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The Anatomy of the Seedling and Roots of the Valencia Orange[1]

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CONTENTS

INTRODUCTION

Studies are in progress to determine the effect of salts on the growth and development of the Valencia orange seedling. These include investigations of the response of seedlings to varying concentrations of chloride, sodium, potassium, calcium, and hydrogen ions. The development of the primary root and the formatipn of its absorbing structures are intimately related to the problems of absorption of water and the intake and accumulation of salts. As there has been little work done on the anatomy of Citrus, the present study was necessary to serve as a basis for the salinity studies referred to above. The importance of this aspect of the salinity problem led to the inclusion of a preliminary study of the secondary roots of the Valencia and other sweet orange rootstocks, Citrus sinensis (L.) Osbeck.

Anatomical investigations of the genus Citrus have centered on the flower and fruit (1, 2, 10, 12, 22, 23, 24),[3] the seed with special reference to polyembryony (4, 21, 30), and the shoot (7, 16, 17 19, 25). Penzig (14) has described the root of Citrus *limonum, and* more recently Cossmann (3) has published an account of the anatomy of citrus roots

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[3] Italic numbers in parenthesis refer to literature Cited, p. 30.

of nine species and varieties, which confirms and extends Penzig's work and describes certain root characters that he found to be of taxonomic importance. The genetics, physiology, and pathology of citrus seedlings have been studied with incidental reference to the anatomy (5,6, 26, 28).

MATERIAL AND METHODS

The majority of the seedlings were grown from selected seeds obtained from the Citrus Experiment Station, Riverside, Calif. Some were produced from seeds of ordinary market stock. In April and August 1939, seeds were sown in quartz sand and grown under the shelter of a lath house. In December a third set was grown in sand in the greenhouse, and a fourth lot of seed was planted in sphagnum moss.

All cultures were watered with tap water having a pH of approximately 7.7 and supplied with a four-salt nutrient solution at regular intervals. No attempt was made to adjust hydrogen ion concentration of the solution, but the pH value of the sand solution at the time the seedlings were harvested was 8.2, whereas that of the sphagnum ranged from 4.6 (first percolate) to 6.2. The maximum temperature of the sand culture was 30" C. and of the sphagnum moss 26° C.

The material used for anatomical analysis was fixed in Navashin's solution, dehydrated in an ethyl tertiary butyl alcohol series, and infiltrated and embedded with a paraffin-beeswax-rubber mixture. Immediately after placing the material in the fixative, air n-as evacuated from the tissues with a vacuum pump. A modified Flemming's triple stain was used. In stndies of the root hairs fresh sections prepared with the freezing microtome were also used.

POLYEMBRYONY

The occurrence of polyembryony (fig. 1) has long been known in Citrus, and the subject has been investigated by Strasburger (21), Webber (26), Frost (4), and others. In most instances the embryos other than the gametic one are of nucellar origin, although Frost has described a few cases which he interpreted as "identical twins."

Webber reported that 40 to 95 percent of the seed contained apomictic embryos in C. sinensis. Tn these studies from 25 to 50 percent of the seed that germinated produced more than one seedling. Two seedlings usually started to develop? and in a few instances three were observed (fig. 2). The development of albino seedlings was not uncommon. and albinism and polyembryony occurred together in one case in which two white seedlings started development. One tricotyledonous seedling was observed.

THE EMBRYO

Owing to the competitive growth of two or more embryos within the seed coat the seedlings vary in size, and one is usually larger and more vigorous than the others. The smaller seedlings frequently show evidence of injury, and there may be considerable distortion of the two fleshy cotyledons, which are commonly very unequal in size.

The oval cotyledons are much thickened, as is usually the case in seedlings with the hypogeal habit (fig. 2). According to Winton and Winton (30), the endosperm is reduced in the mature seed to two or three layers of small thin-walled cells containing minute aleurone, grains. In the cotyledonary traces the arrangement of the

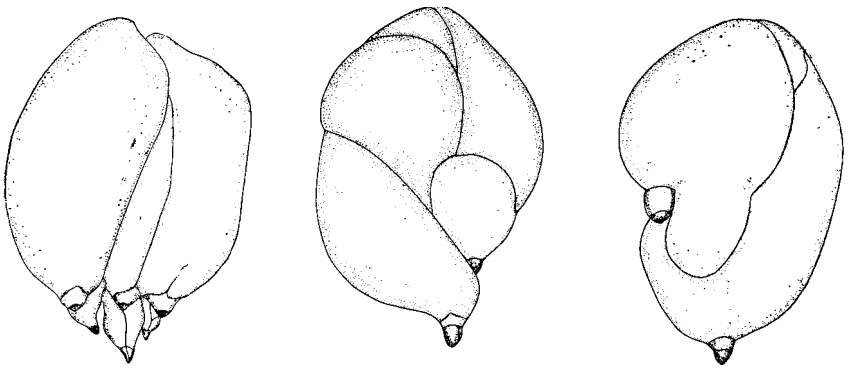

FIGURE 1.-Seeds with seed coats removed showing the polyembryonic condition and the variation in size and shape of the cotyledons. x 4.5.

FIGURE 2.-Valencia seed and seedlings in several stages of development. In three cases the germination of two seedlings from a seed is shown.

primary xylem and phloem is half amphicribral to subamphicribral. The veins branch profusely so that they form a network extending throughout the cotyledons.

ONTOGENY OF THE PRIMARY ROOT

In the development of the primary root the terminal meristem is differentiated so that there are three histogens. The manner in which these initiating layers are arranged corresponds in general plan with that described as Type III by Hanstein (8). There is a definite plerome and periblem and a common initiating zone for the root cap and epidermis, the dermatogen-calyptrogen layer.

Penzig (14), in describing the growing point of the primary root of Citrus limonum, refers to three histogens comparable to those indicated above. He states that they originate from a small group of generative cells or primordial meristem located at the apex of the root tip, and he does not regard them as constituting distinct layers at that point. Observations in the present studies confirm this view in part for the Valencia orange. The plerome is distinct, but the periblem cannot be clearly distinguished from the dermatogen-calyptrogen layer at the extreme apex of the meristematic zone (fig. 3). In embryogeny all tissues may be referred back to a single cell, the zygote (in polyembryony, to a synergid or nucellar cell); and it is clear that the histogenic concept cannot be applied too rigidly. But in root ontogeny.. it does form a convenient basis for the study of tissue differentiation.

The cells of the dermatogen-calyptrogen produce successive layers of the root cap by periclinal divisions. The inner daughter cells of such tlivisions remain meristematic and continue to function as the histogenic layer compensating for root enlargement by anticlinal divisions. The cells that form the proximal margin of this layer at any given time undergo a final periclinal division. The inner daughter cells resulting from this division then function as a dermatogen and may divide anticlinally before differentiating as epidermal cells. The outer daughter cells are added to the root cap. The cells that form the apex of the root cap are in regular alignment, but in the lateral portions some irregularity results from subsequent anticlinal divisions.

The periblem consists of a single layer of cells at the root apex, but laterally it is several-layered as a result of periclinal divisions. The cells of the outermost or hypodermal layer may be much elongated radially later in ontogeny. (See fig. 7, il.) The innermost layer abutting the pericycle differentiates as the endodermis. Between the hypodermis and the endodermis are several layers of parenchymatous cells that are isodiametric in transection and four or five times as long as broad.

Reed and MacDougal (18) have pointed nut that the growth of the shoot in the orange is cyclic and that periods of root growth follow those of the shoot. They have suggested that growth-promoting substances catalyze the growth process.

The activity of the histogens constituting the terminal meristem of the root appears to be conditioned by soil factors. When the pH of the soil solution is high (8) and the available soil moisture is reduced, the activity of the meristem may be inhibited. In such cases the development of the hypodermal periderm proceeds until it may be differentiated nearly to the upper limits of the root cap (fig. 4).

THE EPIDERMIS

DEVELOPMENT OF ROOT HAIRS

Although it has been stated in general works on citriculture (2, 9) that citrus roots do not develop root hairs, it has long been known that they do occur. Penzig (14) refers to long root hairs covering

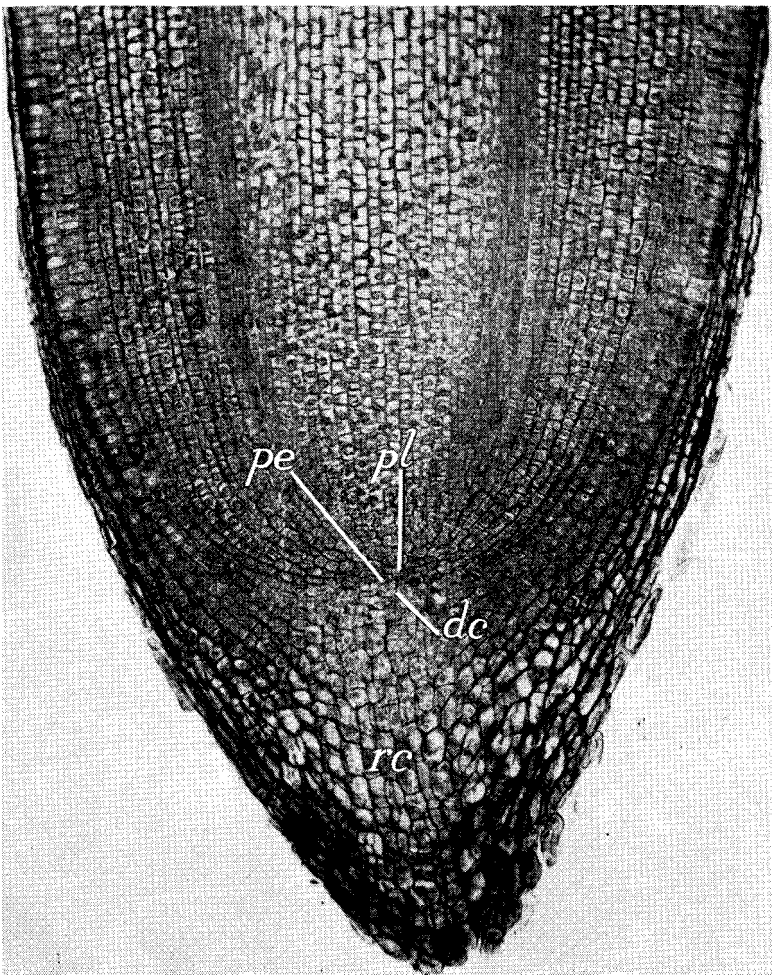

FIGURE 3.-Longisection of the apex of the primary root showing the root cap and histogens :dc, Dermatogen-calyptrogen layer ; pe, periblem ; pl, plerome ; rc, root cap. x 180.

the surface; and, more recently, Girton (5) has studied the effects of various factors on root hair formation. He used a "root hair index" to express the frequency of development and found that root hairs were most abundant when there was good aeration, a soil or solution

temperature of 33" C., and a pH of 5. The optimum pH for root development is reported as somewhat higher than that for root hair development. Girton found best root growth with sour orange seedlings in water cultures at pH 6.5, and Haas and Reed (6) obtained

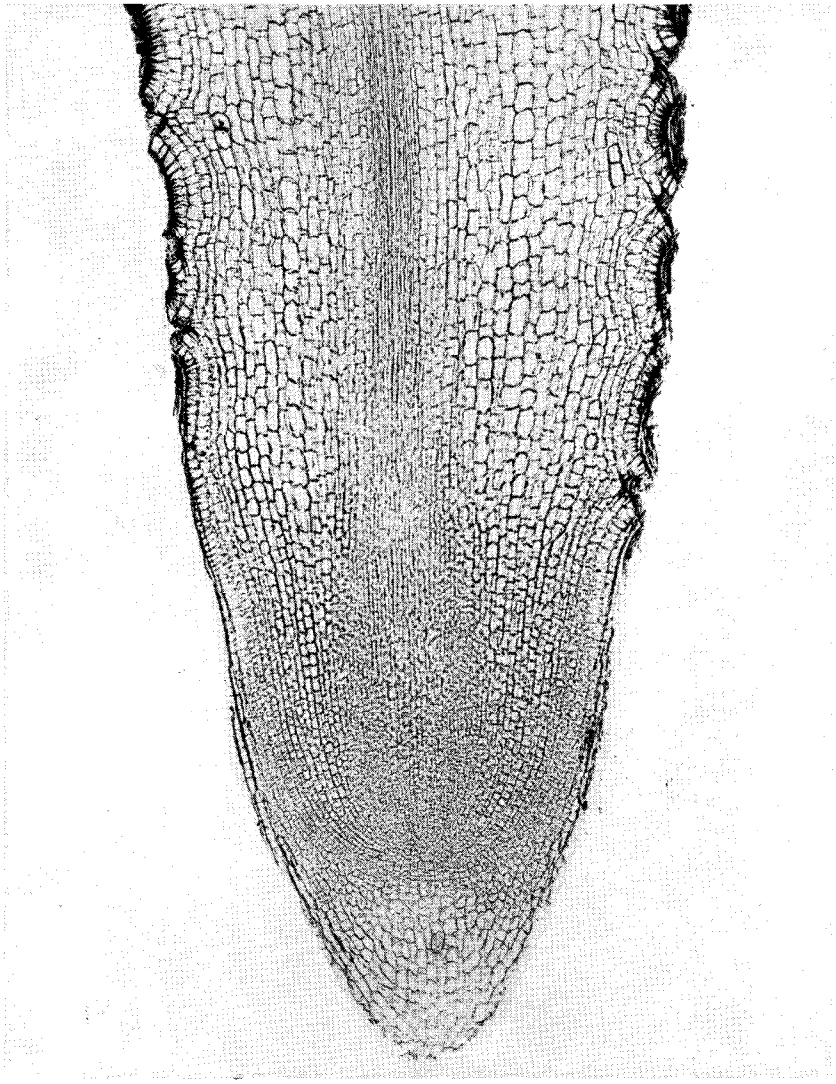

FIGURE 4.-Longisection of a primary root in which growth in length has been inhibited. The periderm is differentiated nearly to the root cap. x 110.

best results with St. Michael orange seedlings at pH 7 to 8, depending upon how the hydrogen ion concentration was established and maintained.

In this study fewer root hairs developed in the sand cultures in which the pH was 8 or higher than in sphagnum moss in which it was 6 or lower. More favorable aeration may also have been a factor in promoting better growth in the latter case. In some roots approximately every other epidermal cell developed as a root hair, whereas in others the occurrence of root hairs was not uniform and they occupied patches or horizontal bxntled areas (fig. 5, A and B).

The root hairs vary in shape, the most common type being the cylindrical form. The shorter hairs frequently develop broad swollen bases ; others are shaped like a spearhead. Some of the epidermal cells form nothing more than short papillate projections, and most of the root hairs are not long, ranging from 50μ to 150μ. Occasional hairs attain a length of 200μ to 250μ exclusive of the basal portion of the cell, which averages 14μ to 20μ for the radial dimension. The length of root hairs has been reported for a large number of plants. The indicated range is from 0.15 to 10.0 mm., so that the average length of the root hairs observed in these studies is at or below the lower limit reported.

The root hairs persist for a longer period than is commonly the case, and they may remain after the hypodermal periderm is well developed (fig. 6). It seems unlikely that they function as absorbing organs at this time, since. their walls are much thickened and give a staining reaction Indicating the presence of some suberin and possibly lignin. No data were obtained to indicate the maximum longevity of the root hairs? as none of the seedlings studied were grown for more than 2 months.

Although the occurrence of persistent root hairs is not common, they have been reported for a number of plants. McDougall (13) observed them in certain legumes, *Gleditsia, Cercis,* and *Gymnocladus;* and Whitaker (29) found root hairs in some Compositae that persisted for 3 years.

Young root hairs taken from the segment just back of the root tip gave positive reactions for pectic substances, callose, and cellulose, but in older root hairs these were not as marked. As the walls thicken, they become yellow to olive brown? and other substances of unknown composition are laid down in them. These materials are also very abundant in the outer tangential walls of the epitlermis. The old root hairs gave a positive reaction for suberin, and there was some indication of lignin in the inner tangential wall. This was associated with the deposition of lignin in the walls of the hypodermal cells, which gave a positive reaction for both suberin and lignin when mature. Where the hypodermal cells develop as root hairs or "transfusion cells" the walls at first' hare characteristics similar to those of the younger root hairs and it seems probable that they perform an absorptive function.

THE CORTEX

THE HYPODERMIS

The hypodermxl cells may develop in several ways. In some cases their inner tangential and radial walls soon become suberized to

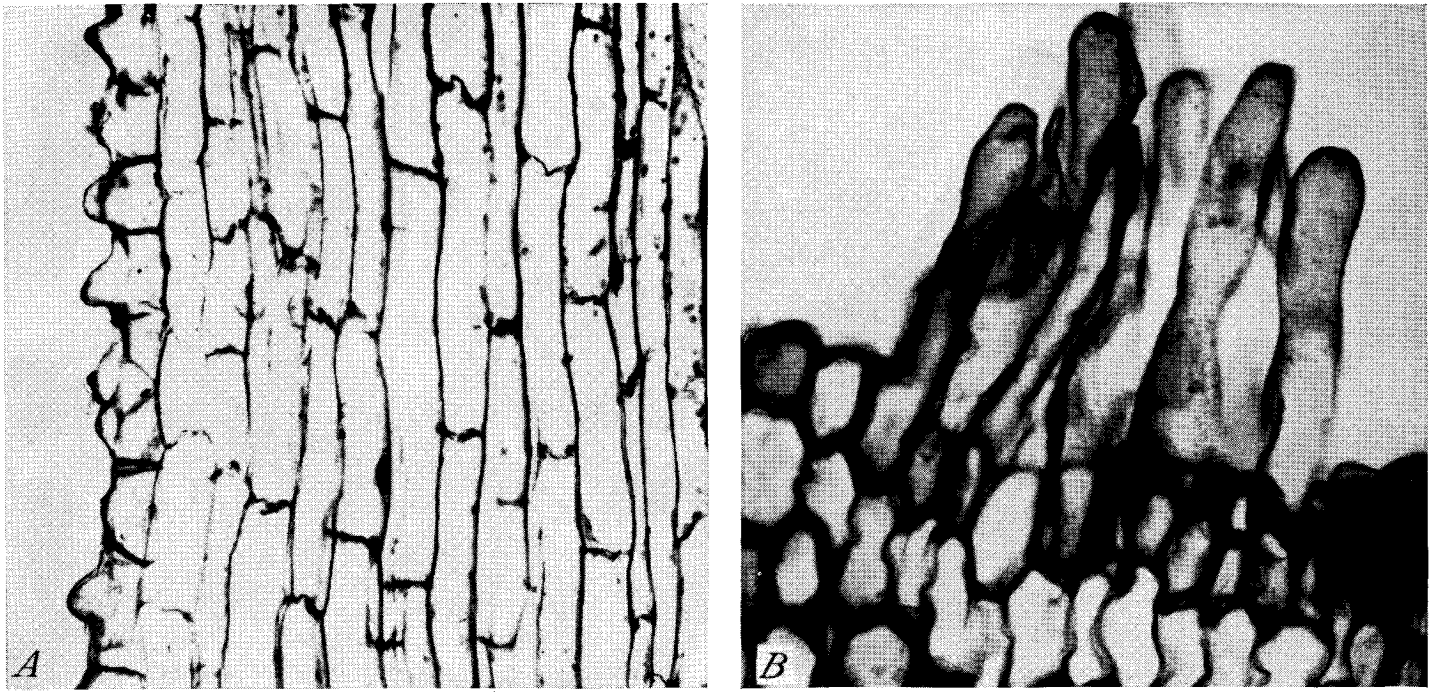

FIGURE 5.—*A*, Longisection of primary root showing early stage in development of root hairs. × 450. *B*, Transection showing older root hairs. × 800.

form a protective layer. Frequently the hypodermal cells enlarge slightly in the radial dimension, and then periclinal divisions occur, the layer functioning as a phellogen to produce a periderm (fig. 6). in other cases the cells may elongate radially and increase in size until the radial dimension approximates 65μ and the tangential one 30μ to 35μ, giving the layer a palisaded appearance (fig. 7, A). This may be restricted to scattered loci and result later in the formation of ienticels. The enlarging hypodermal cells form a convex protrusion on the root surface! and the overlying epidermal cells are eventually ruptured. The hypodermal phellogen produces comple-

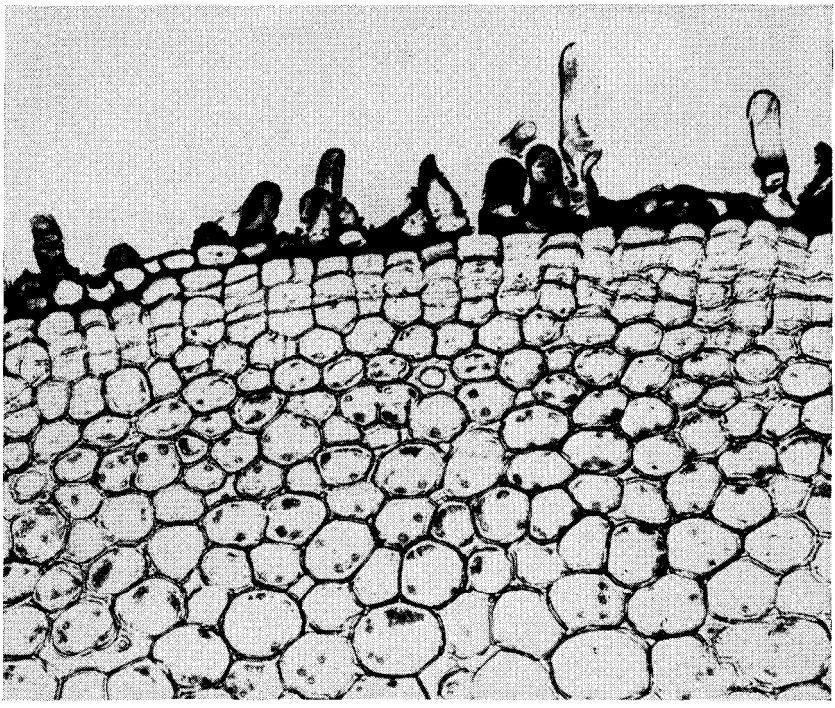

FIGURE B.--Transection of primary root showing the hypodermal periderm and persistent root hairs. X 236.

mentary cells that become somewhat rounded at the angles forming intercellular spaces (fig. 8).

SECONDARY ROOT HAIRS

As the epidermis breaks down single hypodermal cells may elongate and form secondary root hairs, which approximate the length of the shorter epidermal root hairs but have a greater diameter (fig. 9, A). The walls of these cells ultimately become suberized, but. prior to that time they probably function as absorbing structures.

Pinkerton (15) found a somewhat similar development of root hairs in several members of the Commelinaceae in which short, thick,

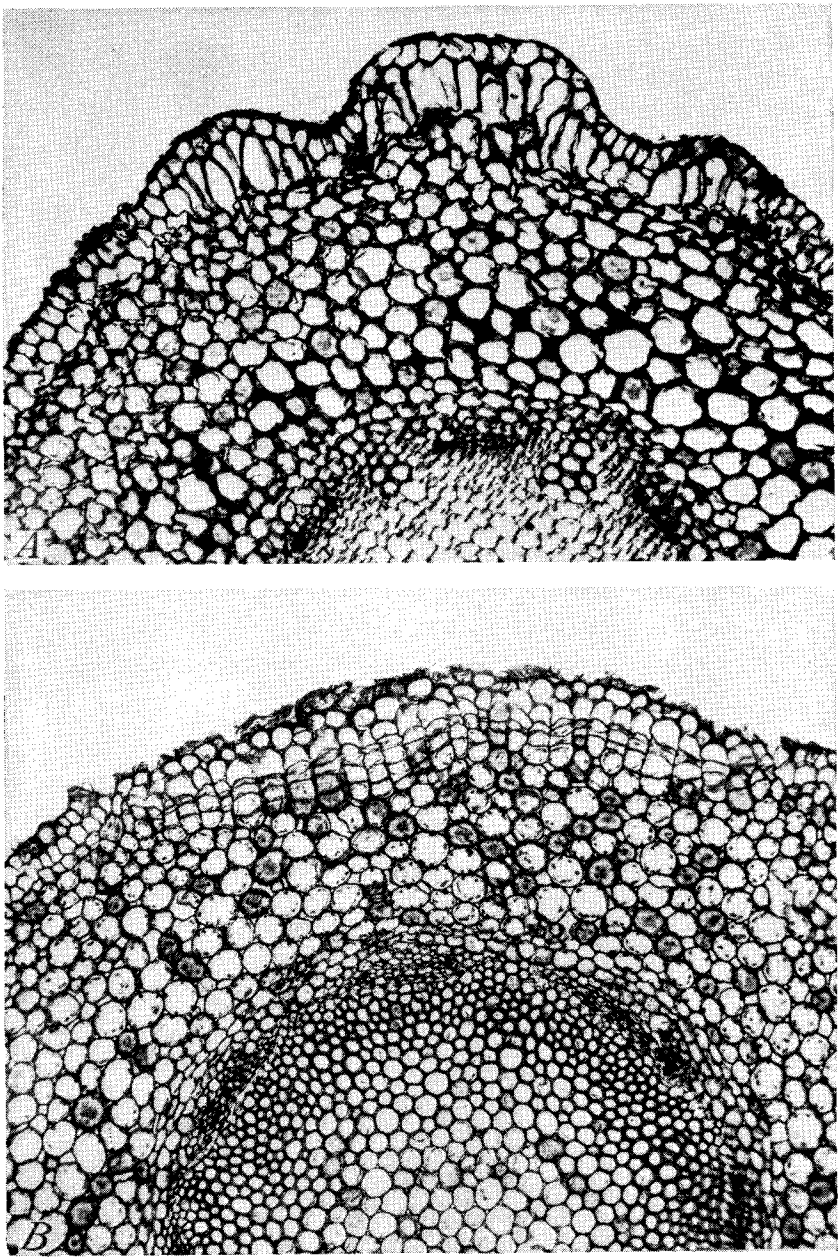

FIGURE 7.—*A*, Transection of primary root showing the development of a palisaded periderm. The differentiation of the primary xylem is about complete. × 190. *B*, A somewhat older portion of primary root showing the hypodermal phellogen. The walls of the conjunctive cells in the stele and the peripheral cells of the pith are thickened. × 135.

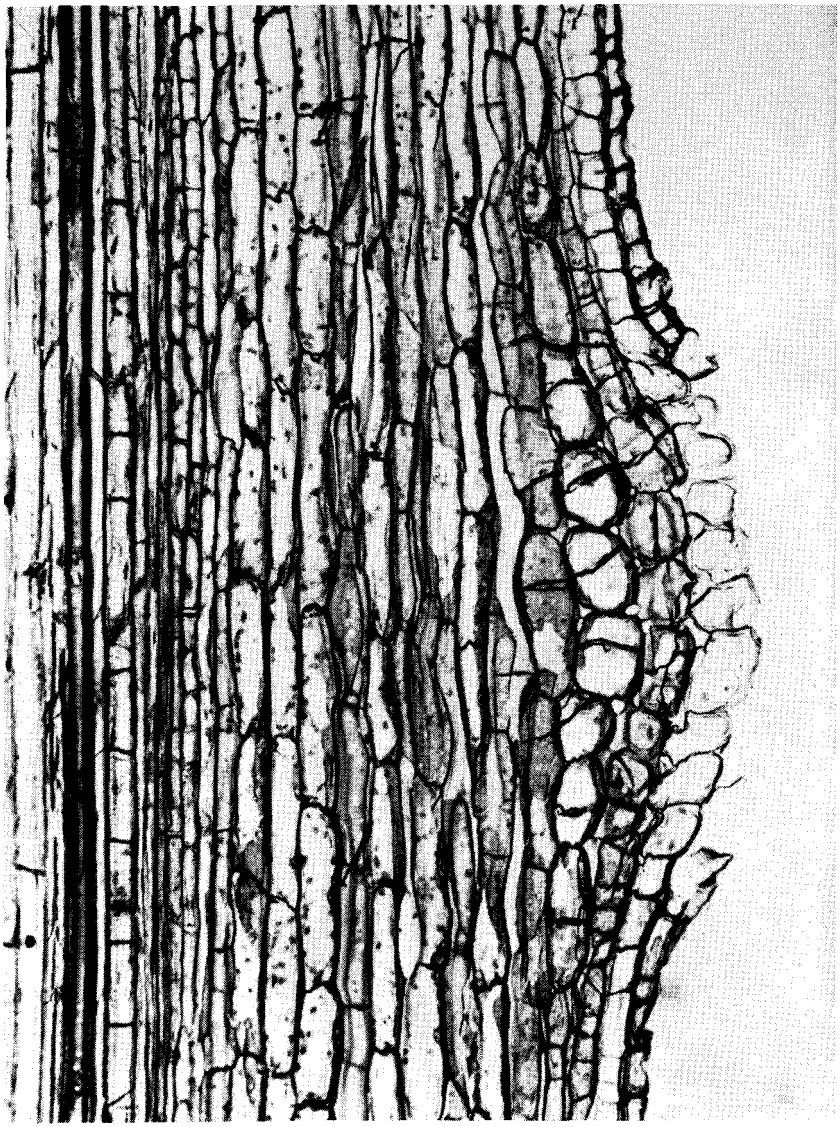

FIGURE 8.--Longisection of root showing development of lenticel as a result of the activity of the hypodermal phellogen. X 215.

russet root hairs mere formed in addition to the long, slender, transparent ones. The former were of secondary origin and came from the esodermis superseding the primary hairs. They usually developed several centimeters from the root tip in the zone bearing the older hairs. She found the physical structure of the secondary root hairs to be different, from that of the primary ones and because of their thick walls suggested anchorage as a function, although she felt that absorption might be possible.

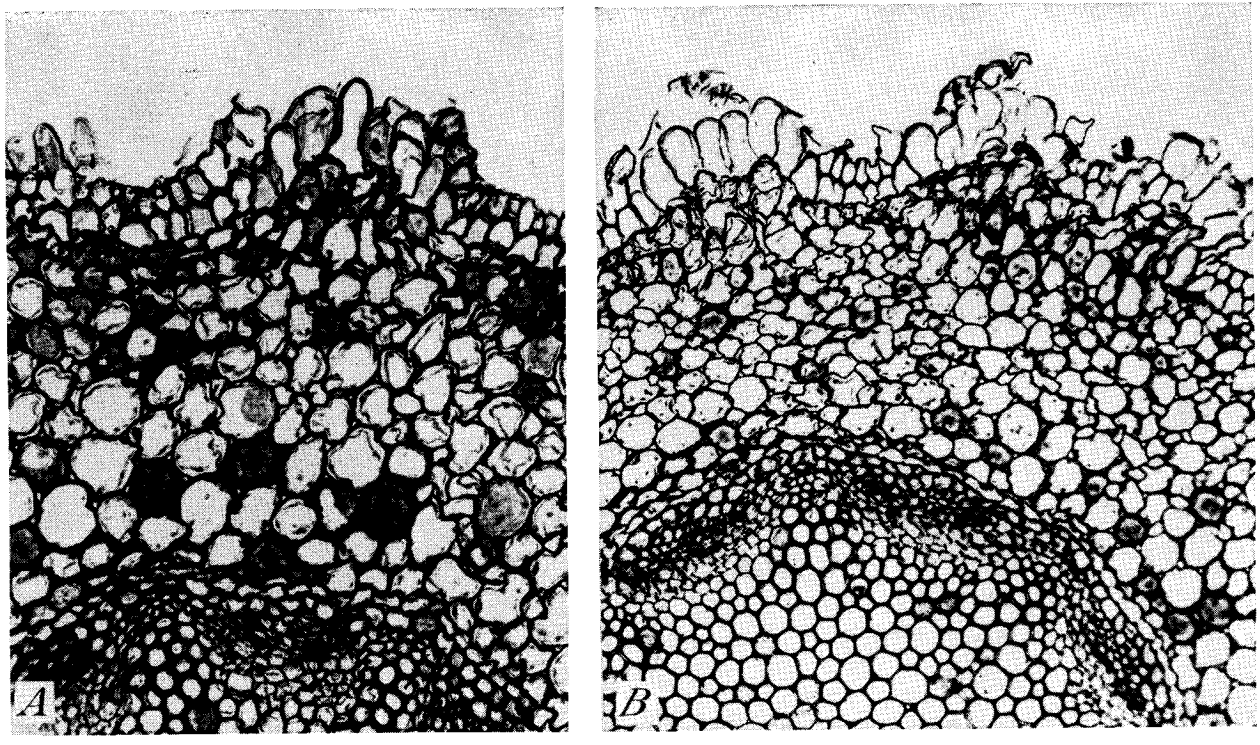

FIGURE 9.—*A*, Transection of root showing secondary root hairs arising from the hypodermal layer. × 210. *B*, transection of root showing absorbing or "transfusion cells" arising from the hypodermal layer. × 155.

HYPODERMAL ABSORBING AREAS

The formation of hypodermal absorbing areas also occurs. In this instance groups of hypodermal cells enlarge radially and tangentially, rupture the epidermis, and become functionally absorptive (fig. 9, B). Unlike the lenticular development the hypodermal cells do not divide periclinally at first, although they may do so later in ontogeny. Leavitt (11) observed that, epidermal root hairs may be replaced by a "transfusion-cell piliferous layer" derived from the cortex. The walls of the "transfusion cells" differed from those of the other hypodermal cells in that they were not cutinized.

CORTICAL PARENCHYMA AND ENDODERMIS

The cortical parenchyma between the hypodermis and the endodermis consists of 10 to 20 rows of cylindrical cells. Longitudinal intercellular spaces occur owing to the curvature of the vertical walls. The endodermal cells have Casparian thickenings on the radial and end walls. These are well differentiated by the time the primary xylem is mature and the walls of the conjunctive tissue have begun to thicken. There is no pronounced secondary thickening of the tangential walls.

THE STELE

The primary root commonly has an octarch radial siphonostele although there are occasionally seven or nine protoxylem strands. The protophloem is the first stelar tissue to develop. In many plants, owing to the absence of distinguishing histological characters, it is difficult to determine the formation of this tissue, but this is not the case with the Valencia seedling owing to the early development of the primary phloem ducts. These occur at the outer limit of the primary phloem abutting the pericycle. As seen in transection there is a large central cell which is surrounded by four to six cells (fig. 10, A). The central cell becomes more vacuolate than the surrounding ones, the cell contents and end walls disappear, and a lysigenous duct is formed consisting of a longitudinal series of central cells. The ducts are not readily observed in the older portions of the root axis as the adjacent cells enlarge, but they apparently function as long as the primary phloem persists.

As the phloem is differentiating the first protoxylem elements are formed on radii alternate with the strands of primary phlocm (fig. 10, B). The development of the subsequent primary xylem elements is centripetal. Unlike most dicotyledonous roots, there is a pith, and the central portion of the axis does not differentiate to form a protostele of xylem tissue (fig. 11). But the eight strands of primary xylem are connected by thick-walled conjunctive tissue, and later in ontogeny the thickening of the walls of the medullary parenchyma continues centripetally until all the cells in this region are thick-walled.

The long, slender protoxylem elements of the root are most commonly scnlariform or reticulate. Annular or spiral elements rarely occur although they are numerous in the stem and in the upper transition region of the hypocotyl, where they form the primary xylem of the cotyledonary traces. In the scalariform elemeuts the bars are very

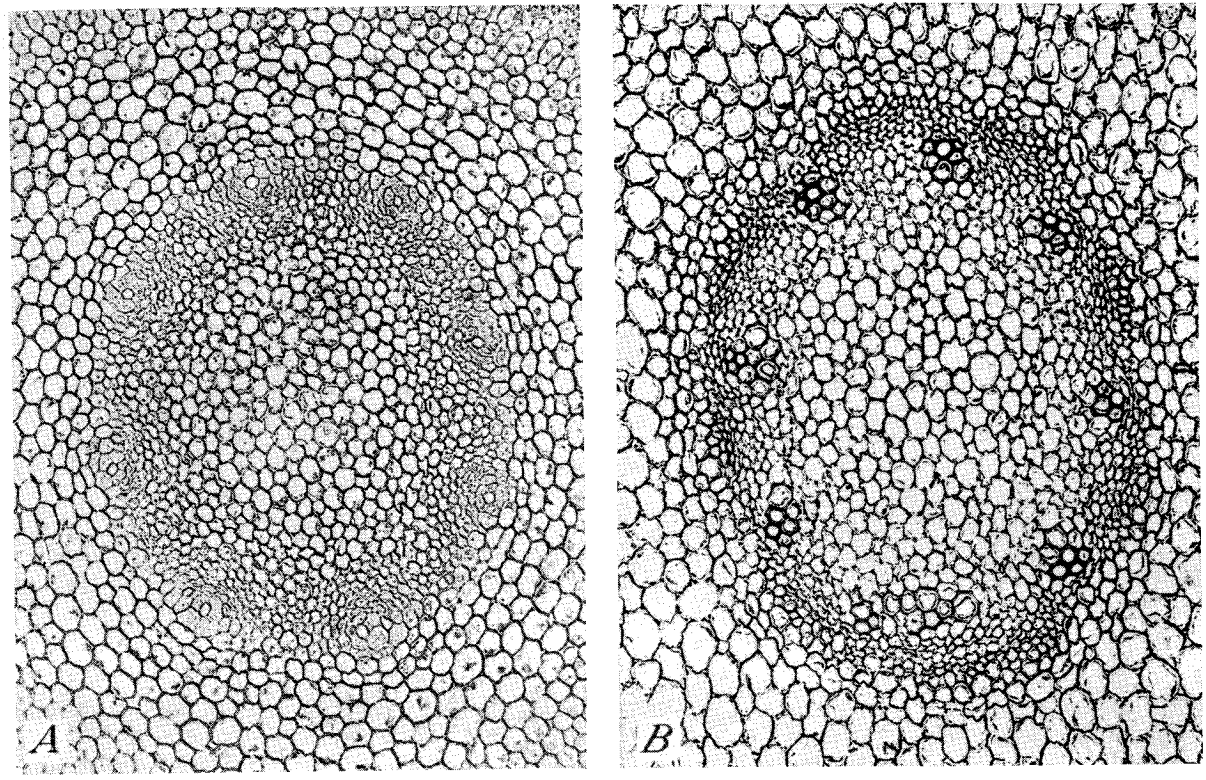

FIGURE 10.—*A*, Transection of primary root showing early differentiation of primary phloem ducts. *B*, Transection at a higher level showing differentiation of protoxylem. × 170.

thin, and this type grades into a loosely reticulate form. The metaxylem elements are pitted, and the end malls that are usually slightly oblique have simple perforations.

As reported by Solereder (20) for other genera of Rutaceae, the pits of the vessel segments are bordered where they are adjacent to xylem parenchyma, and the tracheids also have bordered pits. The wood fibers have long sharply tapered ends and simple pits. The cells of the xylem parenchyma are rectangular in transection, axially elongated, and have simple pits except as noted above.

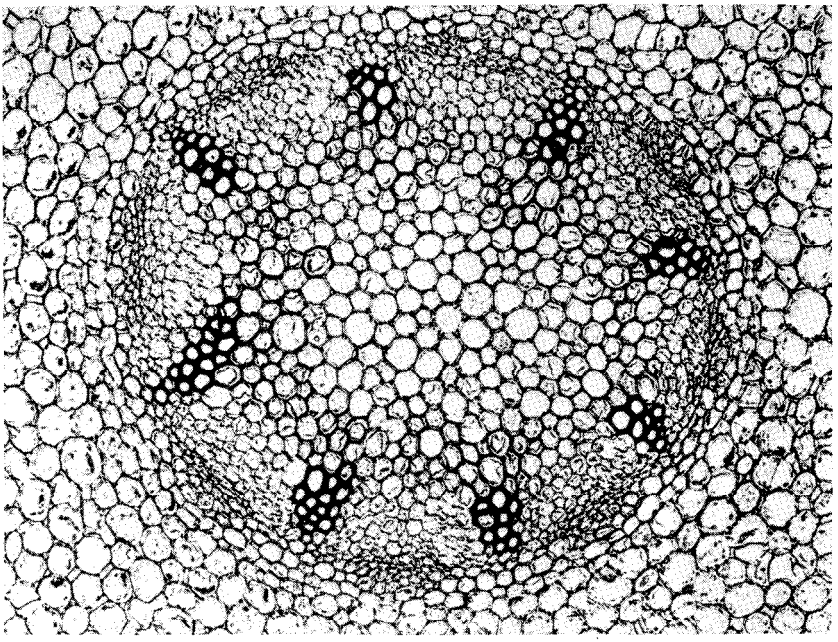

FIGURE 11.--Transection of octnrch primary root showing complete differentiation of protoxylem and metaxylem and the initiation of wall thickening in the conjunctive cells between the xylem strands. X 755.

The early differentiation of the primary phloem duct has been described (p. 18). Abutting the centratl face of the duct is a semicircular zone of protophloem elements that are thin-walled, slender, and as long as the protoxylem cells. The metaphloem elements are larger in caliber, and usually there are solitary sieve plates on the slightly oblique end walls. Companion cells and parenchymu are also differentiated adjacent to the sieve tubes.

LATERAL ROOT FORMATION

The formation of lateral roots is initiated as the metaxylem is maturing. The primordia arise in the pericycle at points abutting the protoxylem (fig. 12, A and B). Periclinal and anticlinal divisions of the pericyclic cells result in the organization of meristematic growing points of the lateral roots. As the secondary root continues to develop, its growth results in rupturing the cells of the cortex, but

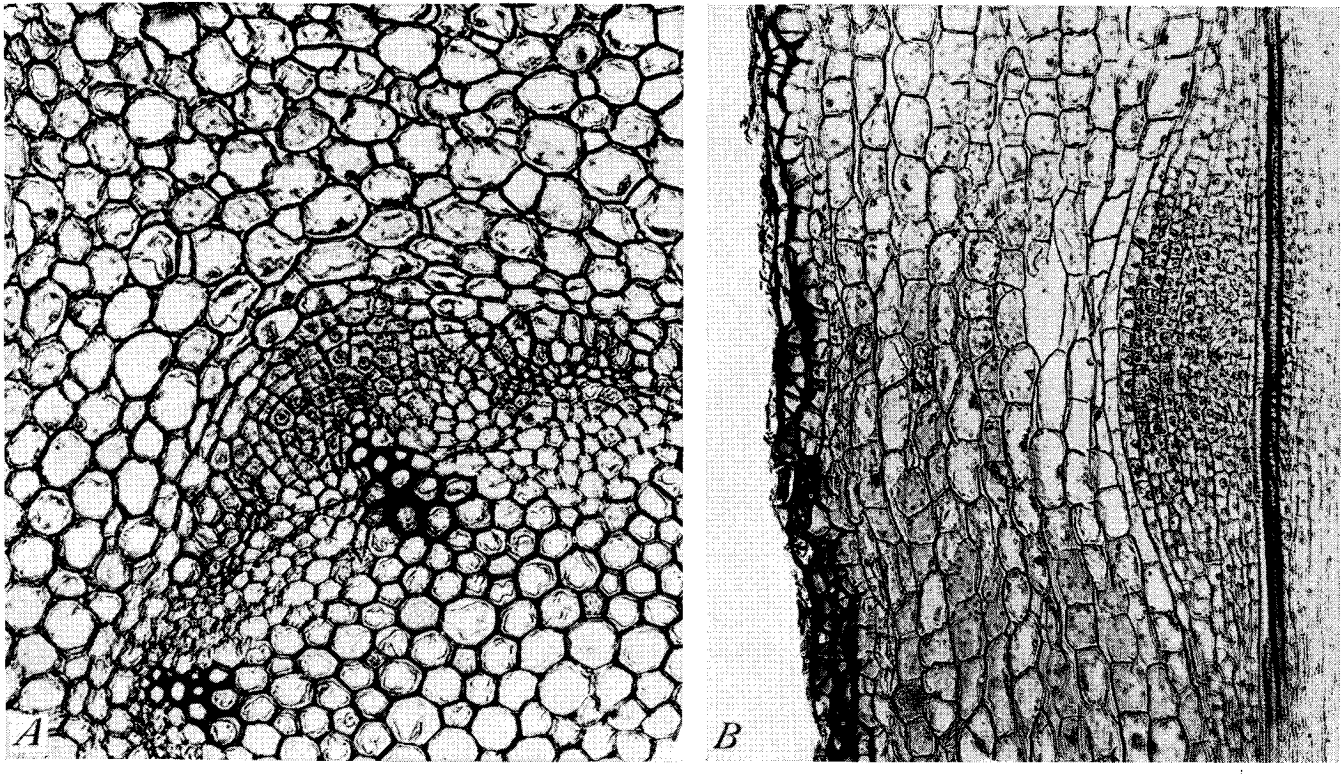

FIGURE 12.—*A*, Transection of primary root showing pericyclic origin of lateral root. × 265. *B*, The same in longisection. The endodermal cells are longitudinally stretched and radially flattened, owing to the growth of the meristem of the lateral root. × 155.

there is also some digestion of cortical tissue. At first the endodermal cells adjacent to the tip of the lateral root compensate for its growth by dividing anticlinally, but ultimately they are stretched and broken by the emerging root (fig. 13).

The ontogeny of the lateral root and its final structure resemble that of the primary root, but there is wide variation in the NUMBER

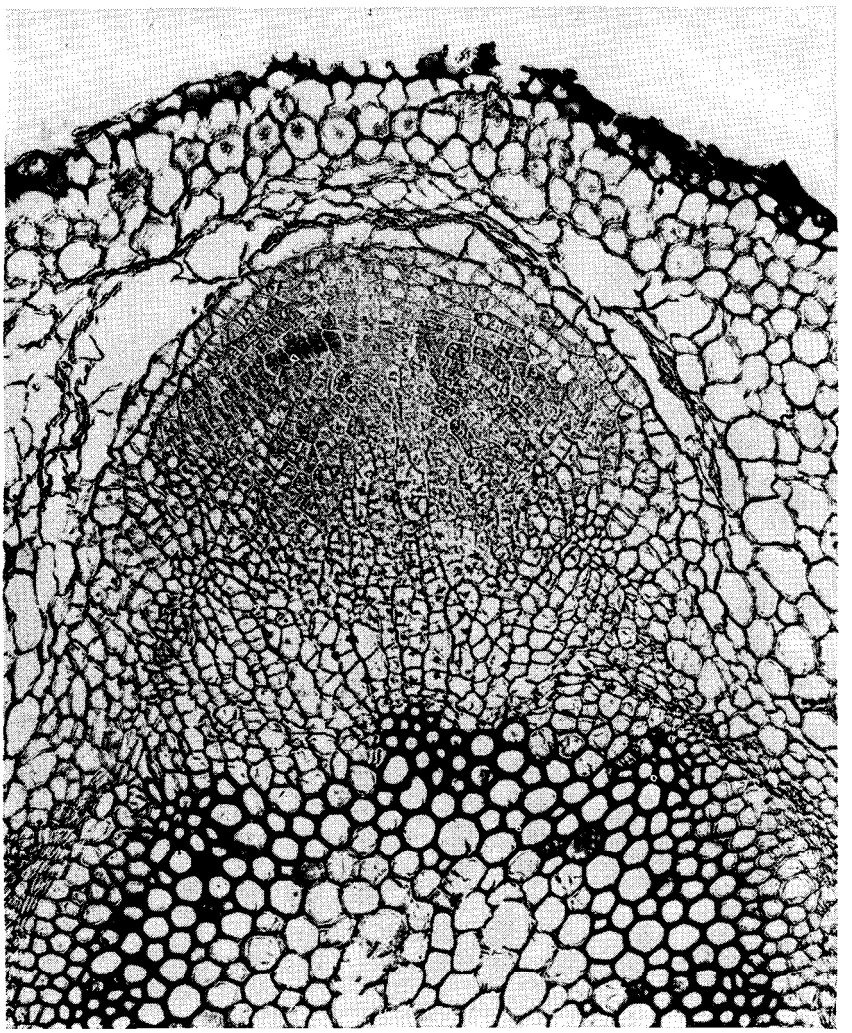

FIGURE 13.--Transection of the primary root showing penetration of lateral root through the cortex. Some of the endodermal cells have divided radially to compensate for the growth of the lateral root. x 196.

of protoxylem strands that are differentiatetl. The lateral roots of Valencia and other strains of sweet orange have been observed with patterns ranging from triarch to octarch, the tetrarch and pentarch being the most common types (fig. 14, A).

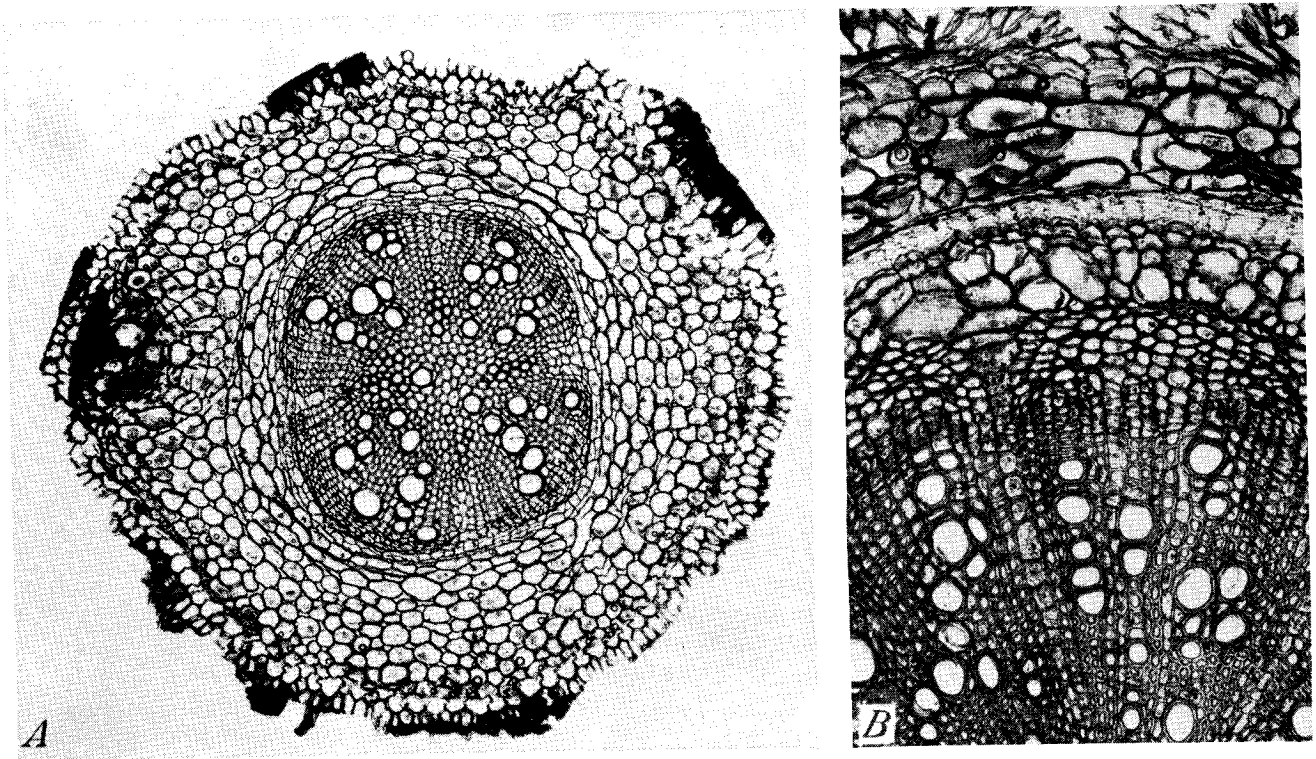

FIGURE 14.—*A*, Transection of a tetrarch lateral root of the sweet orange. The first tangential divisions of the pericyclic cells to form a periderm have occurred. × 115. *B*, Sector of an older root in which the pericyclic periderm is in a more advanced stage of development. × 195.

In view of the character of the primary root of the Valencia seedling it seemed desirable to investigate the lateral roots of the Valencia and other sweet orange rootstocks taken from mature trees, in order to determine whether or not the same absorbing structures occurred. Sweet orange roots from bearing trees in several representative orchards were obtained, as well as roots from a Valencia tree propagated from a cutting of a Valencia parent.

Aside from the variation in the number of arcs noted above, the development of the lateral root resembles that of the primary root in the formation of primary root hairs, the development of hypodermal absorbing areas, and the occurrence of lenticels.

SECONDARY THICKENING OF THE ROOT

The Valencia orange is not usually grown on its own rootstock owing to the limited production of seeds, which may be less than five per fruit. Commonly, the seeds used in growing rootstocks are obtained from carefully selected seedling trees of sweet orange (Citrus sinensis) or sour orange (C. aurantium L.).

Older lateral roots of sweet orange and Valencia were examined to investigate the secondary thickening of the root axis. Secondary thickening begins at about the time that the cell walls of the conjunctive tissue start to thicken, and cambial activity is initiated at points in the fundamental parenchyma between the strands of primary xylem and centrad from the primary phloem.

The secondary tissues of the root are similar in structure and arrangement to those described by Webber and Fawcett (27) for the stem. The wood is diffuse porous! but growth rings can be distinguished owing to somewhat smaller and more compactly arranged vessels at the outer limit of each ring. The vessels are arranged in radial rows and may occur singly or in small groups. The wood fibers are very numerous. forming solid zones between the wood rays except where there are vessels. The xylem parenchyma is diffuse although a vasicentric distribution is not uncommon (fig. 14, A).

The secondary phloem consists of sieve tubes. companion cells, storage and crystal-bearing parenchyma,, and fibers. It has a banded appearance owing to the differentiation of tangential bands of fibers which form the outermost portion of each growth zone. The intervening bands of sieve tubes and companion cells become crushed as the root increases in diameter (fig. 15).

As noted by Solereder (20), one of the characteristics of the Rutaceae is the formation of a hypodermal periderm (figs. 6 and ‘7, B). In the sweet. orange root cambial activity is relatively slow, and the cortex and cortical periderm persist for some time. Later in ontogeny, periclinal divisions of the pericpclic cells form a zone of parenchyma, a phellogen arises in the layer adjacent to the endodermis, and the cortical tissue is crushed and ultimately lost (fig. 14, *B)*.

THE VASCULAR TRANSITION

The two fleshy cotyledons remain within the split seed coat during germination. Because of the hypogeal habit and the frequent. occurrence of polyembryony there may be considerable distortion of the

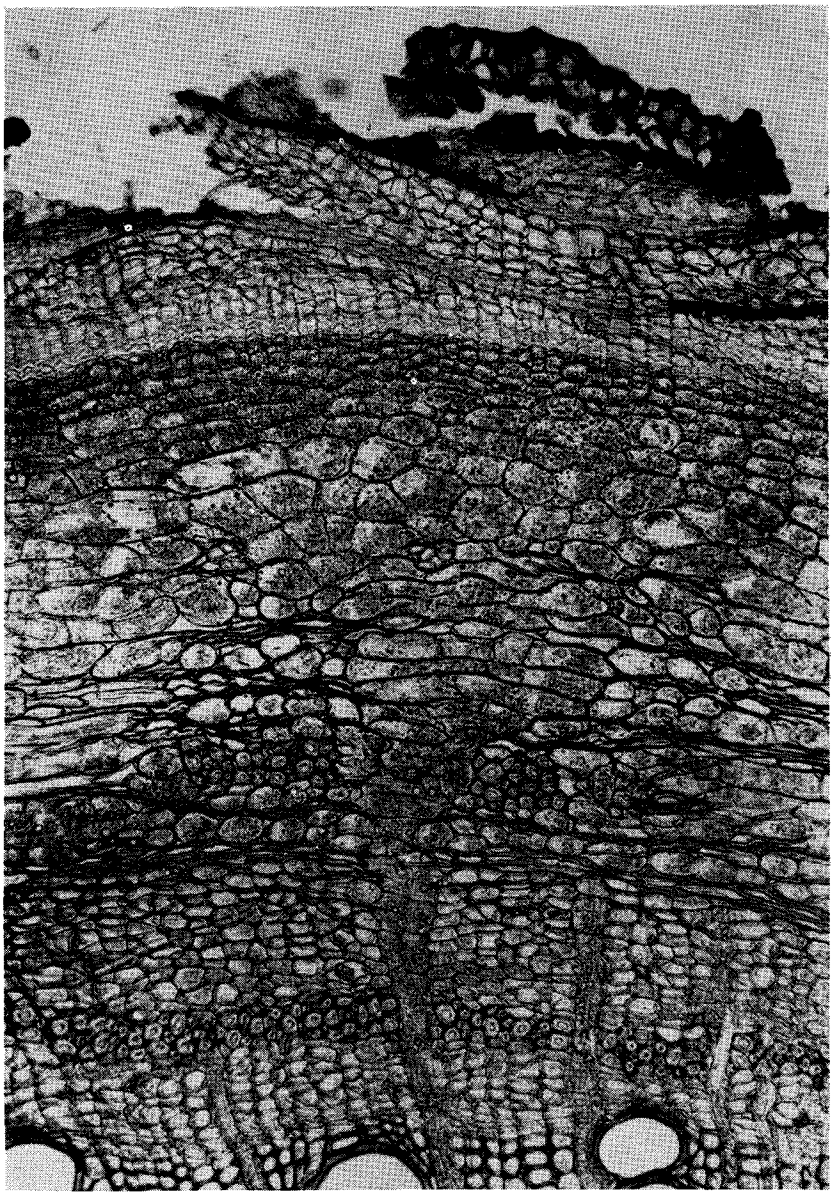

FIGURE 15.—Transection of a 3-year-old lateral root showing banded phloem. The zones of phloem fibers alternate with the bands of parenchyma, sieve tubes, and companion cells. The latter are crushed in the first two cycles of growth. × 180.

cotyledons and variation in their orientation with respect to the hypocotyledonary axis. In some instances the cotyledons are not opposite, one being placed above the other, and the cotyledouary traces enter the axis at different levels.

The cotyledonary bundles are subamphicribal with the primary phloem almost surrounding the endarch primary xylem (see fig. 18, G). In contrast to the root, the protoxylem elements have annular, spiral-annular, and spiral wall thickenings.

At the cotyletlonary node the traces form two arms of vascular tissue in the provascular ring of the axis. At right angles to the cotyledonary plane there are two epicotyledonary bundles which are downwardly differentiating leaf traces of the first foliage leaves (fig. 16). The latter have no direct connection with the primary vascular sys-

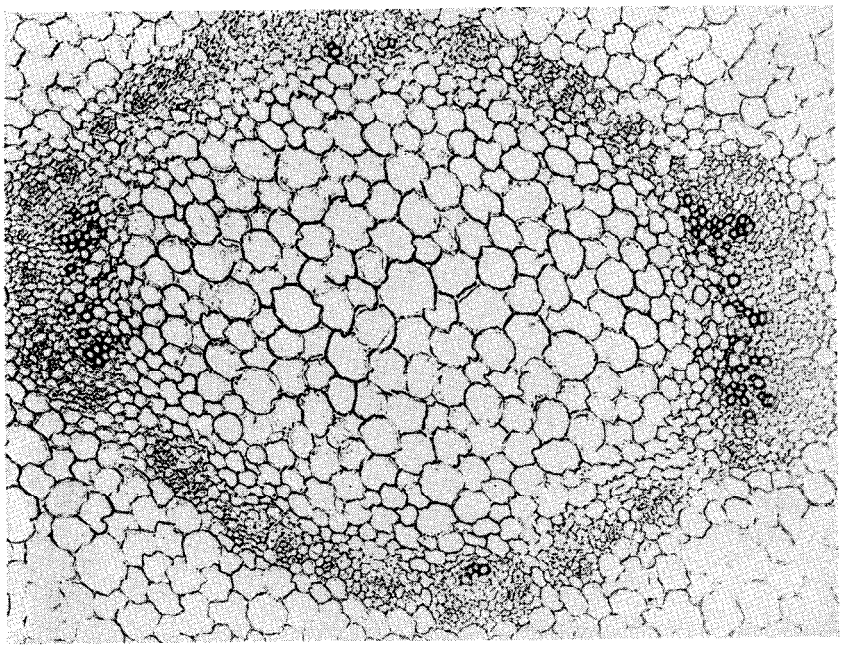

FIGURE 16.--Transection of the seedling axis at the cotyledonary node showing the cotyledonary traces (right and left) and those of the first two foliage leaves (top and bottom). X 126.

tem of the hypocotyl until later in ontogeny when the cambium produces a continuous cylinder of secondary xylem.

Below the cotyledonary node each cotyledonary trace is broadened tangentially and at the lower level forms three strands of primary xylem with the phloem in a collateral position with respect to them (see fig. 18, F). As in the root the differentiation of the phloem precedes that of the xylem, and there is a complete cycle of phloem strands differentiated around the periphery of the provascular cylinder in **advance** of the primary xylem elements.

As in many hypogeal types the transition region is short and the reorientation of primary vascular tissues from the endarch collateral to the alternate exarch relationship is abrupt, occurring within a few millimeters of the cotyledonary node. At the lower limit of the transition region the xylem strands occupy alternate radii to the phloem groups (fig. 17, 4 and B) The general arrangement of the primary vascular tissue in the root and transition region is shown diagrammatically in figure 18, A to G.

THE FIRST INTERNODE

The first internode is oval or round in transection. Its length varies considerably depending in part upon the depth at which the seed is planted; but it is commonly 4 to 5 cm. long by the time the first pair of foliage leaves is fully expanded.

In the young internode the epidermis is glabrous except for a few short conical unicellular hairs, which are more numerous near the second node. There is an early development of lenticels, which arise from a hypodermal phellogen subjacent to the somewhat raised stomata. The stomata are not numerous, but they may occur on the subterranean portion of the internode and occasionally on the hypocotyl near the cotyledonary node.

The cells of the cortical parenchyma are cylindrical and about three to four times as long as broad, with intercellular spaces at their angles. Those adjacent to the epidermis are smaller and more compactly arranged than those nearer the stele; and oil glands, similar to those occurring in the leaves, develop in the peripheral region (fig. 19).

In the stele the development of the primary phloem precedes that of the xylem, forming an almost continuous cylinder of strands. The development of the primary xylem is endarch, and the protoxylem elements have annular: spiral, and spiral-annular wall thickenings fig. 20).

The walls of the conjunctive cells begin to thicken as the differentiation of the primary xylem is completed and cnmbial activity is initiated. The secondary xylem is like that described for the root. Pericyclic fibers develop outside the strands of primary phloem. In the tlevrlopment of secondary phloem each growth ring consists of an outer zone of fibers and an inner one of sieve tubes, companion cells, and parenchyma. As in the root the older intervening groups of sieve tubes and companion cells become crushed as the diameter of the stem increases.

THE FIRST FOLIAGE LEAVES

The first foliage leaves are opposite and simple, differing in this regard from the other leaves, which are alternate and unifoliately compound. The deep-green, glabrous blade is oval or ovate, unequally rounded at the base and acute, obtuse or retuse at the apex (fig. 2). The margin is undulate or crenate and thickly beset with translucent oil glands These are also distributed rather regularly in the vein islets of the mesophyll. The venation is pinnate and the main lateral veins anastomose near the leaf margin, so that the vas-

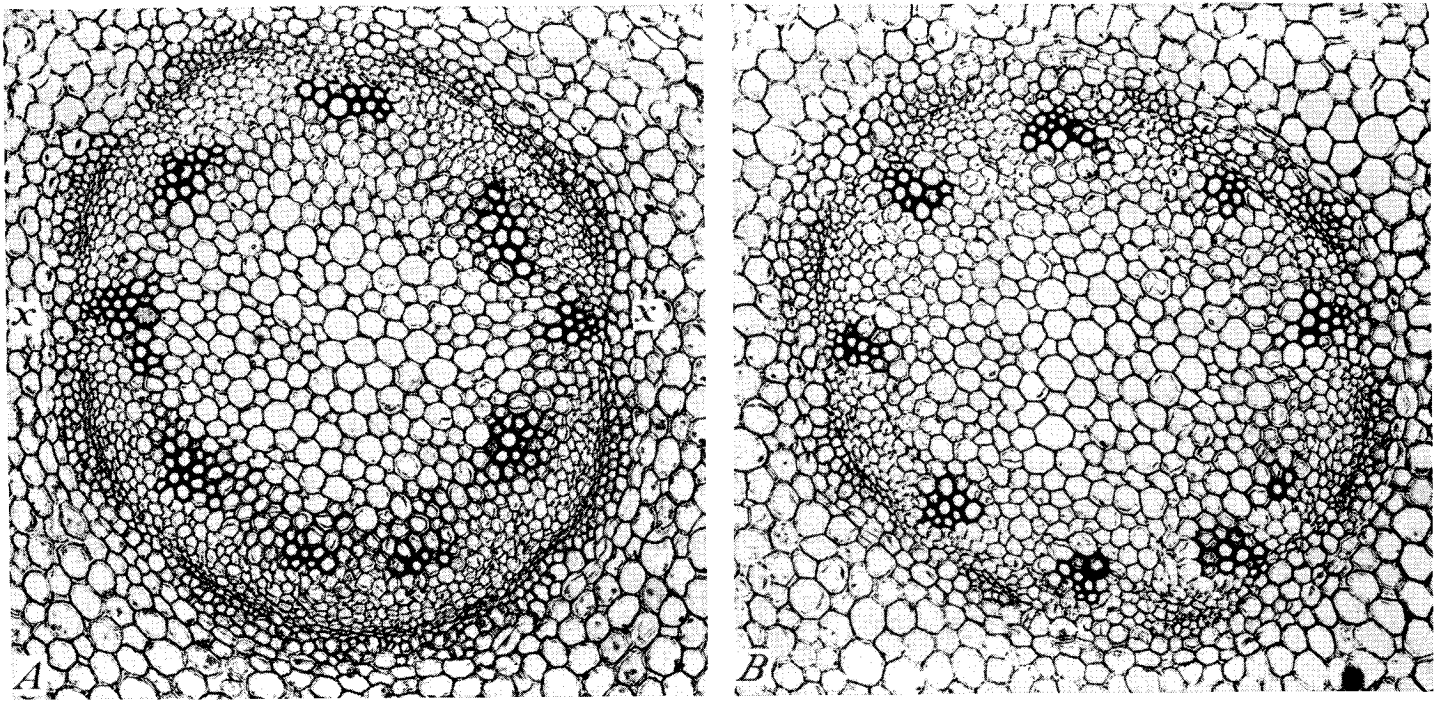

FIGURE 17.—*A*, Intermediate stage in vascular transition. The plane of the cotyledons is indicated by the letters *x–x*. *B*, Lower transition zone in which the octarch pattern is essentially rootlike. × 150.

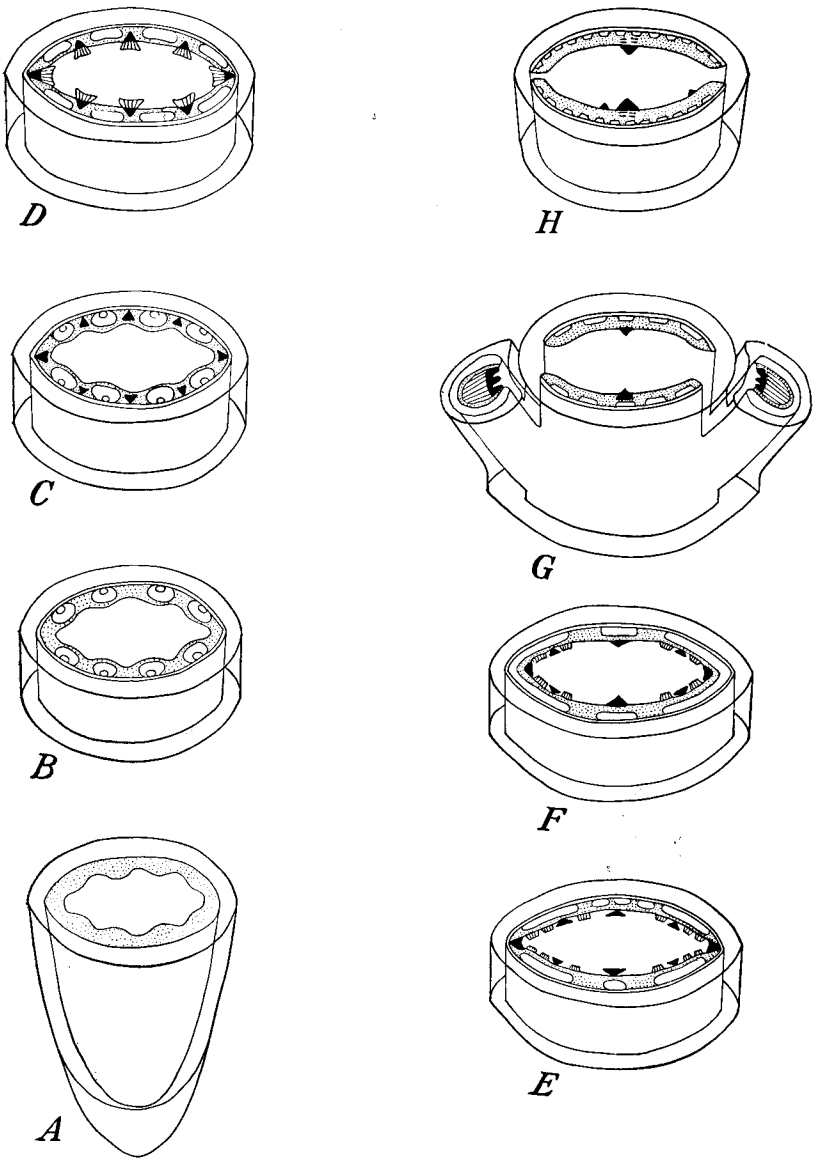

FIGURE 18.—Diagrammatic representation of the vascular transition showing segments of axis from root tip (*A*) to first internode (*H*). The solid black areas represent protoxylem; lined regions, metaxylem; clear zones, primary phloem; and stippled ones, provascular tissue.

cular system is closed except for the ultimate veinlets that terminate in the vein islets.

At first the subconical primordium elongates to form the short petiole and midrib. This is followed by a lateral growth, which results in the formation of the lamina. At this time the two halves of the blade are oriented with their adaxial surfaces opposed, and they remain in this position until the leaf is several millimeters in length.

Except in the region of the provascular strands the young leaf primordium is usually 12 cell lagers in thickness (fig. 21, fl). The 2 protodermal layers differentiate as the upper and lower epidermal layers. Stomata develop only in the lower one. The 10 internal layers of the ground meristem produce the mesophyll. These

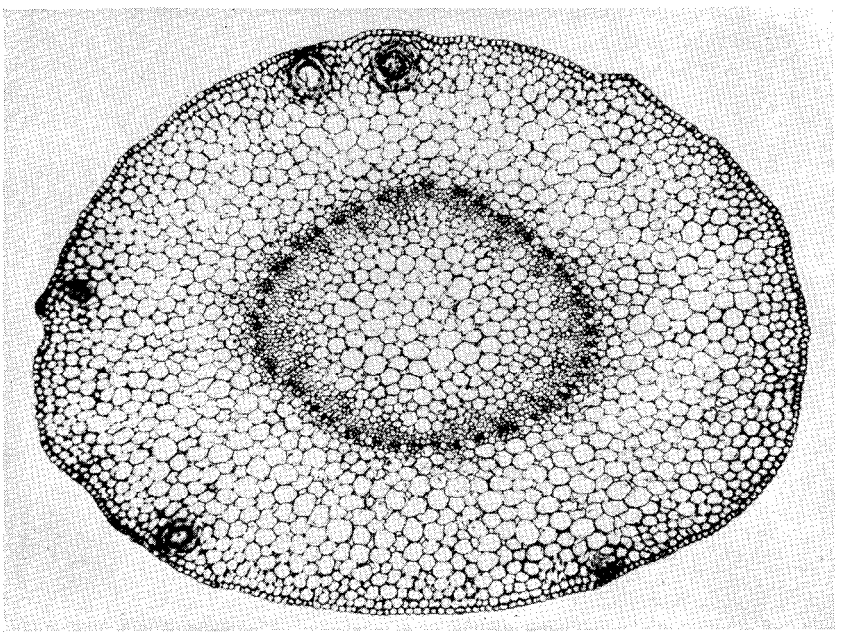

FIGURE 19.--Transection of the first internode prior to secondary thickening showing vascular ring with numerous primary phloem groups and oil glands in cortex. X 80.

layers are compact and without intercellular spaces at first (fig. 21, *A)*. The 2 adaxial layers form a palisade region, and the cells of the remaining layers enlarge and stop dividing before the palisade cells and the epidermal layers do. The continued growth and division of the cells of the palisade and epidermis create stresses that result in the development of schizogenous air passages in the spongy parenchyma. The cells of the spongy parenchyma adjacent to the palisade cells and those abutting the lower epidermis are more compactly arranged than the intervening ones (fig. 21, B).

The mature leaf resembles the unifoliate compound leaf in the structure of the mesophyll (fig. 33, *A)*. Schizolysigenous oil glands

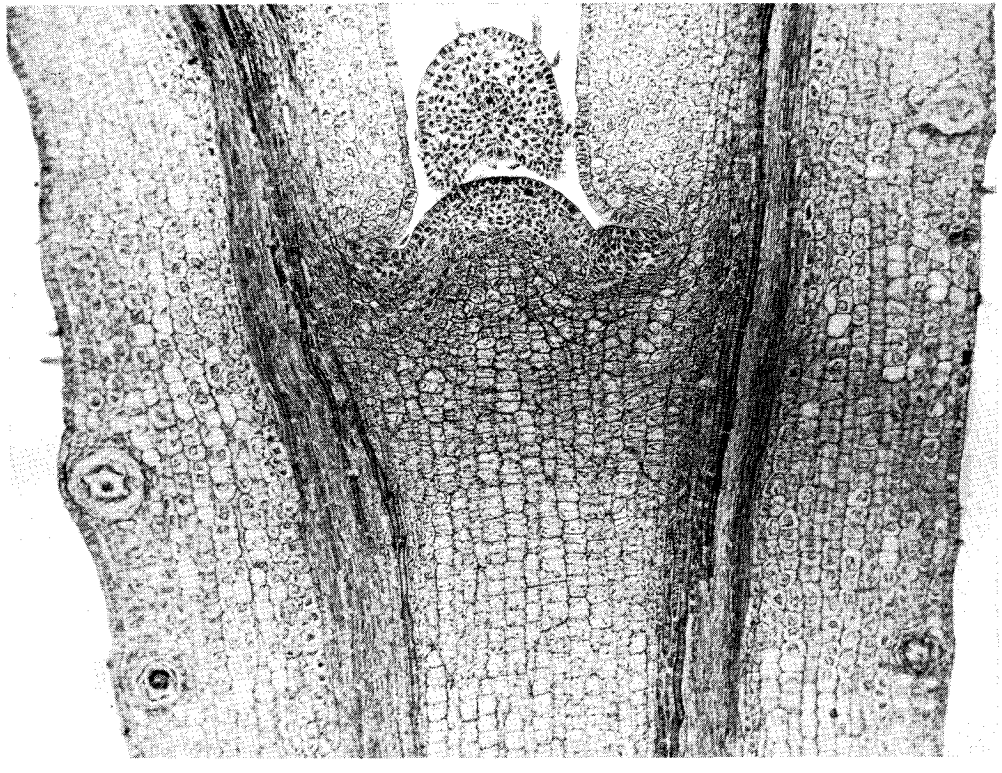

FIGURE 20.—Longisection of the apex of the seedling axis showing the growing point and the divergence of the first pair of foliage leaves. The young third leaf is shown in transection. × 115.

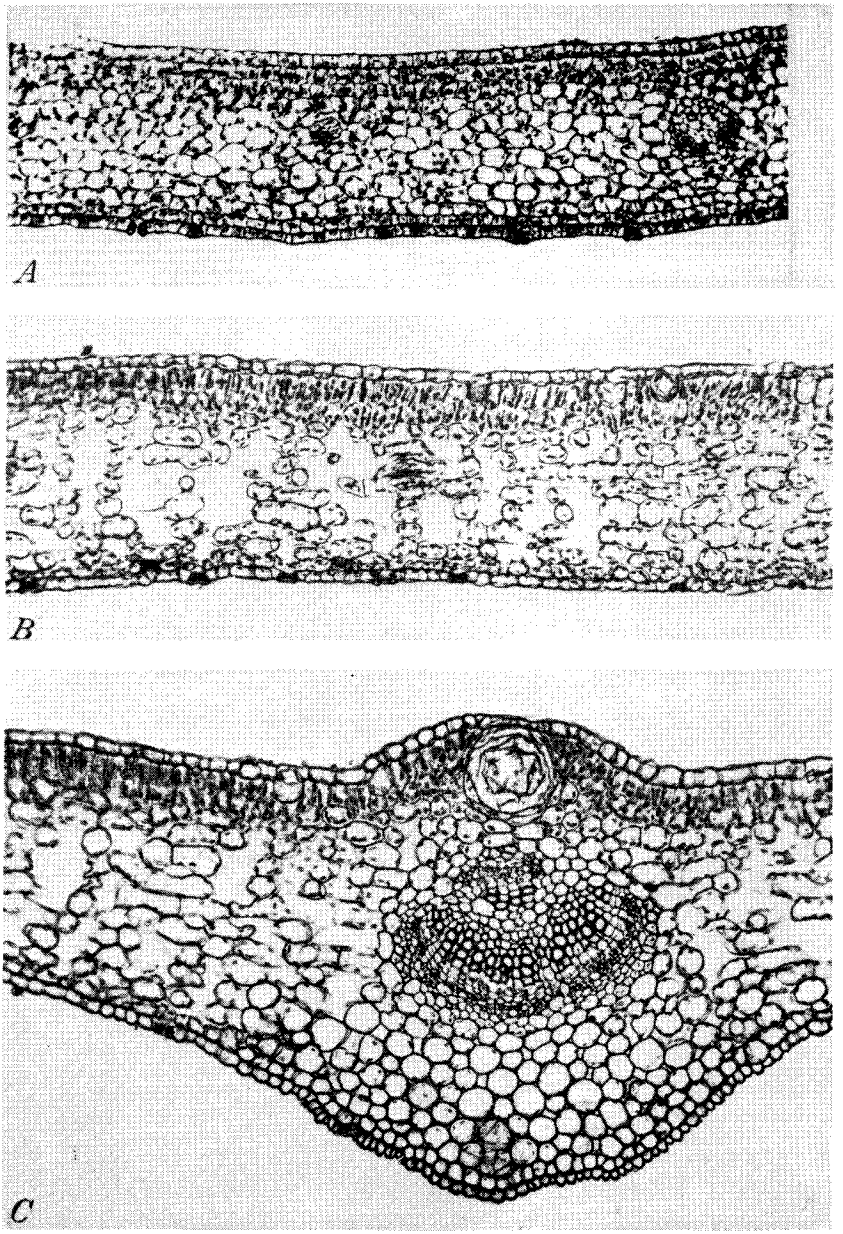

FIGURE 21.—*A*, Transection of a portion of the blade of a young first foliage leaf. The mesophyll is still compact with few intercellular spaces, and two rows of potential palisade cells can be distinguished from the spongy cells. Stomata develop only on abaxial surface. *B*, Transection of a nearly mature first foliage leaf showing compact palisade and spongy parenchyma with larger intercellular spaces. *C*, Transection through the midrib of the first foliage leaf, showing arrangement of vascular tissue. An oil gland has formed above the vein and crystal-containing cells arising in the palisade layer have grown between the adjacent epidermal cells. × 170.

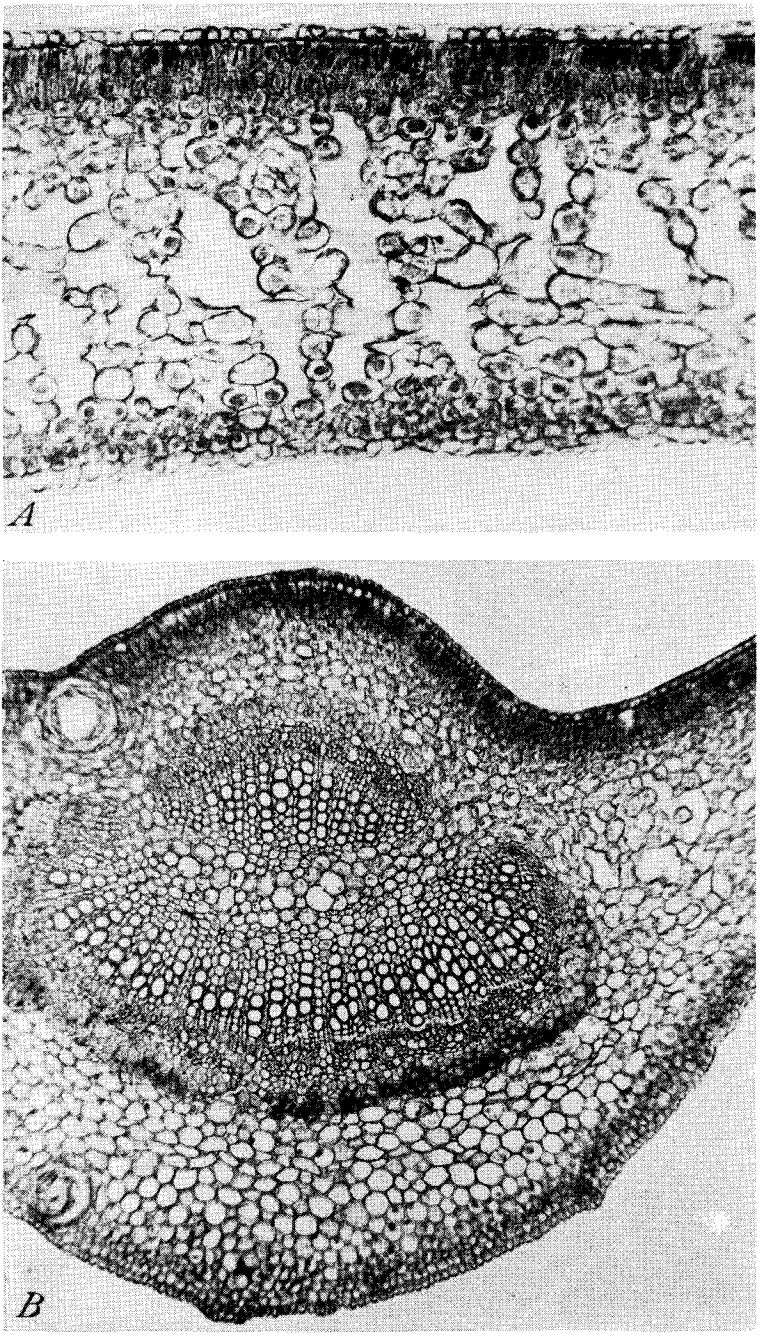

FIGURE 22.—*A*, Transection of a portion of the blade of a mature foliage leaf taken from a bearing tree. × 185. *B*, Transection of the midrib of the same leaf showing arrangement of the vascular tissues. × 100.

are present in the mesophyll, arising early in ontogeny (fig. 22, B). Calcium osalate crystals are numerous in the subepidermal layer of the palisade and slightly less so in the subepidermal spongy layer. The crystal-containing cells frequently appear to be of epidermal origin owing to the manner in which they become wedged between the overlying epitlermal cells (fig. 21, B).

The main vein of the leaf consists of two groups of vascular tissue which are smaller than those 'in the other foliage leaves, but similar to them in arrangement. The larger crescentic segment lies toward the abaxial face of the vein with phloem outermost. The smaller bundle occupies an adaxial position with the xylem and phloem in reverse orientation, so that the primary xylem elements of the two bundles lie opposed to each other separated by a narrow zone of parenchyma (fig. 21. C). Outside the phloem is a zone of mechanical tissue consisting of fibers. These are more numerous in the later formed leaves (fig. 22, B) . Both segments of the vein have a cambium, but there is more secondary thickening in the abaxial than in the adaxial unit. The lateral veins are collateral with adaxial xylem, and fibers occur only on the abaxial face of the bundle.

SUMMARY

The hypogeal development of the multiple seedlings of the Valencia orange (Citrus sinensis (L.) Osbeck) occurring in one seed complex is described, and the effects of resultant competition noted.

The terminal meristem of the primary root consists of three histogens-plerome, periblem, and dermatogen-calyptrogen. The plerome gives rise to the stele and the periblem to the cortex. The dermatogen-calyptrogen is a dual layer. Its distal cells produce the root cap, and the epidermis is derived from the cells at the proximal margin of the layer.

Cells of the epidermis develop as root hairs, and these may be very numerous under favorable soil conditions.

The root hairs finally become suberized or lignified and may then persist until after the hypodermal periderm is well developed.

The hypodermal layer may produce secondary root hairs or absorbing areas consisting of groups of thin-walled radially elongated hypodermal cells. In other instances lenticels are formed.

The primary root commonly has an octarch radial siphonostele in which the cells of the medullary region ultimately become lignified.

The primary phloem begins to differentiate before the primary xylem and is characterized by the early formation of primary phloem ducts which persist until the primary phloem is crushed.

The lateral roots of Valencia and other sweet orange strains have an ontogeny like that of the primary root and produce similar absorbing structures. They frequently differ from the primary root, in the number of strands of primary xylem. Patterns ranging from triarch to octarch have been observed, the tetrarch and pentarch types being the most common.

The growth in length and the secondary thickening of the root is slow. Under unfavorable conditions elongation may be so inhibited that the formation of the hypodermal periderm extends to the proximal margin of the root cap.

The vascular transition occurs in a very short portion of the hypocotyl immediately below the cotyledonary node.

The structure of the first internode and the development of the first pair of foliage leaves is described.

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