle cells opposite the protoxylem poles have split off daughter cells that later will give rise to cambial cells.

The first protoxylem elements and the first sieve tubes are obliterated at the beginning of the secondary growth—a process that occurs somewhat earlier in the hypocotyl than in the root.

The seedling completes the primary development of the base of the root and of the hypocotyl just before the leaves emerge from the plumule. The plant depicted in figure 1, *A*, shows early stages of secondary growth.

THE TRANSITION REGION

The transition from the root to the stem structure is very gradual and occurs through most of the hypocotyl. The branching of the primary xylem plate in the formation of the cotyledonary traces[4] is, however, rather abrupt (plate 8); and the change from the exarch to the endarch xylem occurs in the cotyledons. The hypocotyl therefore resembles the root rather than the stem in its internal structure. As was earlier pointed out, the hypocotyl resembles the root also in external morphology.

The beginning of transition is indicated in the vascular tissues by the change in the arrangement of the elements. In the root the first sieve tubes form compact clusters; in the transition region they are somewhat dispersed among parenchyma cells. In the root the succeeding sieve tubes develop centripetally with respect to the first (fig. 5, *C–E*); in the hypocotyl they appear laterally from the protophloem poles (figs. 6, *A–C*, and 8, *A*). In the root the first protophloem sieve tubes lie next to the pericycle; in the hypocotyl they are separated by parenchyma from the pericycle (fig. 6, *C*).

In later stages of the primary development and during secondary growth in transition region, the lateral spread of the oldest phloem becomes less obvious because numerous sieve tubes differentiate centripetally with regard to the first (fig. 8, *B*).

The xylem of the hypocotyl differs from that of the root in the occurrence of parenchyma between the protoxylem and the pericycle in the former (fig. 6 and plate 3). This characteristic appears at the base of the hypocotyl. Somewhat higher, the order of vessel development is also

[4] The term *trace* is applied here to each individual bundle that connects the leaf with the stem and hypocotyl.

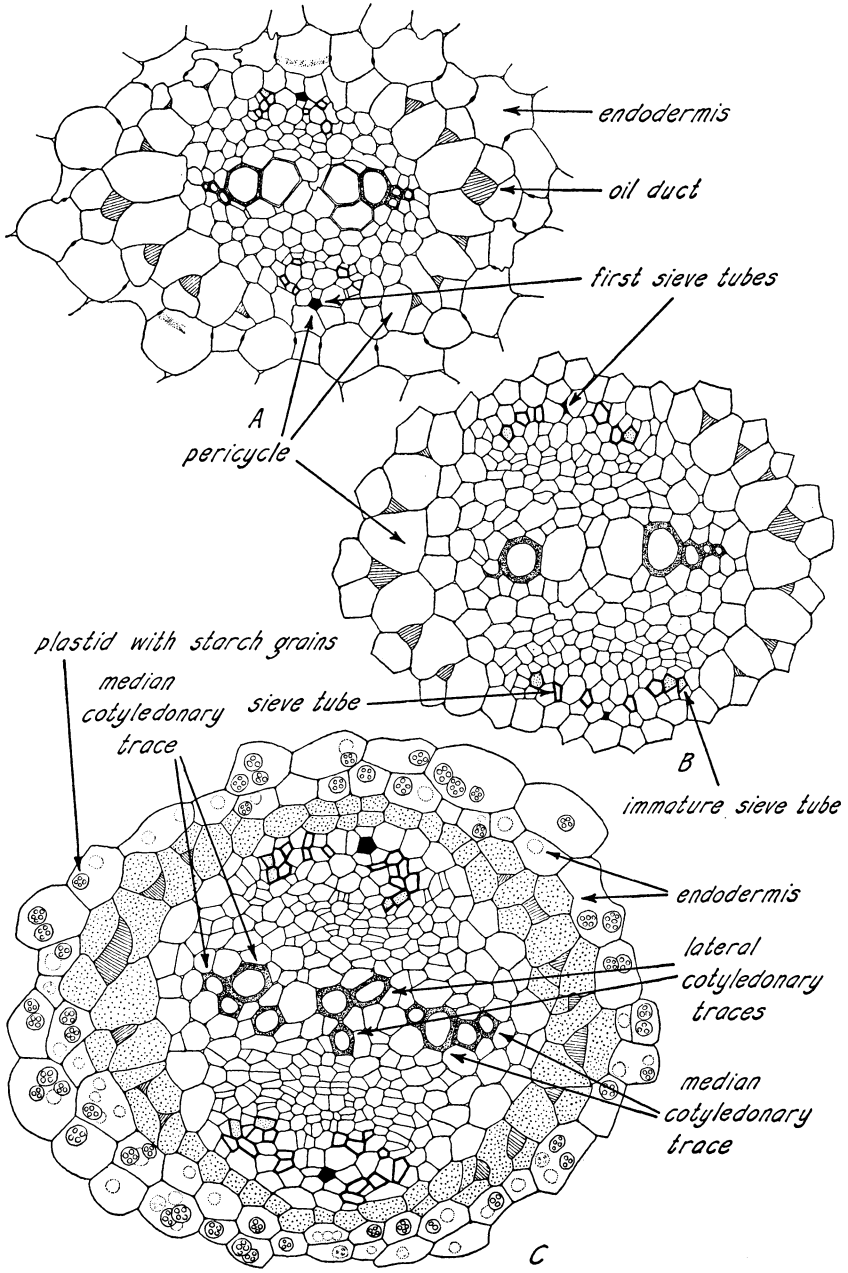

Fig. 6.—Successive transverse sections of a hypocotyl, showing the beginning of transition from root to stem structure. *A* is nearest the root base; *C*, farthest away. Details are as in figure 5 except that the pericycle cells are stippled in *C*. The plant was sampled four days after the seed had been sown. (*A*, × 269; *B* and *C*, × 400.)

modified. At first the xylem differentiates centripetally from two points as in the root. Then some elements mature in the middle of the plate so that the latter appears broken up into three bundles (fig. 6, *C*). Some of the cells separating the bundles are parenchyma; others are vessel mother cells. When the latter mature, the xylem appears as one strand (fig. 8, *A* and *B*).

The successively higher levels of the hypocotyl show an increasing parenchymatization of the xylem. Whereas in the root the xylem plate consists of vessels only (fig. 5, *E*), in the upper transition region it encloses considerable parenchyma (fig. 8, *B*).

Below the insertion of the cotyledons the xylem is represented by two large and three small groups of vessels (fig. 7, *C*). The large groups are the median cotyledonary traces; the small ones contain the first xylem elements of the lateral cotyledonary traces. One of these small groups gives, at higher levels, two branches, so that altogether four lateral traces are formed, two for each cotyledon (fig. 7, *D*, and plate 7). The median traces of the cotyledons are continuous with the protoxylem poles of the root, showing a centripetal order of differentiation for some distance within the cotyledons. The lateral traces are branches of the central portion of the xylem plate. In the early stages of development this portion appears, in the lower hypocotyl, as a separate bundle (fig. 6, *C*). The lateral traces show centrifugal xylem differentiation throughout their extent. At successively higher levels all these traces differentiate somewhat more obliquely and farther away from the center of the axis, where cells mature into the parenchyma of the pith (fig. 7, *C*, and plate 8).

The phloem also develops at an increasingly greater distance from the center and, at the same time, continues to spread laterally from the protophloem poles. Just below the level where the xylem forms the cotyledonary traces, the first two sieve tubes disappear as such (fig. 7, *C*). However, these elements form connections with the sieve tubes differentiating to the right and to the left of them (fig. 7, *A* and *B*).

Whereas the xylem differentiates in six bundles at the base of the cotyledons, the phloem forms eight strands. The median traces of the cotyledons have each two strands of phloem flanking the xylem on two sides; the lateral traces are collateral bundles, each with one strand of xylem and one of phloem (fig. 7, *D*, and plate 7).

In the upper hypocotyl the pericycle does not form a continuous layer as in the root. Like the vascular elements, the oil ducts differentiate farther away from the center of the axis and also somewhat obliquely. Moreover, their number is reduced so that two or three ducts below are

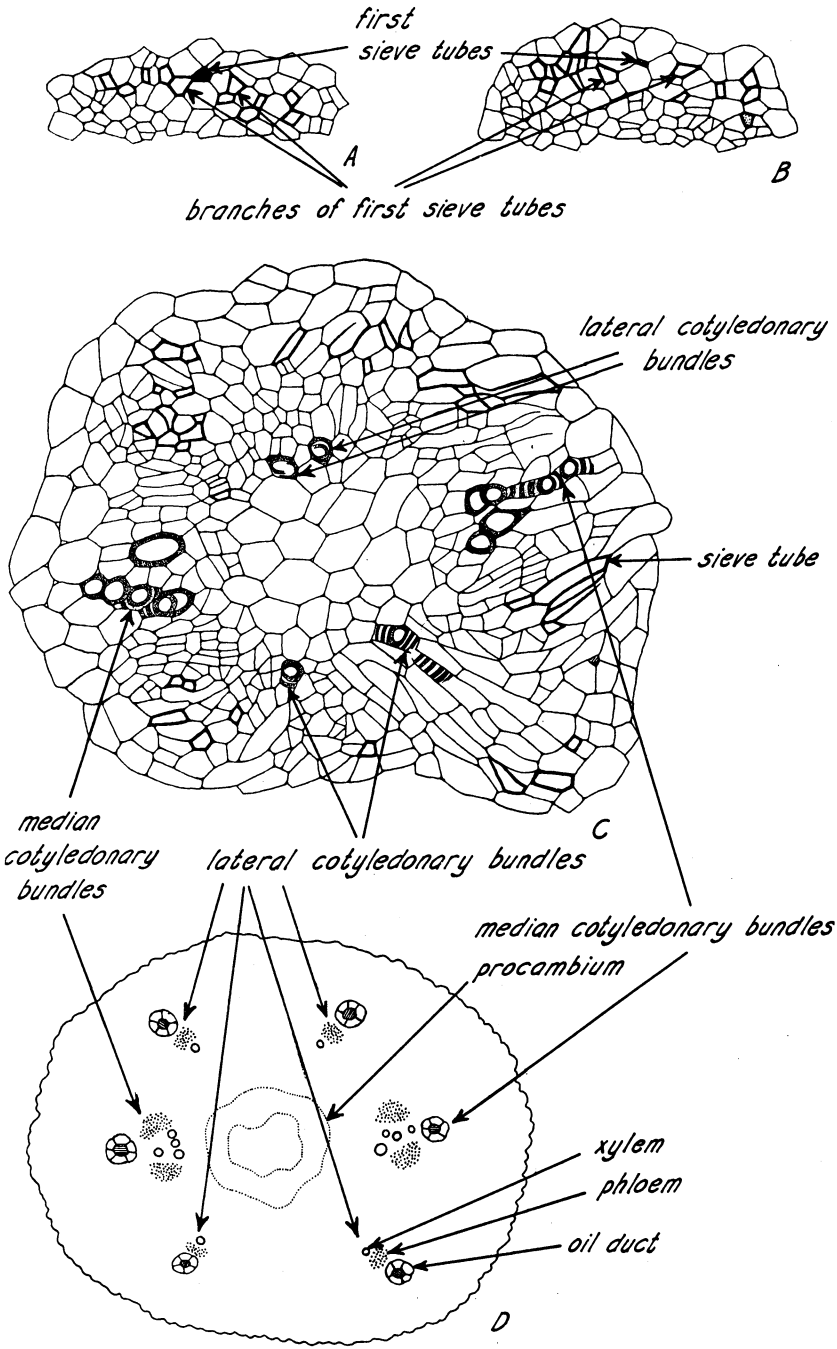

Fig. 7.—Successive transverse sections of the hypocotyl of the same plant as in figure 6. *A, B,* Details of branching of phloem in the transition region. *C,* Reorientation of the vascular tissues in the formation of the cotyledonary traces. *D,* Fused bases of cotyledons enclosing the procambium cylinder of the plumule. Compare with plates 6 and 7. (*A–C,* × 400; *D,* × 134.)

connected with one above. At the base of the cotyledons two groups of three ducts differentiate (fig. 7, *D*) instead of two groups of six to nine ducts as in the root and lower hypocotyl (figs. 5 and 6). These ducts occur on the abaxial sides of the cotyledonary bundles (fig. 7, *D*, and plate 7, *A*). As seen in transverse sections the secretory cells lining the ducts are more numerous in the cotyledons than in the root. In the latter, three or four cells surround the oil cavity (fig. 5); in the cotyledons, five or six (fig. 7, *D*). In the foliage leaves, the structure of the oil ducts is the same as in the cotyledons. Since the cells between the ducts do not differ from other parenchyma cells surrounding the cotyledonary bundles, the pericycle appears to consist of the individual oil ducts with their secretory cells (plate 7, *A*).

In contrast to the lower hypocotyl (fig. 6, *A*) and the root (plate 3, *B*), the endodermis of the upper hypocotyl is characterized by starch accumulation (fig. 6, *C*, and plate 3, *A*). The lowermost starch-containing endodermal cells also have Casparian strips, structures that do not differentiate at the higher levels. Within the cotyledons no specialized endodermis is evident (plate 7, *A*).

Although starch appears also in the cortex of the hypocotyl, it is less prominent there than in the endodermis (plate 3, *A*). The epidermis of the upper hypocotyl has stomata.

The primary vascular tissues of the root are continuous with the traces of the cotyledons. The foliage leaves differentiate after the initiation of secondary growth in the root, forming direct connection with the products of the cambium and perhaps also with the small amount of centrifugal primary xylem.

At first the vascular tissues of the cotyledons appear much more prominent than those of the foliage leaves. Later, because of the secondary growth, the leaf traces develop to a much larger size than the entirely primary cotyledonary strands (plates 6 and 7).

Above the insertion of the cotyledons in very young seedlings, the procambium of the foliage leaves forms an uneven ring within the circle of the cotyledonary bundles (fig. 7, *D*). At lower levels, where the traces of the cotyledons appear nearer the center of the axis, this procambium and later the leaf traces occur in strands among the cotyledonary traces (plate 6, *B*). Still lower the cotyledonary vascular supply appears imbedded in the xylem of the leaf traces (plate 6, *A*).

Two of the lateral bundles of the cotyledons become discrete near the center of the hypocotyl (fig. 7, *C*, below, and plate 6, *B*, left). The other two are united for some distance, then separate (fig. 7, *C*, above, and plate 6, *B*, right). The pair of separate lateral cotyledonary strands

occurs among the traces of the second foliage leaf; the united pair between those of the first leaf (plate 6, *B*).

ORIGIN OF THE LATERAL ROOTS

In the primary body the lateral roots are initiated in the pericycle to the right and to the left of the protophloem poles, making an angle of about

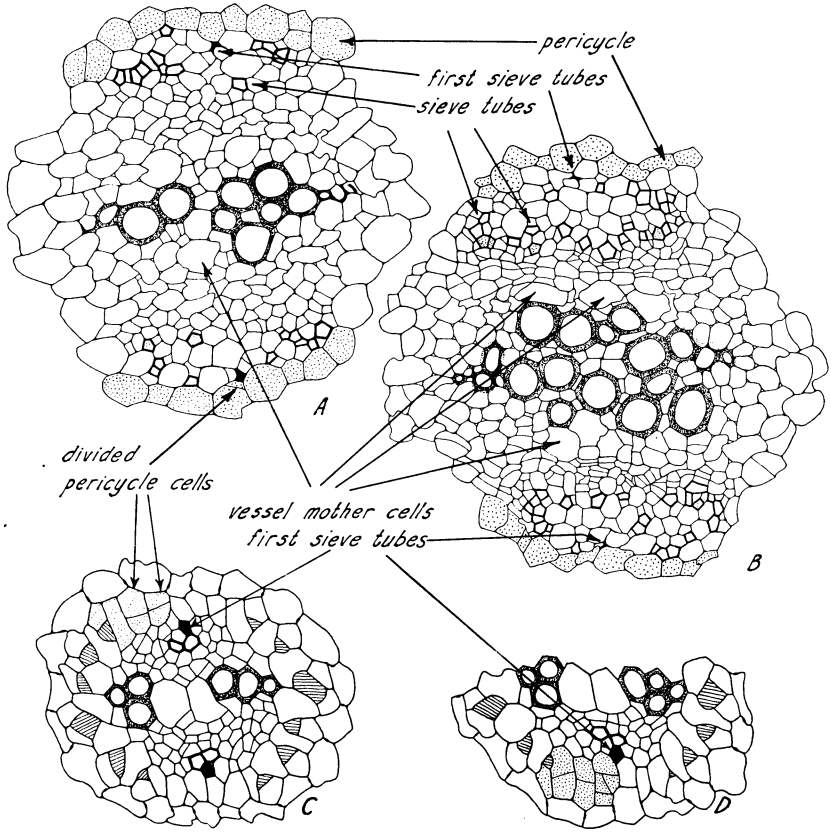

Fig. 8.—*A*, *B*, Transverse sections of the lower transition region, showing two stages of development of vascular tissues. *B* was taken from the lower hypocotyl of a plant similar in size to that in figure 1, *A*; *A*, from a younger plant. *C*, *D*, Transverse sections of a root of a seedling, showing initiation of lateral roots. In *C* two pericycle cells have divided by periclinal walls; in *D* three cells, one of which is a secretory cell of an oil duct. In *A* and *B*, all pericycle cells shown are stippled; in *C* and *D* only those that were concerned with lateral-root formation and showed very dense protoplasts. Other details as in figure 5. (*A*, × 421; *B–D*, × 283.)

45° with the xylem plate. There are, accordingly, four points of origin of lateral roots, two on each side of each phloem strand.

As seen in transverse sections, one or two pericycle cells to the right

or left from the first sieve tube undergo periclinal divisions (fig. 8, *C*, two of the stippled cells). Soon the secretory cells of the nearest oil duct undergo similar divisions (fig. 8, *D*); then those of the ducts that are farther removed. The divisions may spread to the median oil duct lying opposite the nearest protoxylem pole, the oil ducts being obliterated in the process (fig. 10, *A*). The cells participating in the divisions have densely staining protoplasts.

In longitudinal sections also, divisions are initiated in two or three cells and then spread to the adjacent ones. At first the cells divide transversely; then they elongate radially and divide periclinally (fig. 9, *A* and *B*); later, more periclinal and anticlinal divisions occur (fig. 9, *C*).

The endodermis remains intact until the lateral emerges on the surface of the main root. It shows dense protoplasts over the area of dividing pericycle cells, eventually forms anticlinal walls, and thus keeps pace with the growth of lateral root (fig. 9, *B* and *C*). The first new walls in the endodermis sometimes develop Casparian strips, structures not formed in the later divisions. The parenchyma of the cortex is destroyed in front of the advancing primordial root (fig. 9, *C*).

Before the lateral root emerges on the surface of the main root, the derivatives of the endodermis become stretched—a process most pronounced at the base of the lateral organ (fig. 10, *A*, above), where eventually the endodermal cells are torn apart. Although the emerging lateral carries the upper portion of the endodermis to the surface, these cells soon die off. They may begin to disintegrate while the lateral is still imbedded in the cortex of the main root (fig. 10, *A*, cells indicated by cross hatching).

The main part of the lateral root consists of the derivatives of the pericyclic cells. These are organized into a stele, a cortex, and a rootcap before the root emerges on the surface (fig. 10, *A*). As in the taproot of the seedling, the epidermis and the cortex appear to merge with the rootcap. The stele, which is clearly outlined, seems independent of the other root regions (fig. 10, *A*). As in the taproot, the cortex increases in thickness by periclinal divisions (fig. 10, *A*); and the endodermis differentiates in the last and innermost products of these divisions. The Casparian strips are evident before the lateral root breaks through to the surface. The new endodermis is connected with the endodermis of the main root through cells at the base of the lateral root. These cells develop Casparian strips before the endodermis develops in the lateral root proper (fig. 10, *A*, upper left).

The vascular tissues appear in the lateral after it has passed through the cortex of the mother root. The young root forms a connection, first

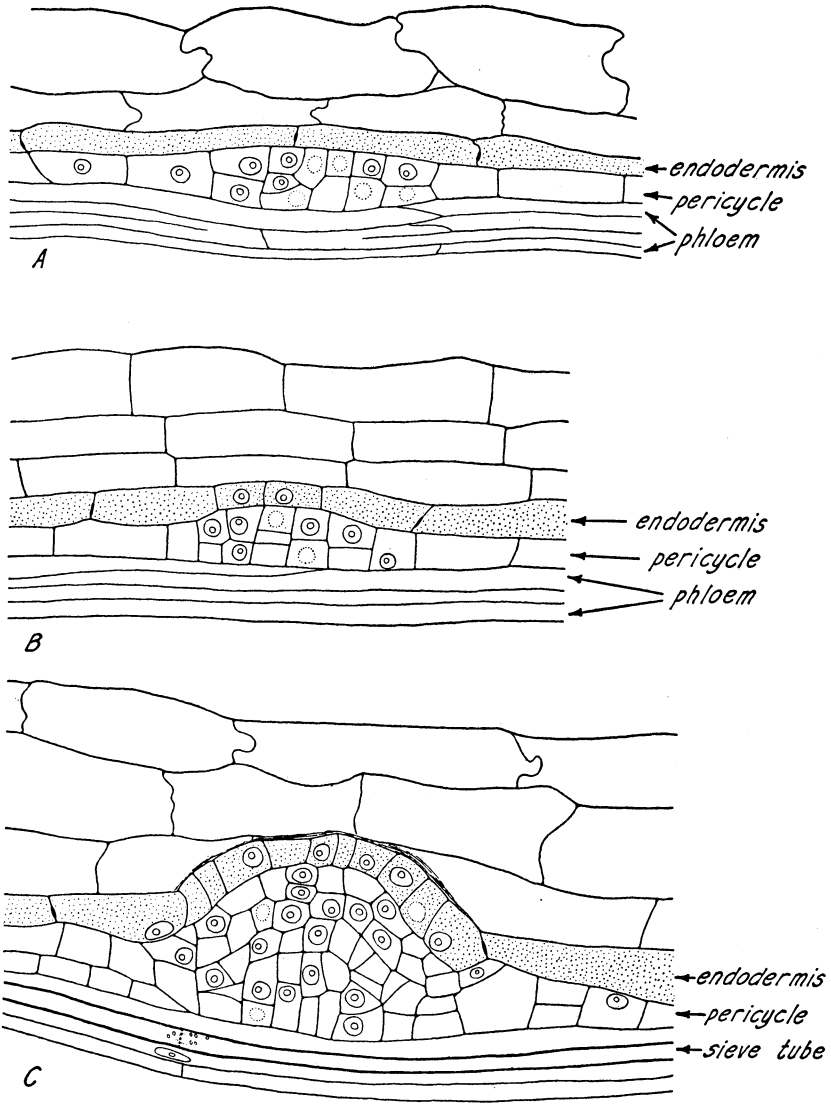

Fig. 9.—Three successive stages of development of a lateral root as seen in a longitudinal section of a young taproot. (All × 421.)

with one side of the primary xylem plate of the main root and with one phloem strand; later, when secondary growth occurs, also with the other phloem strand. Such is the orientation of the diarch xylem plate in the lateral that a line connecting the two protoxylem poles is more or less parallel with the long axis of the main root.

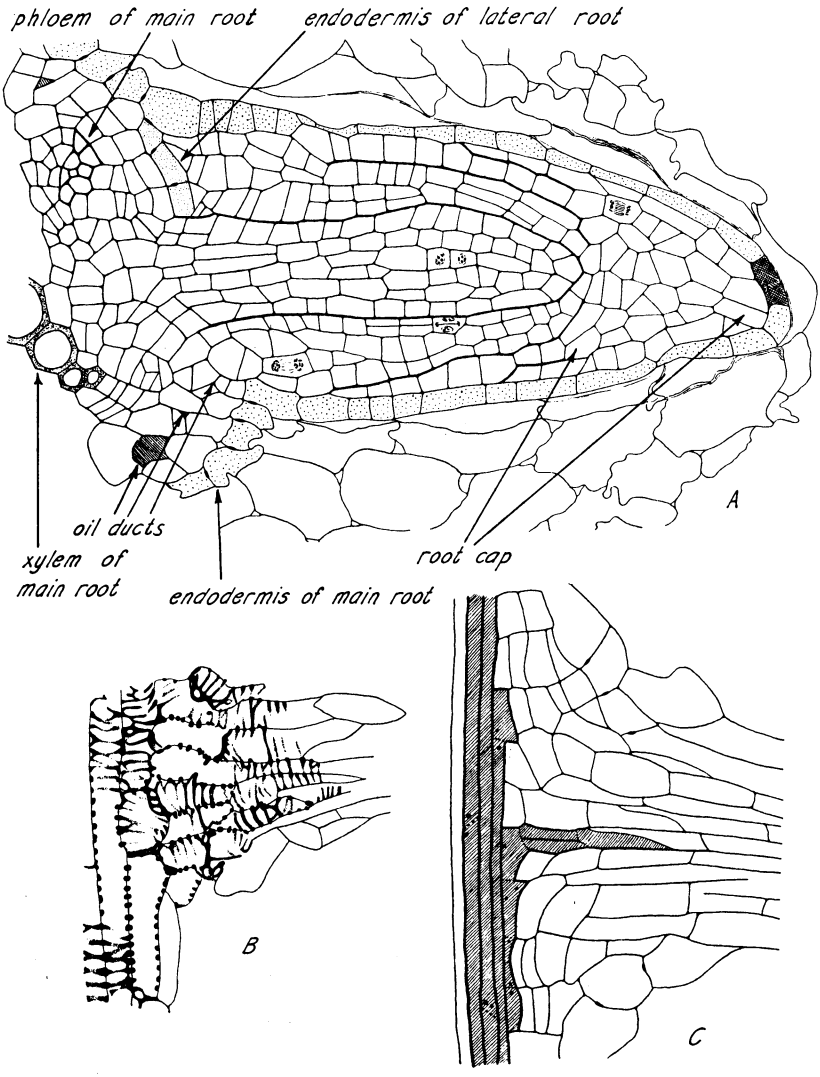

Fig. 10.—*A*, Lateral root just before emerging on the surface of the main root. A small amount of vascular tissues of the main root is seen in transverse section, at the left. The heavy lines indicate the probable limits of the plerome, the periblem, and the dermatogen. *B*, Xylem, and *C*, phloem, at the point of connection between the main and lateral roots. In *B* and *C* the vascular elements of the main root extend vertically to the left; those of the lateral roots are arranged horizontally to the right. The sieve tubes in *C* are indicated by hatching. (All × 380.)

The connection between the vascular tissues of the main and the lateral roots is formed through cells of pericyclic origin lying outside the protophloem and protoxylem of the main root. These are parenchyma cells of short diameters arranged like the derivatives of a cambium (fig. 10, *A* and *C*). Near the xylem they differentiate into scalariform tracheids and vessel elements (fig. 10, *B*), near the phloem, into sieve tubes (fig. 10, *C*) with which companion cells are associated.

Lateral roots continue to arise in the fleshy root and hypocotyl even after the cortex sloughs. At this time the lateral organs usually originate at the base of the older lateral roots from cells of pericyclic origin. They form vascular connections with the xylem and phloem of the main and the older lateral roots.

SECONDARY GROWTH IN THE ROOT AND THE HYPOCOTYL

The enlarged underground storage organ of the carrot plant is developed largely by secondary growth from the vascular cambium. As is usual in roots with secondary tissues, the periclinal cambial divisions first become evident between the xylem and phloem. Later they occur in the parenchyma outside the protoxylem, so that a complete cylinder of cambium is formed.

In the root region, where the protoxylem lies next to the pericycle, the cells of the latter divide before the secondary growth is initiated (fig. 5, *D*). Thus at the end of the primary growth some parenchyma occurs between the protoxylem and the secretory cells of the oil ducts (fig. 5, *E*). In the hypocotyl the conducting elements of the protoxylem do not differentiate next to the pericycle (figs. 6 and 8, *A* and *B*).

The amount of secondary vascular tissues produced by the cambium is greater in the upper than in the lower portion of the storage organ (plates 4 and 5). On the other hand, in the root the vessels tend to have larger diameters and are more compactly arranged than in the hypocotyl (plates 4 and 5). The change from one cell pattern to the other is, of course, gradual.

Except in the earlier stages of secondary growth (plate 4, *A*), the secondary xylem contains a large proportion of parenchyma (plates 5, *A*, and 11). In the hypocotyl considerable parenchyma occurs outside the protoxylem poles (plates 4, *A*, and 5, *A*). These islands of parenchyma cells are the first products of the cambium in this region. Later the cambium produces xylem and phloem, and the parenchyma becomes imbedded between the primary and secondary xylem. At the same time the vascular cylinder becomes continuous (plate 5, *A*). On the inside of the

primary phloem the cambium forms xylem as soon as the meristem begins to function (plate 4, *A*). Although secondary in origin, the vessel elements are scalariform and reticulate.

Besides the parenchyma of the longitudinal system, ray parenchyma occurs in the xylem. The rays, though not conspicuous in transverse sections (plate 11), are evident in longitudinal ones (plate 13). Tangential section through the cambium show the striking contrast between the ray and the fusiform initials (plate 9, *B*).

During the later stages of the secondary development, the parenchyma cells of the primary xylem enlarge and occasionally divide (plates 5, *A*, and 13, center). As a result of this growth the primary vessels become widely separated from each other and from the secondary vessels. During this process, there is also some crushing of the primary xylem. The dilation, very pronounced in the hypocotyl, gradually diminishes toward the apex of the fleshy root because there the xylem parenchyma is less abundant and the secondary growth less active. The occurrence of dilation makes it appear as though pith were present in the mature organ.

Like the xylem, the secondary phloem contains a large proportion of parenchyma (plate 11). The sieve tubes, companion cells, and phloem parenchyma occur in strands separated from each other by comparatively large parenchyma cells (plate 5). Anastomosing strands join the longitudinal bundles. The rays are just as inconspicuous in the phloem as in the xylem (plate 11). Oil ducts occur in the secondary phloem, with the secretory cells arranged in circles around the cavities.

The sieve tubes have companion cells, arranged in longitudinal series, which are shorter than the sieve-tube elements (fig. 12, *C* and *D*). The wall between a sieve tube and a companion cell is very thin, with no obvious pits (fig. 12, *B–D*). The parenchyma cells are connected by pit fields with each other and with the sieve tubes and the companion cells (figs 11, *C* and *D*, and 12, *B*). The immature sieve tubes have slime bodies, one spindle-shaped body in each element. The sieve-tube plastids contain starch that stains red with iodine. In the parenchyma cells ordinary starch occurs (plate 11).

The two strands of the primary phloem remain evident for a considerable time during the secondary growth (plates 4 and 5). The sieve tubes and the companion cells of this phloem are gradually obliterated, while the parenchyma cells enlarge and develop rather thick walls (plates 4, 5, and 10, *B*). Opposite the protoxylem poles, where no primary phloem is present, the secondary phloem is separated from the pericycle by parenchyma (plates 4 and 5). These cells arise from the cambium and, in the

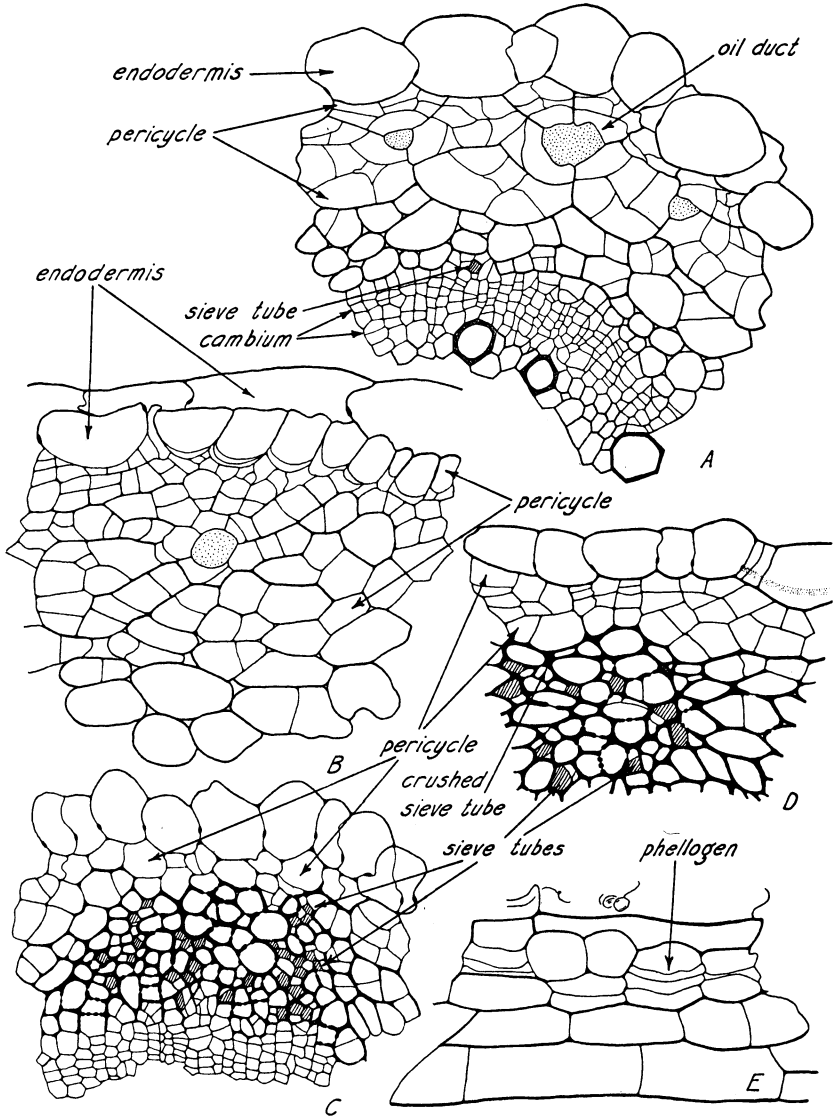

Fig. 11.—Secondary growth in the pericycle in transverse section of a hypocotyl before the rupture of the cortex. *A*, An earlier, *B*, a later stage of cell multiplication in the pericycle opposite the protoxylem. *C*, An earlier, *D*, a later stage of cell multiplication in the pericycle opposite the protophloem. *E*, Phellogen from the same hypocotyl region as in plate 14. *A* and *C* were taken from a plant similar in size to that in figure 1, *C*; *B* and *D*, as in 1, *D*; *E*, as in 2, *D*. The oil ducts are indicated by stippling; the sieve tubes by hatching. (All × 245.)

hypocotyl, also from the parenchyma originally present between the protoxylem and the pericycle.

The older secondary sieve tubes and their companion cells become functionless and are crushed. The remaining parenchyma cells elongate tangentially and divide anticlinally.

When the stele begins to enlarge through secondary growth, the cortex at first keeps pace with the increase in circumference of the organ by tangential stretching of cells and by occasional anticlinal divisions. The endoderms also shows divisions (fig. 11, *D*, and plate 4), the new walls frequently developing Casparian strips. Later the cortex, together with the endodermis, is ruptured and shed.

As was mentioned previously, the cortex sloughs first in the root, then in the hypocotyl (fig. 1, *D*, and plate 5). It persists longest on the sides along the primary phloem strands (plate 5, *A*).

When the cortex is lost, the periderm becomes the protective layer. As in most roots, this tissue layer arises in the pericycle. The secretory cells of an oil duct become subdivided into many cells, so that only a small portion of each cell remains associated with the duct (fig. 11, *A*). In shape and arrangement these new secretory cells (fig. 7, *D*) resemble the analogous cells in the secondary phloem and in the aerial parts of the plant. The first divisions of the original secretory cells occur in all planes (fig. 11, *A*) but eventually periclinal divisions predominate in the cells outside the oil ducts (fig. 11, *B*), and the groups of cells originating from one secretory cell form fan-shaped layers in cross sections (plates 5, *A*, and 10, *A*). In longitudinal sections these groups of cells appear in radial rows. Plates 9, *A*, and 12 show two stages of secondary growth in the pericycle in longitudinal sections. During the further expansion of the fleshy organ the fan-shaped arrangement is destroyed, while the cells elongate tangentially and divide radially. Toward the apex of the root, pericyclic divisions are less abundant than in the hypocotyl (plate 5).

Outside the primary phloem, where no oil ducts are present, secondary growth in the pericycle is less vigorous than elsewhere. The divisions begin here later than in the cells connected with the oil ducts (compare *A* and *C* of fig. 11) and are less numerous (compare *B* and *D* of fig. 11; *A* and *B* of plate 10). As a result of this comparatively sluggish growth, the surface of the rather young fleshy organ shows shallow grooves on the sides along the primary phloem strands (plate 5, *B*).

Periderm, defined as a tissue composed of the phellogen and its derivatives, arises in the superficial layers of the pericycle. Cells outside the oil ducts become orderly arranged because of successive periclinal divi-

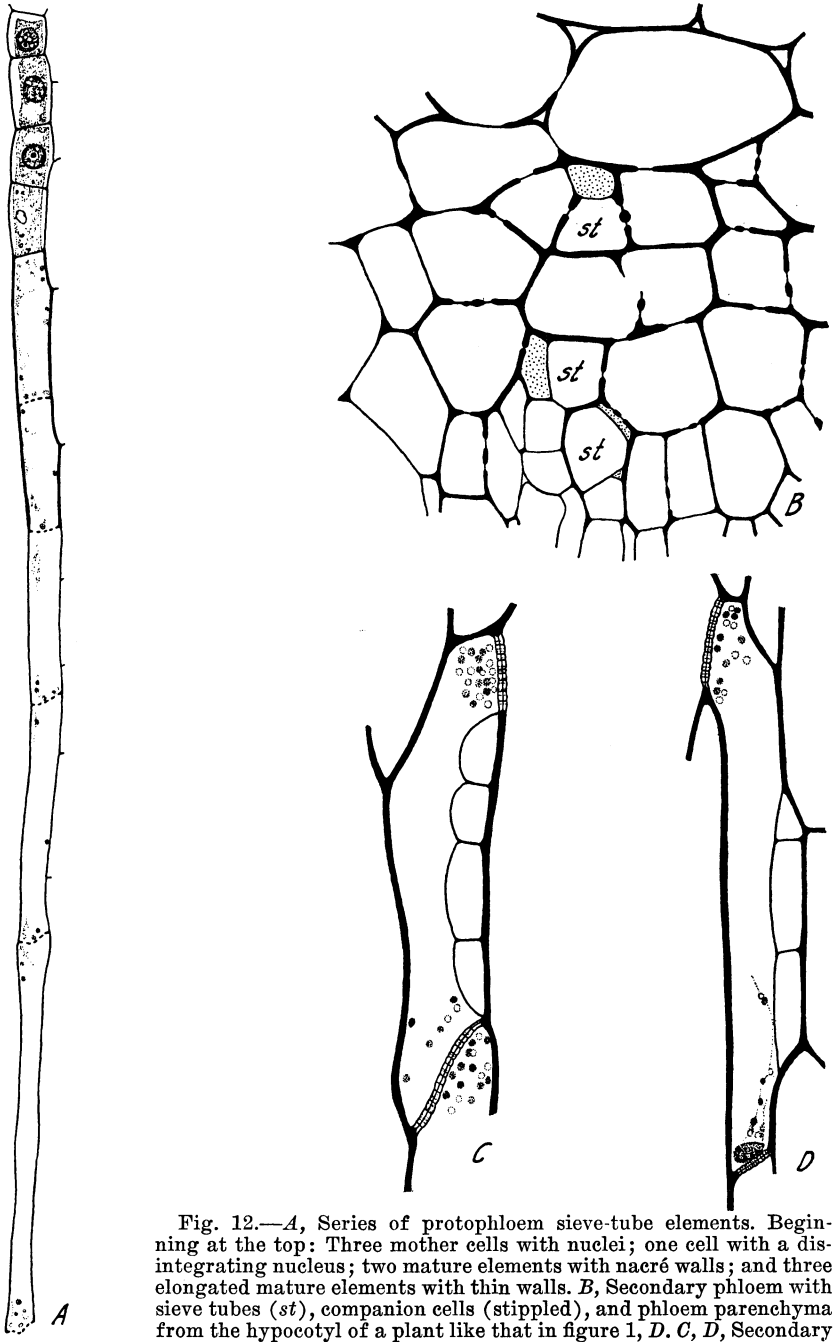

Fig. 12.—*A*, Series of protophloem sieve-tube elements. Beginning at the top: Three mother cells with nuclei; one cell with a disintegrating nucleus; two mature elements with nacré walls; and three elongated mature elements with thin walls. *B*, Secondary phloem with sieve tubes (*st*), companion cells (stippled), and phloem parenchyma from the hypocotyl of a plant like that in figure 1, *D*. *C*, *D*, Secondary sieve tubes with companion cells in tangential views. (*A* and *B*, ×605; *C* and *D*, × 472.)

sions (fig. 11, *E*, and plates 10 and 12). The outermost of these cells differentiate as cork cells, the innermost function as a cork cambium producing additional cork cells toward the periphery. Beneath the periderm are the oil ducts. These, because of the increase in circumference of the fleshy root and hypocotyl, become considerably removed from each other.

The phloem parenchyma remaining after the obliteration of the sieve tubes and companion cells, merges with the parenchyma of the pericycle lying centripetally from the oil ducts. The pericyclic cells, however, are somewhat smaller than those of the phloem (plates 12 and 13).

The pericycle, together with the periderm, forms a thin layer. The secondary xylem and the secondary phloem constitute the major portion of the storage organ (plates 13 and 14).

Since the secondary xylem and phloem contain a high proportion of parenchyma and since all their cells have rather short diameters, the tissues of the fleshy root and hypocotyl appear rather homogeneous in longitudinal and transverse sections (plates 13 and 14).

In fresh sections examined without magnification, the cambium and the youngest vascular regions together appear as a very sharply outlined uneven and narrow circle. Within the mature xylem and phloem and in the pericycle the parenchymatous areas are translucent, whereas those containing the conducting elements are opaque. The phloem is usually deeper orange than the xylem. Under the microscope the carotin crystals are seen to be most abundant in the sheets of tissue containing the sieve tubes. The phloem region also shows, to the naked eye, certain concentric opaque areas. These contain the phloem oil ducts arranged transversely and longitudinally. Their secretory cells are comparatively small and form a denser tissue than the adjacent parenchyma.

DISCUSSION

Although *Daucus carota* resembles other Umbelliferae in the peculiar structural details of the root and hypocotyl (van Tieghem, 1870–71; Warning, 1934; Hayward, 1938, chap. 15; and others), it shows fewer unusual features in the anatomy and the ontogeny of its hypogeous parts than certain other plants with fleshy storage organs. The development of the fleshy organ of the carrot occurs through the activity of a normal cambium cylinder and does not involve the occurrence of an anomalous meristematic activity as in the beet (*Beta vulgaris*) or the sweet potato (*Ipomoea Batatas*). The carrot resembles the long varieties of the radish (*Raphanus sativus*) in the morphology of the storage organ (Golinska, 1929; Hayward, 1938, chap. 10). In both, the hypocotyl and the root partake in forming this organ through excessive secondary growth; and

in both, the largest part of the hypocotyl has essentially the structure of a root. In contrast to the carrot, however, the radish, according to Hayward (1938, p. 301), has some anomalous cambial activity within the secondary xylem.

Havis (1939) interpreted the enlarged hypogeous organ of the carrot as largely hypocotyl. This region, of course, elongates considerably between the germination of the seed and the inception of secondary growth, but reaches only about 1 inch in length at the end of this period. The mature storage organ is, however, usually several inches long; hence the hypocotyl constitutes a comparatively small part of the entire structure.

The mature storage organ consists mainly of secondary vascular tissues. As Havis (1939) has indicated, the relative amount of xylem is a variable characteristic. The pericycle contributes comparatively little to the thickness of the organ. Havis (1939), on the contrary, reported a rather thick layer of pericyclic origin. It seems, he included in this layer some phloem parenchyma that remained after the obliteration of the sieve tubes and companion cells, and the parenchyma intervening between the pericycle and the first secondary phloem cells opposite the protoxylem poles.

The presence and the arrangement of the pericyclic oil ducts in the primary condition are perhaps the most unusual features of the root and hypocotyl of the carrot and other Umbelliferae (de Bary, 1884, p. 448–49; van Tieghem and Douliot, 1888; Hayward, 1938, p. 458–59; and others). Only two more families, the Araliaceae and the Pittosporaceae, are listed by de Bary (1884, p. 450–51), Courchet (1884), and Solereder (1908, p. 1101) as having a similar structure of the pericycle.

The lateral roots are initiated in the pericycle near the protophloem poles, as in figure 108, *D*, page 236 in Eames and MacDaniels' (1925) text. Courchet (1884), van Tieghem (1870–71), van Tieghem and Douliot (1888) explained the characteristic position of the lateral roots by the absence of pericyclic oil ducts opposite the phloem. As the present study shows, the first divisions in the formation of lateral roots appear in cells not connected with the oil ducts, but later the secretory cells divide and contribute to the development of the laterals and to the secondary growth in the pericycle.

Certain observations on the development of the storage organ of the carrot have a bearing upon some general questions of histogenesis and ontogeny.

The literature gives diverse data on the structure of the meristematic apices of the roots of Umbelliferae. Eriksson (1877) distinguished two

layers of initials, one giving rise to the central cylinder with its pericycle; the other to the cortex, the epidermis, and the rootcap. Holle (1876), using different kinds of roots, and van Tieghem and Douliot (1888), who studied only lateral roots, reported the presence of three sets of initials—those of the stele, those of the cortex, and the common initials of the epidermis and the rootcap. Certain recent workers similarly interpreted the meristem organization of umbelliferous roots (Warning, 1934; Hayward, 1938).

Schüepp (1926, p. 70–71), summarizing the information on root meristems, places the Umbelliferae into three different categories showing the following histogenetic relationships: (1) The cortex and the dermatogen contribute toward the rootcap (the stele, presumably, having a distinct set of initials). (2) The epidermis and the rootcap have common initials, separate from those of the cortex and those of the stele. (3) The primary tissues merge at the summit into a transverse generative layer.

Though the present study does not furnish conclusive information on the meristems of the carrot root, it indicates that the taproot of this plant, at least in seedling stage, approaches the third category listed by Schüepp. In young lateral roots, however, the stele is well marked off from the other regions. Nägeli and Leitgeb (1868) also remarked that the apical structure was clearer in lateral than in taproots, while Holle (1876) reported that the organization of the apex is sometimes more obscure in the radicle of the embryo than in the root of the seedling. The structure of root apices is obviously a complex problem. A comprehensive study of this problem should include different kinds of roots, of the same plant, in different stages of development.

In previous papers, the writer (Esau, 1938, 1939) has pointed out the close ontogenetic relationship between the pericycle and the protophloem of stems. Usually, in fact, the term *pericycle* is applied to the outer region of the phloem.

As appears from the literature on root apices, the pericycle may have independent initials or may arise from the same initials as the rest of the central cylinder; but, in any case, it is early individualized (Janczewski, 1874*a*; Flahault, 1878). In the carrot also the pericycle becomes early defined, forming a continuous layer independent of the vascular tissues until it contributes some cambium to the stele at the beginning of the secondary growth.

In some families, as in the Gramineae and Cyperaceae, the protoxylem elements lie next to the endodermis, and the pericycle appears to be a discontinuous layer. According to Janczewski (1874*a*) and Chau-

veaud (1896), however, in such families the first protoxylem elements arise from pericyclic cells, so that really the pericycle is originally continuous. If this interpretation is correct, the structure of the roots of the Gramineae and Cyperaceae, as well as the observation that the pericycle frequently has common initials with the rest of the stele, indicates a close ontogenetic relationship between the pericycle and the vascular tissues of the root.

The increase in the thickness of the root cortex of *Daucus,* through periclinal divisions of the innermost layer, and the comparatively late maturing of the endodermis are common phenomena in dicotyledonous roots (Janczewski, 1874*a;* Flahault, 1878). Monocotyledons usually show centrifugal growth in the external part of the cortex (Flahault, 1878).

The primary xylem plate of the carrot root becomes delimited before the differentiation of any vascular elements. The central vessels, commonly termed the *metaxylem,* vacuolate before the protoxylem elements, although the latter are the first to mature. Other workers have observed a similar pattern of vacuolation in many representatives of ferns, dicotyledons, and monocotyledons (Russow, 1872, p. 17; Janczewski, 1874*a*; Chauveaud, 1896, 1900; Stover, 1928; Esau, 1935; Hayward, 1938, p. 295). Nevertheless the primary xylem of roots is interpreted as having a centripetal order of differentiation, because such is the order of development of the secondary walls and of the loss of protoplasts—that is, because the peripheral elements become specialized and begin to function before the inner ones.

The first protophloem sieve tubes of the carrot root mature earlier than the first protoxylem elements; in other words, they lie closer to the terminal meristem than do the water-conducting elements. This observation agrees with the conclusions of several other workers who have studied vascular differentiation in root tips. (See review by Esau, 1939.)

Since the first two sieve tubes resemble the pericyclic oil ducts in their shape and clearness of contents, they have often been interpreted, in the Umbelliferae, as secretory canals (Courchet, 1884; van Tieghem and Douliot, 1888; Warning, 1934; Hayward, 1938, p. 459, 461). Crooks (1933) also regarded as ducts the first phloem elements in the flax root. In the carrot, however, as the present study shows, the cells in question are sieve tubes with all the usual characteristics of these elements.

The position and the characteristic appearance of the first protophloem sieve tubes of roots have been studied in much detail by Chauveaud (1896, 1900, 1903) in numerous representatives of cryptogams, gymnosperms, and angiosperms. These contributions have markedly fa-

cilitated the recognition and interpretation of the first phloem elements in differentiating roots.

In the development of the lateral root the behavior of the endodermis of the main root deserves some attention. In the carrot this tissue layer forms a temporary covering of the young root and is discarded as the organ emerges on the surface of the main root. A similar development of the endodermis has been observed in other Umbelliferae by van Tieghem and Douliot (1886*b*, 1888), who interpreted the layer derived from the endodermis as a digestive pocket.

The endodermis frequently participates in the formation of lateral roots in dicotyledons and monocotyledons (Nägeli and Leitgeb, 1868; Lemaire, 1886; van Tieghem and Douliot, 1886*a*, 1886*b*, 1888; Crooks, 1933; Hayward, 1938, p. 51–52). According to Janczewski (1874*b*), plants vary considerably in the degree of this participation; but usually the endodermis forms a single exterior layer.

As van Tieghem and Douliot (1888) have observed in other plants, the lateral root of the carrot forms its own endodermis in connection with the endodermis of the main root.

A study of differentiation of the vascular tissues involves the problem of distinguishing between the different kinds of primary and between the primary and the secondary tissues. Russow (1872, p. 3) introduced the name *protoxylem* for the first mature xylem elements, which, in the root, appear farthest away from the center of the axis. The term *metaxylem* was apparently first used by van Tieghem (1887) who applied it to the centrifugal xylem elements that occupy the same position as the secondary elements but are not yet derived from the cambium. Plants may or may not have such metaxylem. Van Tieghem regarded the entire centripetal xylem plate as protoxylem, apparently without considering the nature of the secondary walls.

In current usage, the term *metaxylem* is applied, in roots, to the innermost centripetal vessels (Jackson, 1928); and only the outermost groups represent the protoxylem. The secondary xylem is, of course, the tissue derived from the vascular cambium. Definite wall sculpturings are ascribed to the different kinds of xylem (Eames and MacDaniels, 1925, p. 92).

In the carrot the innermost vessels are scalariform and reticulate, the latter type being—according to the current concept—a representative of the metaxylem. The cambium, however, produces largely scalariform and some reticulate vessels—that is, elements considered characteristic of the primary xylem. Apparently, therefore, a certain kind of wall sculpturing is not necessarily correlated with the method of formation

of xylem elements, and the distinction between the different kinds of xylem is uncertain. A similar difficulty exists in the attempts to distinguish between the protophloem, the metaphloem, and the secondary phloem.

As the writer (Esau, 1938) has previously emphasized, the distinction between the cambium and procambium in stems and leaves is uncertain because the vascular tissues called *primary* commonly arise from a radially seriated meristem. In the root the entire central cylinder is interpreted as procambium. This meristematic region seems to fit the definition of procambium better than does the corresponding vascular meristem in the stems and leaves, since in the former the walls are formed in many planes and the divisions are largely completed before the appearance of any mature vascular elements.

In this respect it seems significant that, as exemplified by *Daucus,* the centripetal xylem and the corresponding phloem—tissues not derived from a radially seriated meristem—are connected only with the cotyledons. The plumule, developing after the primary body of the seedling plant has been practically completed, forms vascular connections with the secondary tissues of the hypocotyl and root (perhaps also with the small fraction of primary xylem differentiating centrifugally). Thus the collateral arrangement and the radial seriation of the vascular tissues are continuous from the root into the aerial parts of the plant above the cotyledons. Such a relation is, of course, not only true of *Daucus* but probably common in the dicotyledons (Chauveaud, 1911; Havis, 1935, 1937; McMurry and Fisk, 1936; Simonds, 1938).

Apparently, then, homologous vascular tissues are interpreted as primary in the leaf and stem and as secondary in the root. In criticizing this concept, Chauveaud (1911) suggested that the vascular tissues of stem and leaf should be regarded as largely secondary. Studies of seedling anatomy considering the ontogeny and interconnection of xylem and phloem in different parts of the plant would be particularly valuable for the solution of the problem of distinguishing between the primary and the secondary vascular tissues.

SUMMARY

In the primary state the root of the *Daucus carota* L. shows a diarch xylem plate and two strands of phloem lying opposite each other. Vascular differentiation begins with the delimitation of the xylem plate through expansion and vacuolation of the future vessels. Though the central vessels vacuolate first, they are last to develop secondary thickenings and to lose their protoplasts. After having been set aside, the xylem

mother cells do not divide longitudinally any further; but the cells on both sides of the plate—that is, in the two future phloem regions—divide in all planes until the maturation of the vascular elements sets in.

The first mature elements are two protophloem sieve tubes lying opposite each other next to the pericycle in a plane at an angle of 90° to the future xylem plate. In seedlings grown in moist chambers in the laboratory the sieve tubes complete their differentiation about 300 microns from the apex of the root. The first protoxylem vessels, also located next to the pericycle, show secondary walls approximately 1 millimeter from the root apex, but do not lose their protoplasts through another millimeter of the root.

A centripetal differentiation of additional xylem and phloem elements follows, and a few centrifugal xylem elements complete the primary vascular development of the root.

The pericycle becomes individualized before the beginning of vascular differentiation and, through a series of oblique divisions, gives rise to oil ducts. These are arranged in two arcs, each with its central oil duct opposite a protoxylem pole.

The cortex, about two cells wide near the apex, increases in width to four or five cells by tangential divisions of the innermost cortical layer. Thus the endodermis is the last cortical layer formed and develops Casparian strips in the region where the first vessels reach maturity.

The outermost cortical layer divides periclinally near the apex of the root, the outer daughter cells becoming part of the rootcap, the inner differentiating into epidermal cells.

Throughout most of its extent, the hypocotyl resembles the root. The change from the centripetal to the centrifugal order of xylem differentiation occurs in the cotyledons, and the primary vascular tissues branch into the cotyledonary traces just below the insertion of the cotyledons. The xylem, however, shows an increasing parenchymatization from the base of the root toward the top of the hypocotyl; the phloem strands become wider; and the entire stele increases in diameter. In the upper hypocotyl the Casparian strips disappear, and starch accumulates in the endodermis.

The centripetal xylem and the corresponding phloem are connected with the cotyledons only. The plumule forms direct vascular connections with the secondary vascular tissues of the root and also, possibly, with the centrifugal primary xylem.

The lateral roots of the taproot and the hypocotyl are initiated near the protophloem poles in the part of the pericycle that lacks oil ducts, but later the nearest secretory cells also contribute to the growth of these

roots. The endodermis partakes in the lateral root development by forming a temporary covering over the young organ. It is destroyed as the root emerges on the surface. At the same time the lateral root develops its own endodermis and also its primary vascular tissues. The endodermis and the xylem and phloem of the lateral root are connected with the corresponding tissues of the main root. Some lateral roots arise in the periderm after the secondary growth has occurred in the root and the hypocotyl.

The fleshy underground storage organ of the carrot is formed through secondary growth in the taproot and the hypocotyl. The cambium, arising in the usual manner between the primary xylem and primary phloem, forms highly parenchymatous secondary vascular tissues. During this growth the cortex is ruptured and shed. The pericycle, through active divisions externally and internally to the oil ducts, gives rise to several layers of parenchyma. Outside the oil ducts the parenchyma cells give rise to a phellogen producing cork after the cortex sloughs. As the tissues arising from the pericycle form together only a narrow zone, the fleshy storage organ consists mainly of the secondary vascular tissues.

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PLATES

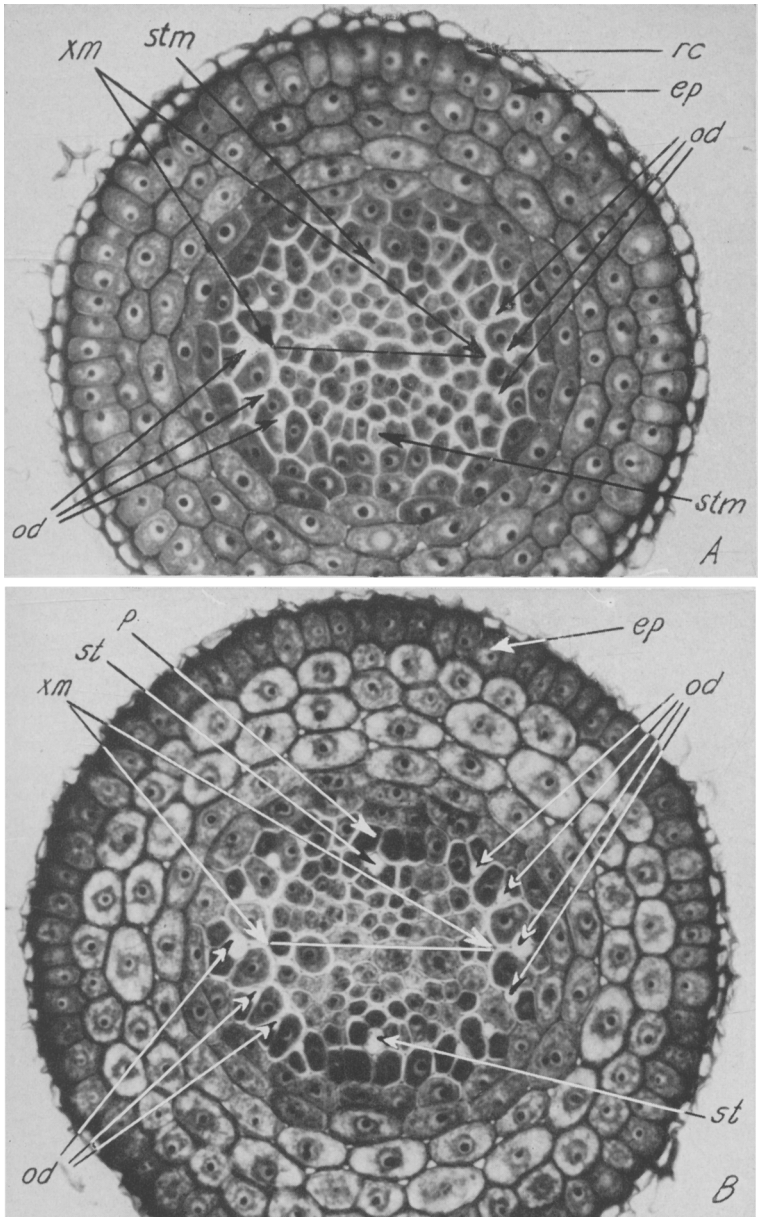

Plate 1.—Transverse sections of a root apex of a seedling, showing structure before (*A*) and after (*B*) differentiation of the first two protophloem sieve tubes. The section in *B* was taken 300 microns from the apex of the root. Details are: *ep*, epidermis; *od*, oil duct; *p*, pericycle; *rc*, rootcap; *st*, sieve tube; *stm*, sieve-tube mother cell; *xm*, xylem mother cells. (Both × 400.)

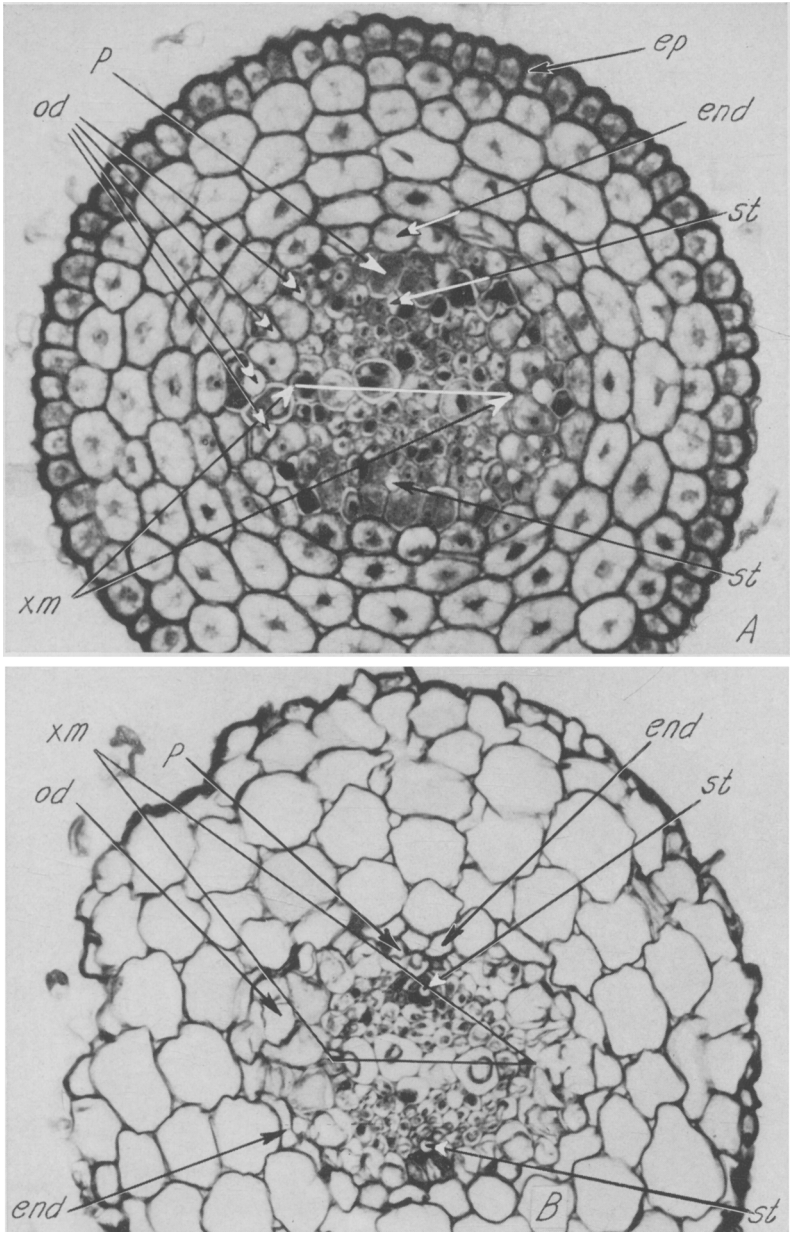

Plate 2.—Transverse sections of a root taken at successively higher levels of the same seedling as in plate 1. Details are: *end,* endodermis; *ep,* epidermis; *od,* oil duct; *p,* pericycle; *st,* sieve tube; *xm,* xylem mother cells. (Both × 400.)

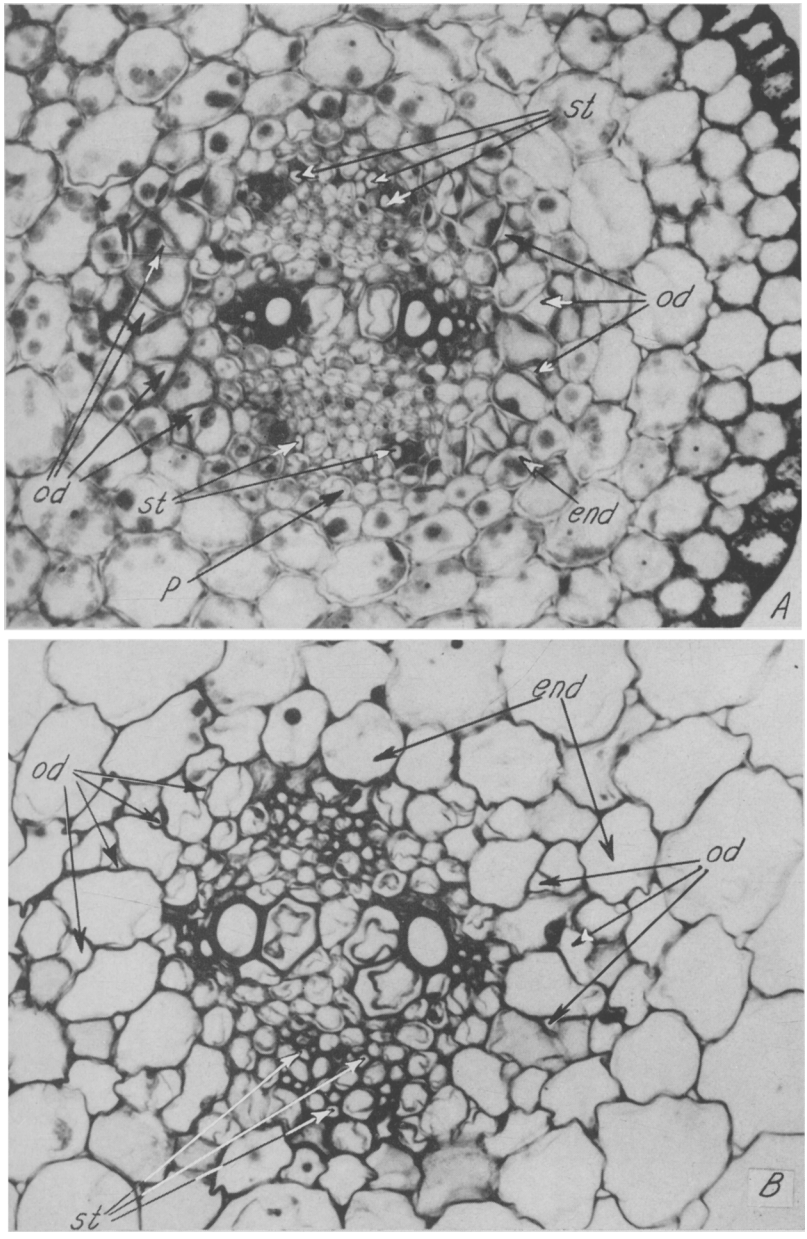

Plate 3.—Transverse sections of the hypocotyl of the same seedling as in figure 6. *B* was taken near the root base; *A*, farther away. The dark bodies in the endodermis and the cortex of *A* are plastids with starch grains. *A* shows a few epidermal cells to the right. Details are: *end*, endodermis; *od*, oil duct; *p*, pericycle; *st*, sieve tube. (Both × 400.)

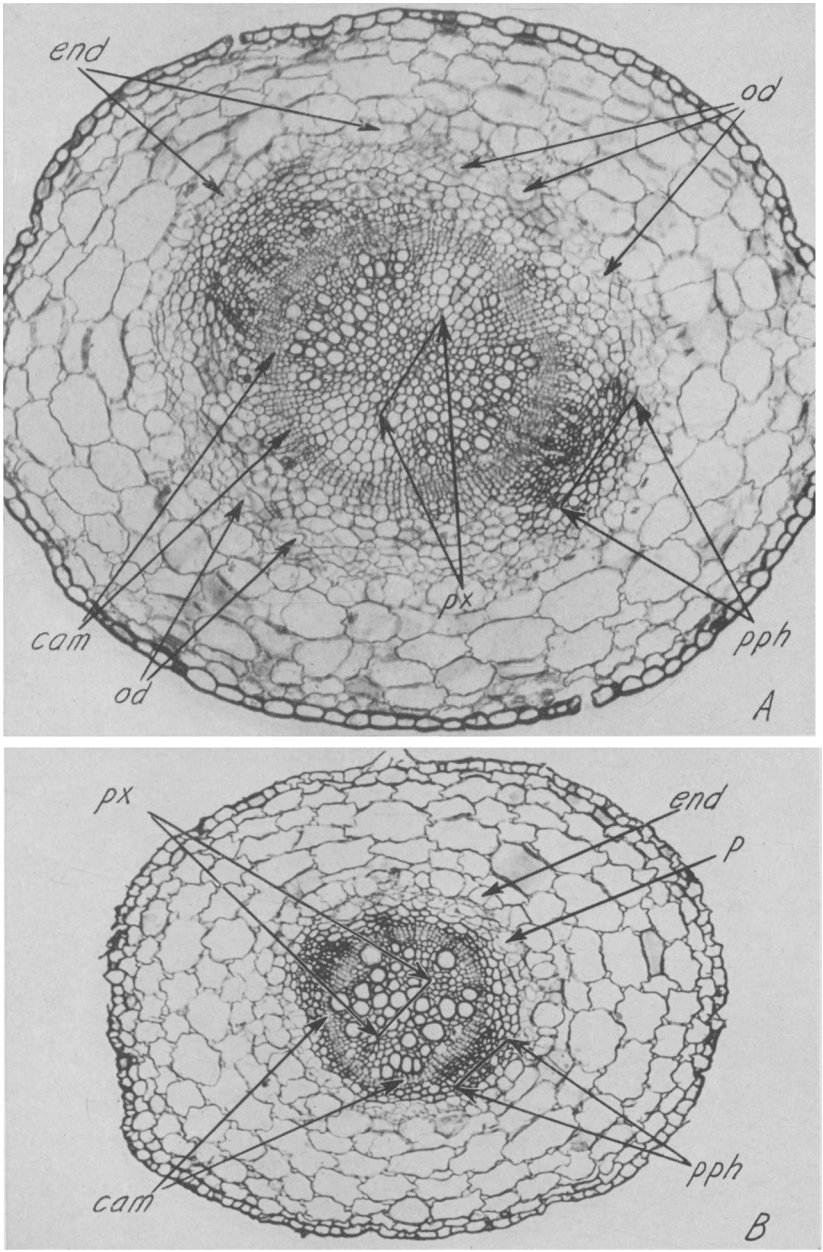

Plate 4.—Transverse sections showing the structure of hypocotyl (*A*) and root (*B*) of a plant like that in figure 1, *C*. Some secondary vascular tissues have been produced, but the cortex is still intact. Details are: *cam*, cambium; *end*, endodermis; *od*, oil duct; *p*, pericycle; *pph*, primary phloem; *px*, primary xylem. (Both × 92.)

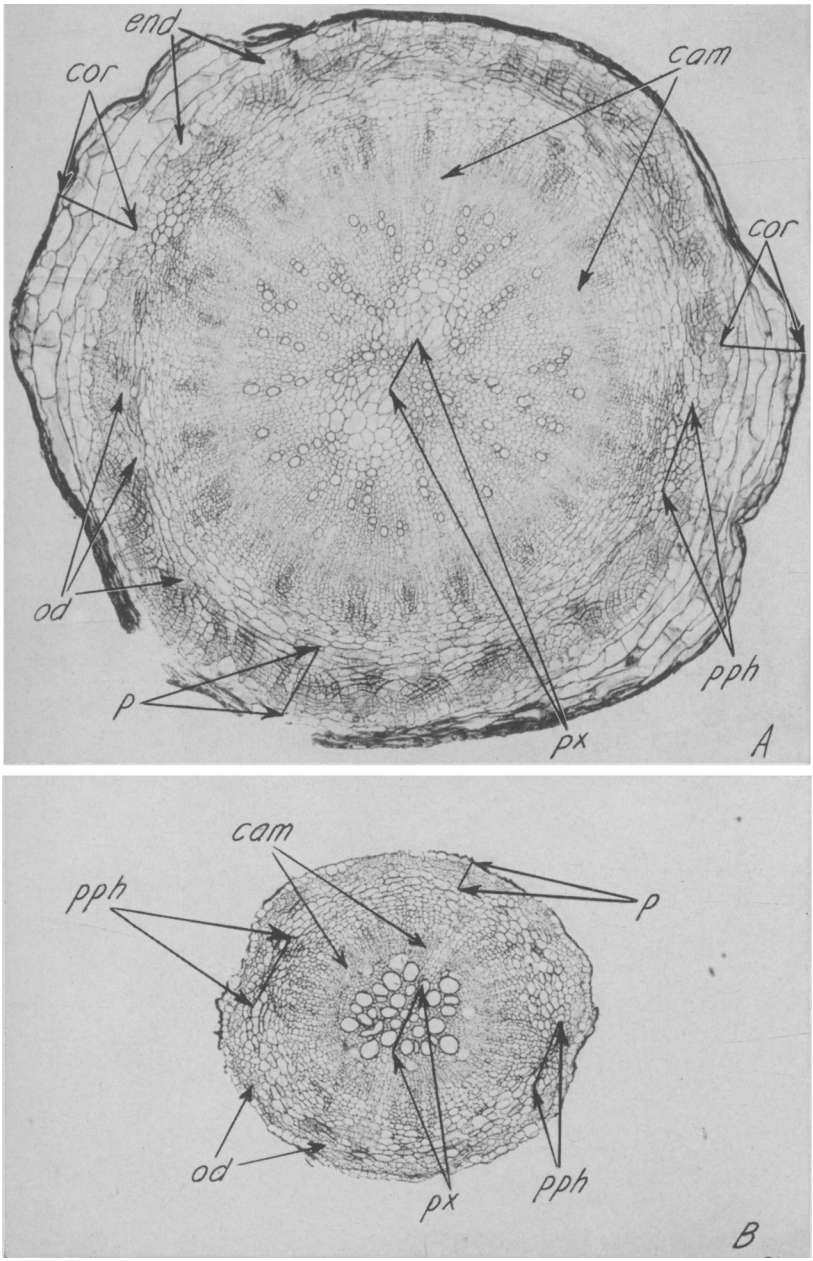

Plate 5.—Transverse sections of hypocotyl (*A*) and root (*B*) of a plant like that in figure 1, *E*. In the hypocotyl some of the cortex is still present; in the root this tissue region has sloughed. Details are: *cam*, cambium; *cor*, cortex; *end*, endodermis; *od*, oil duct; *p*, pericycle; *pph*, primary phloem; *px*, primary xylem. (Both × 50.)

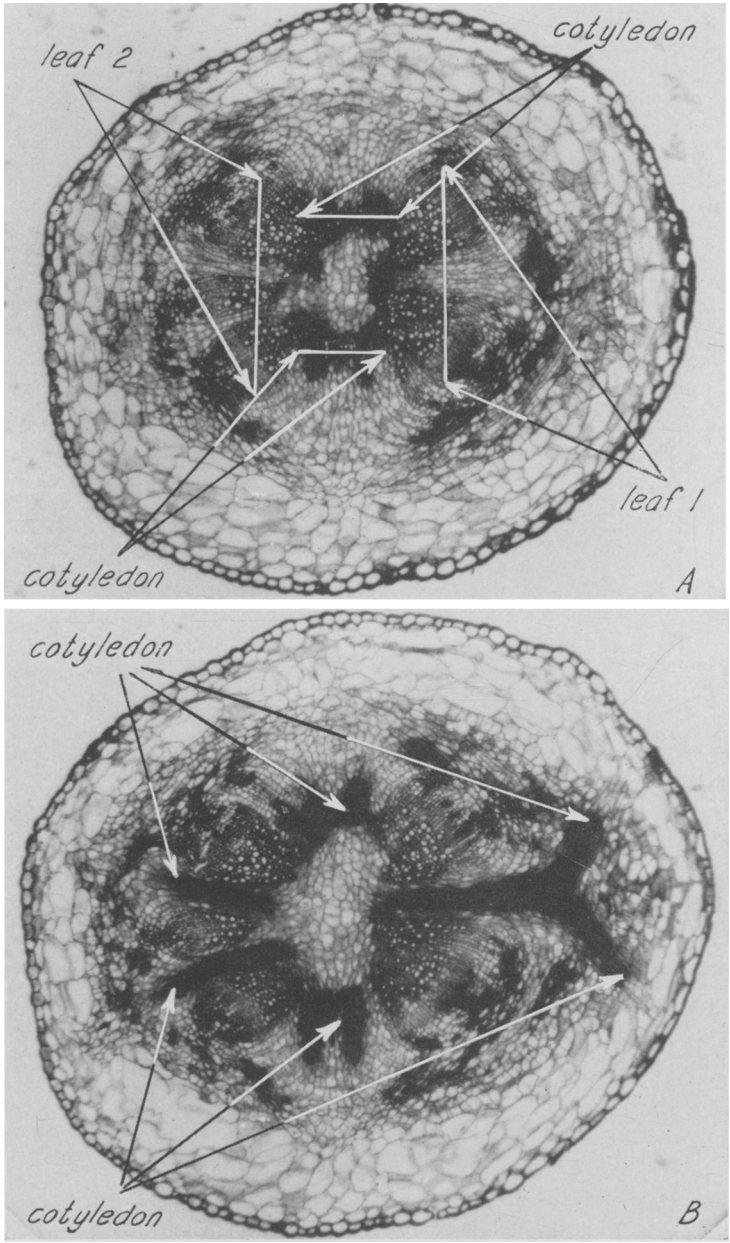

Plate 6.—Transverse sections of upper hypocotyl of a plant like that in figure 1, *C*. *A* was taken at a lower, *B* at a higher level below the cotyledons of the same plant as in plate 4. The sections show the arrangement of traces of the cotyledons and of the first two foliage leaves. Compare with figure 7, *C* and *D*. (Both × 50.)

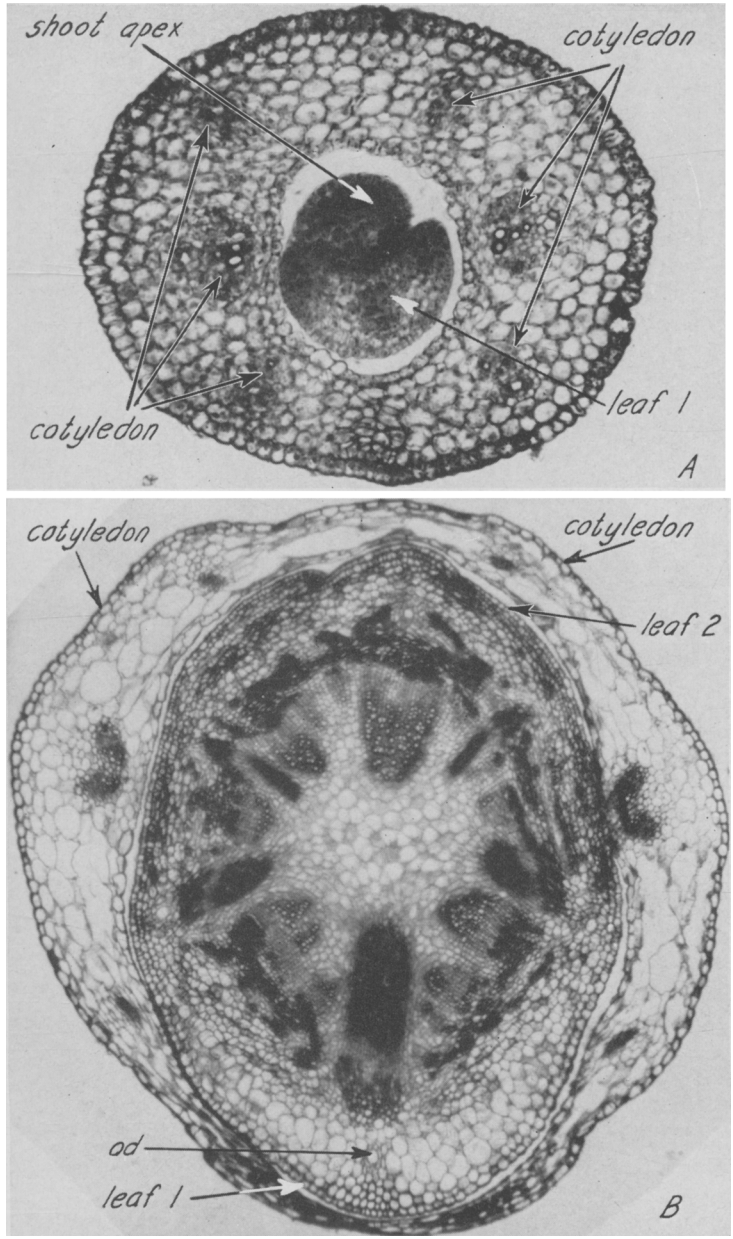

Plate 7.—Transverse sections of a younger (*A*) and an older (*B*) plant showing the structure of the axis above the insertion of the cotyledons. *B* was taken from the same plant as the sections in plates 4 and 6. The bases of the cotyledonary petioles are fused. (*A*, × 168; *B*, × 50.)

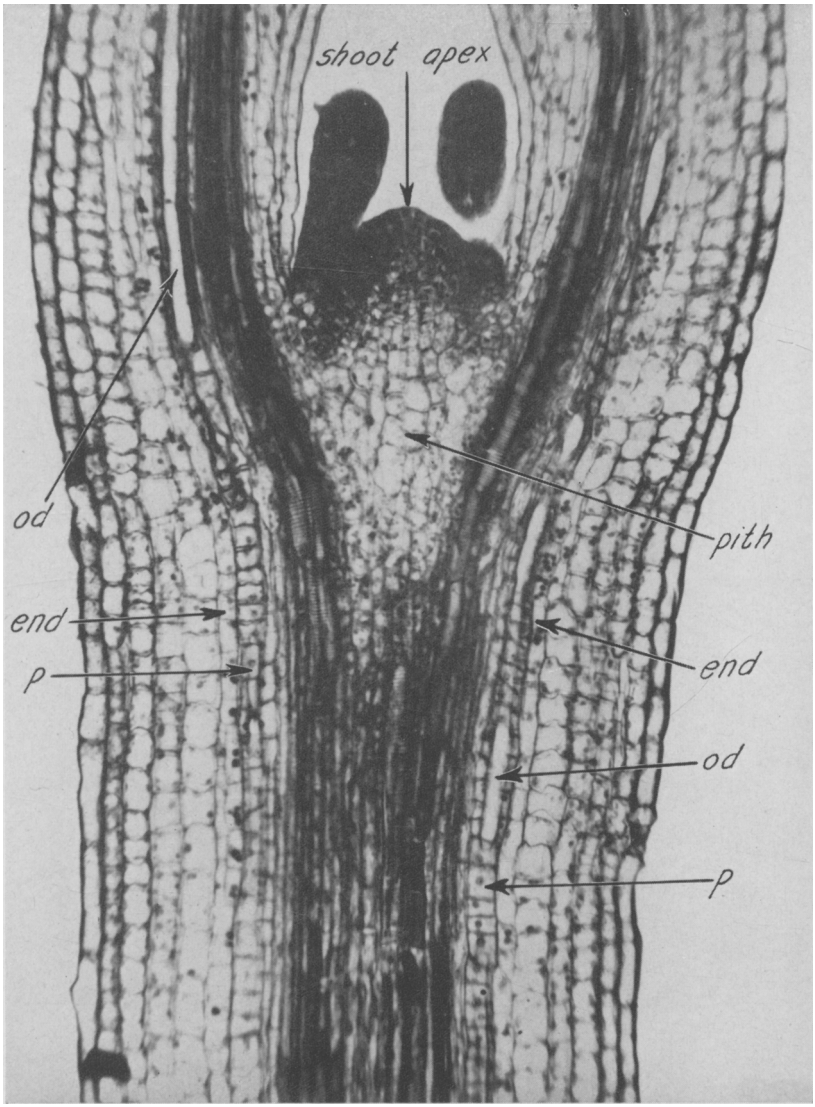

Plate 8.—Longitudinal section of the epicotyl and upper hypocotyl of a plant similar in size to that used for plate 3. This section shows the union of the cotyledonary traces below the primordial shoot. Details are: *end*, endodermis; *od*, oil duct; *p*, pericycle. (× 188.)

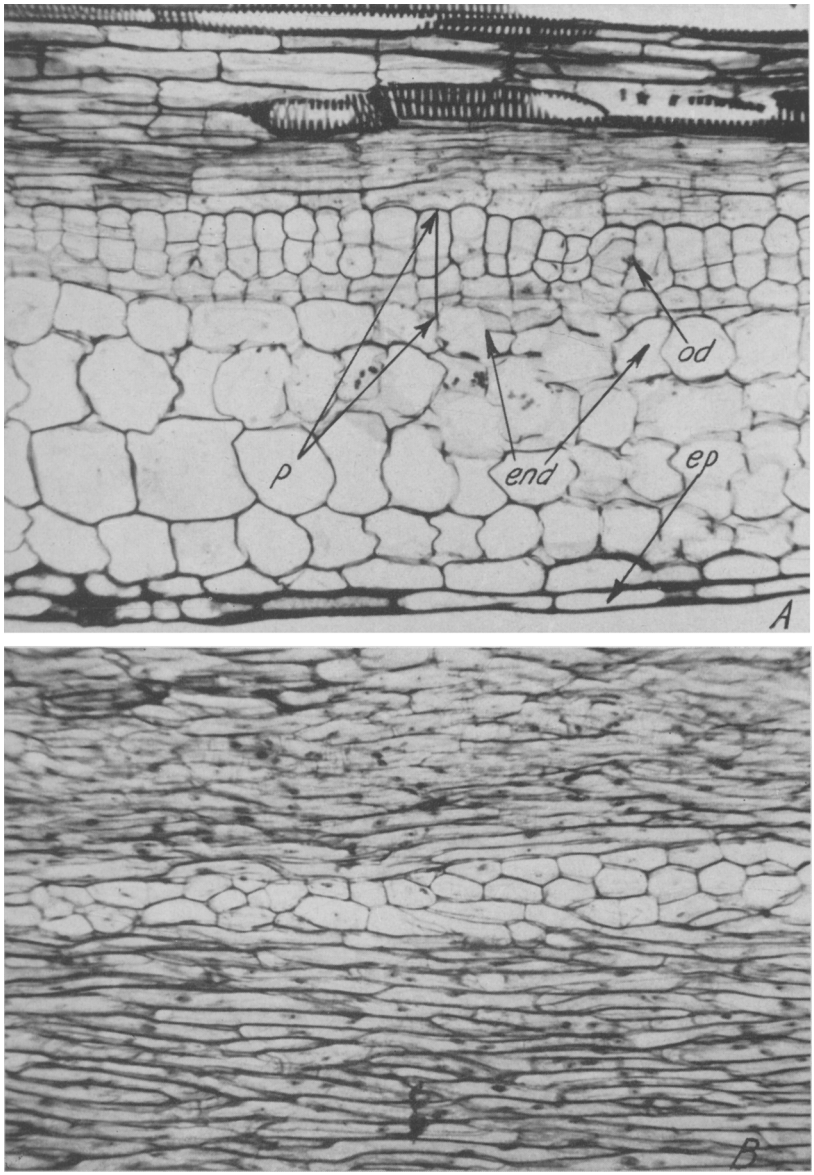

Plate 9.—*A*, Longitudinal section of the lower hypocotyl of a plant like that in figure 1, *C*. A similar region appears in transverse section in plate 4, *A*. Some secondary cell division has occurred in the pericycle. The longitudinal section does not include the primary phloem but shows some cambium below the xylem. *B*, Tangential section of the vascular cambium from the root of a plant like that in figure 2, *A*. The large, nearly isodiametric ray initials contrast sharply with the fusiform initials. Details are: *end*, endodermis; *ep*, epidermis; *od*, oil duct; *p*, pericycle. (Both × 188.)

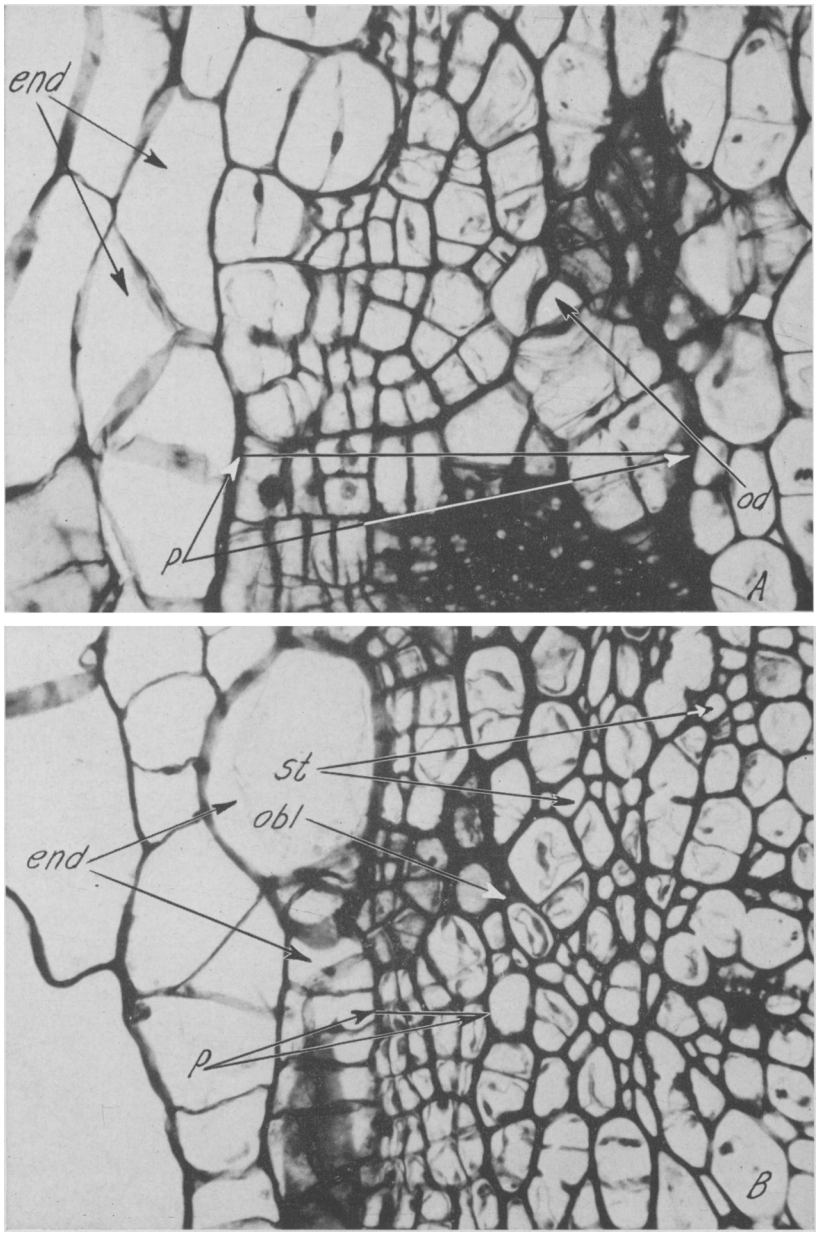

Plate 10.—Transverse sections of a hypocotyl showing cell multiplication in the pericycle before rupture of the cortex. Earlier stages of this process are shown in figure 11. *A* was taken opposite the primary xylem; *B* opposite the primary phloem, from a plant like that depicted in figure 1, *D*. Details are: *end*, endodermis; *obl*, obliterated elements; *od*, oil duct; *p*, pericycle; *st*, sieve tube. (Both × 400.)

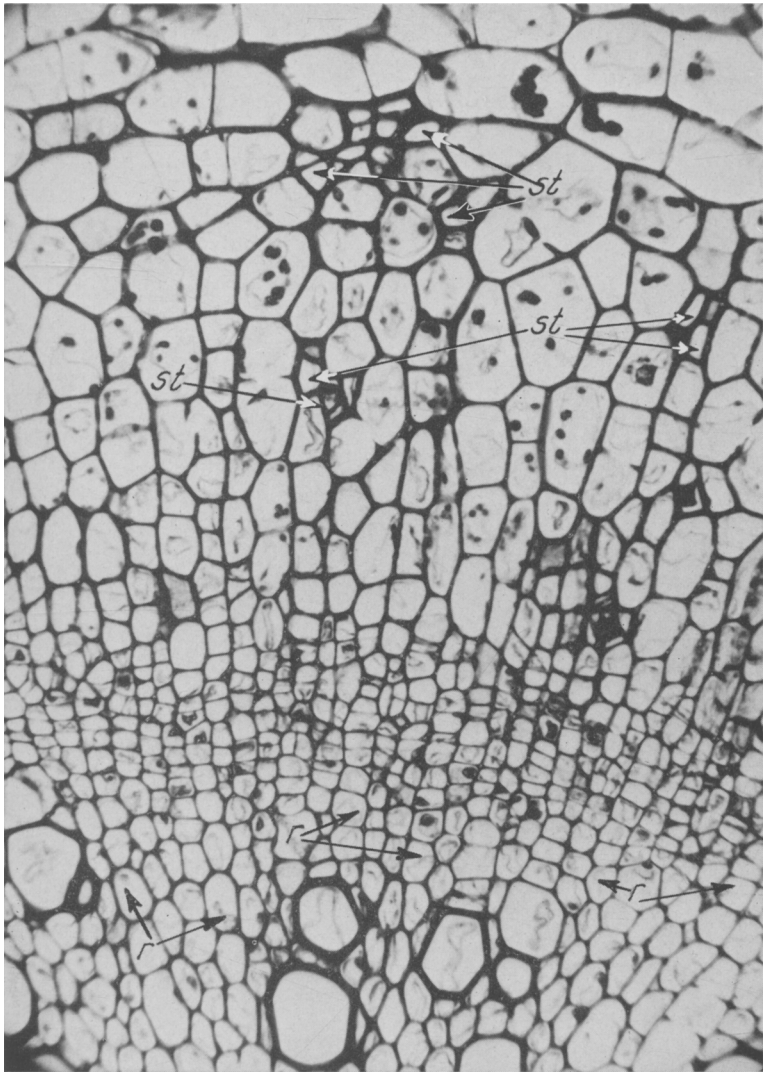

Plate 11.—Transverse section of secondary vascular tissues of the hypocotyl of a plant like that in figure 1, *D*. This photograph was taken from the same section as those in plate 10. Details are: *r*, ray; *st*, sieve tube. (× 400.)

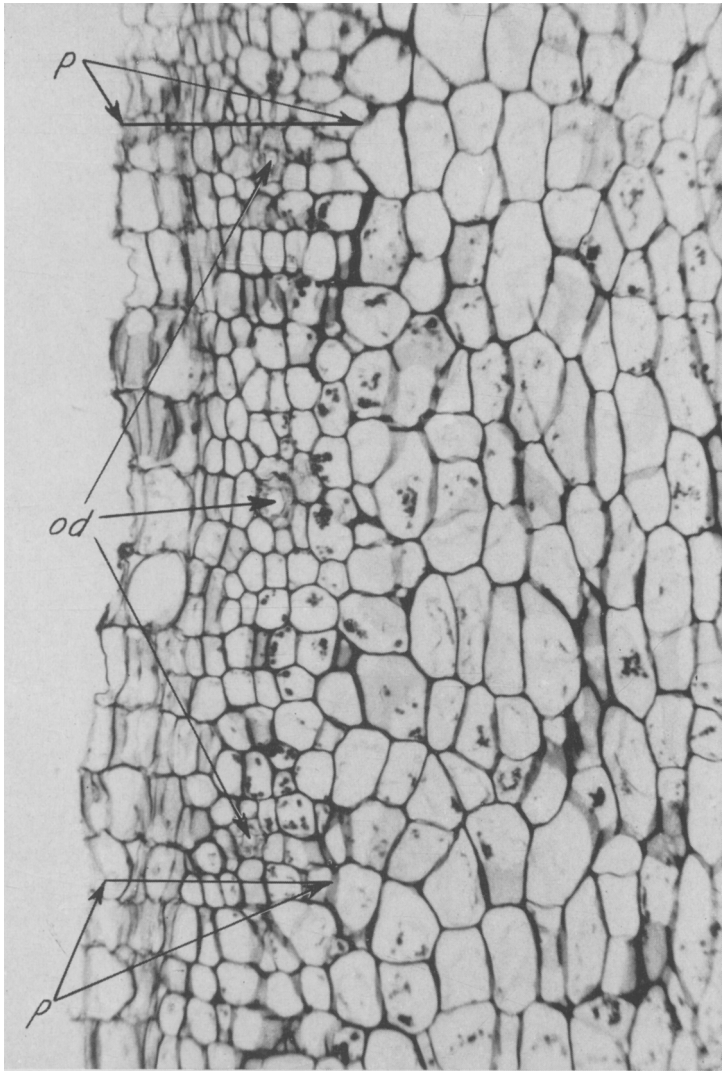

Plate 12.—Radial longitudinal section of outer phloem and pericycle with periderm of the root of a plant like that in figure 2, *A*. Details are: *od*, oil duct; *p*, pericycle with periderm. (× 188.)

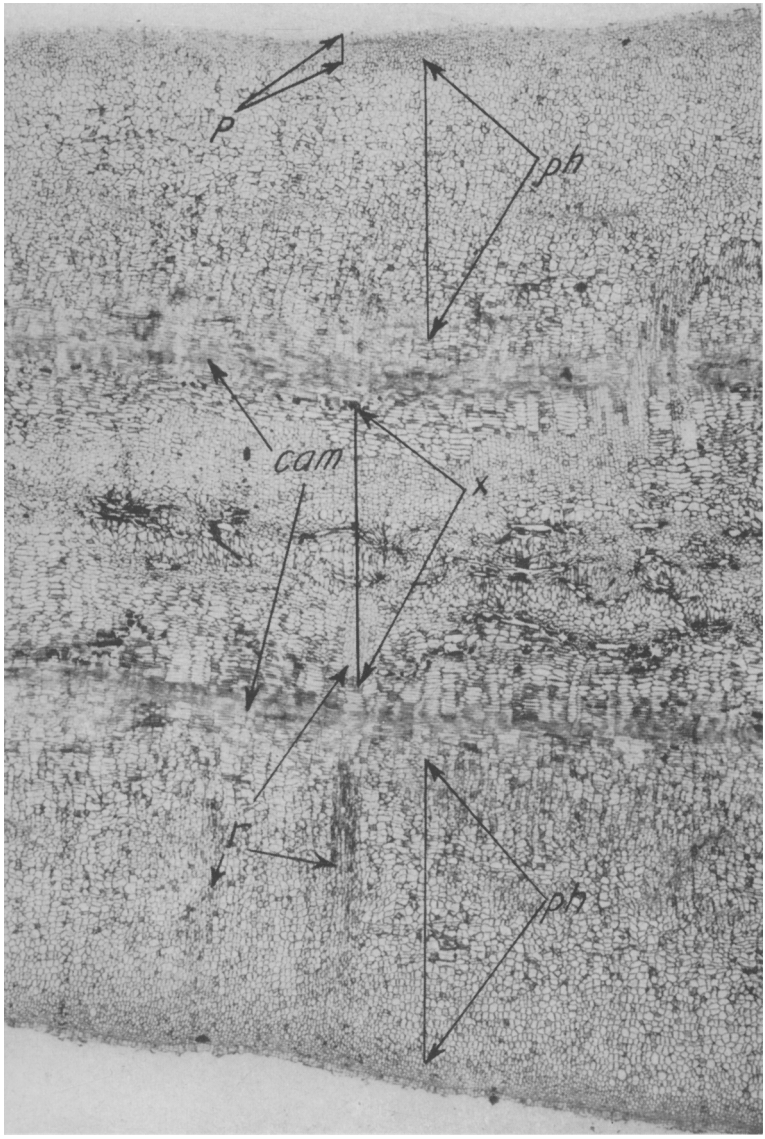

Plate 13.—Radial longitudinal section of root of a plant somewhat smaller than that in figure 2, *C*. Details are: *cam*, cambium; *p*, pericycle with periderm; *ph*, phloem; *r*, ray; *x*, xylem. (× 16.)

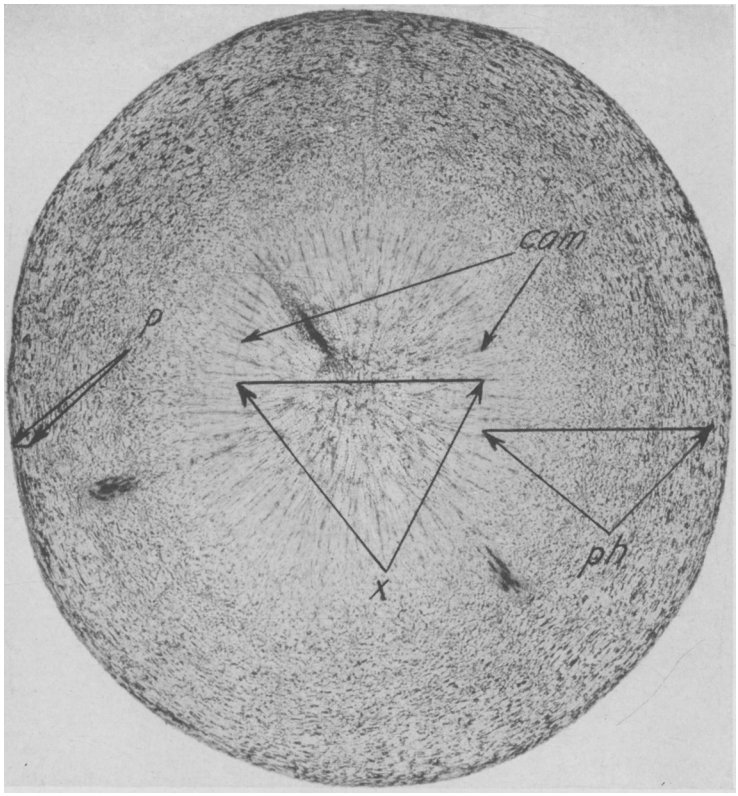

Plate 14.—Transverse section of hypocotyl 1 centimeter below the insertion of leaves in a plant like that in figure 2, *D*. Details are: *cam*, cambium; *p*, pericycle with periderm; *ph*, phloem; *x*, xylem. (× 6.)