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ANATOMY OF PHASEOLUS VULGARIS
L. VAR. BLACK VALENTINE

THESIS FOR THE DEGREE OF PH. D.

Margaret T. Doult

1932

THESIS

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Doctor of Philosophy
Michigan State College

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THESIS

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ANATOMY OF PHASEOLUS VULGARIS L. VAR. BLACK VALENTINE.

Introduction

The first anatomical work on the genus Phaseolus was published by Nägeli (1858). He used two species, P. vulgaris and P. multiflorus, in his investigations of the course of the vascular bundles in the stem. Van Tieghem (1871) was interested primarily in the structure of the root and studied it during both primary and secondary growth.

It was not until 1872 that any very detailed studies were made on the anatomy of Phaseolus vulgaris. In that year Dodel (1872) published an extensive paper dealing with the course of the vascular bundles as well as with the structure of the tissues; however, this was only in the hypocotyl and root. Petit (1887) and Plitt (1886) investigated the petiole of the bean, and de Bary (1884) the differentiation of tissues in the root tip.

De Bold (1894) worked on three hundred species of the tribe Phaseolae, in an attempt to obtain anatomical criteria for the differentiation of the species. In his systematic work on the dicotyledons, Solereder (1908) pointed out various features of the anatomy of Phaseolus vulgaris.

More recently, Compton (1912) carried on an extensive study of the seedling structure of the Leguminosae. Harris (1921) investigated variations in the number of vascular bundles at different heights in seedlings. Within the last few years, many studies have been made on bean mosaic, a virus disease of great economic importance.

This study of Phaseolus vulgaris has been made with the purpose of tracing the course of the vascular tissue throughout the plant, and of

studying the development of the various tissues. The writer has endeavored to make this as complete a study as possible, with the idea in view that such an investigation of the normal structure of the plant may prove to be of value to those working on the mosaic and other diseases of the bean.

Material and Methods

The material for study was obtained from plants grown in the greenhouses at Michigan State College and at the University of California. The Black Valentine variety was used in the investigation. The material was fixed in chromacetic acid, and the microtome sections were stained with Delafield's haematoxylin and safranin. Phloroglucin and hydrochloric acid were used for xylem studies in the free-hand sections. Portions of the plant were cleared by using equal parts of turpentine and phenol.

Gross Morphology

Phaseolus vulgaris L. var. Black Valentine, a member of the Leguminosae, is a dwarf bean, twelve to fourteen inches high, and erect (Jarvis, 1908). The root system is fibrous; the primary root persists but is equaled by the secondary roots. Adventitious roots commonly arise from the lower portion of the hypocotyl.

The stem below the cotyledons, i. e. the hypocotyl, is round in cross-section, and especially enlarged in the lower portion. Above the cotyledons, it is more or less angular or ridged. The cotyledons are epigeal, and oppositely arranged at the first node. The first leaves to develop appear at the second node; they are simple and also opposite. The base of each is deeply cordate. The subsequent leaves which develop are all compound, composed of three leaflets, and they have an alternate

arrangement on the stem.

The petioles of the leaves are enlarged for a length of two millimeters at their base, thus forming a definite pulvinus in this region. Above the pulvinus, the petiole in cross section is round except for a groove on its ventral surface. There is present on either side of this depression a wing or ridge, which ends in a stipel several millimeters from the base of the blade. The leaflets of the compound leaf are shortly petiolulate. The margin of the simple leaf and of the leaflets is entire. The venation of the leaves is of the netted type and the main veins are three in number, branching from the same point at the base of the blade. Lateral branches arise from these and anastomose.

Stipules regularly occur in connection with both the simple and compound leaves. Two ovate, acute stipules originate at the base of the petiole of the compound leaf. At the second node, where the two opposite leaves are attached, there is one pair of stipules. It is interesting to note that each of these is double-toothed at the apex, but united at the base. Perhaps these represent two united stipules. Stipels occur at the base of the leaflets of the compound leaf. A pair is evident at the base of the terminal leaflet, and on the petiole where the two lateral leaflets originate.

The flowers are born in small racemes, the peduncle arising in the axils of the leaves. The pedicels of the flowers bear bracts at the point on the peduncle from which they originate. A pair of bracts also occurs just beneath the flower. The flowers are papilionaceous, consisting of five united sepals, an irregular corolla of an outermost large standard, a lateral pair of clawed wings, and the innermost pair of petals,

united and pressed together over the stamens and pistil to form the keel. The ten stamens are inserted at the same height as the corolla and are diadelphous, nine being united, with the tenth one free. The pistil consists of a single carpel; the style is rolled. In fruit, a typical legume or pod is formed, which encloses the shiny, black seeds.

Anatomy

Root

A cross section through the primary root, at a stage when secondary growth is just beginning, shows a central core of vascular tissue which is limited on the outside by the endodermis and cortex (Plate I, F). The vascular tissue has a tetrarch arrangement. In the phloem, the most evident cells are a group of thick-walled fibers, which are long and pointed. Just outside of these is the more or less crushed protophloem, and inside, the remaining primary tissues of sieve tubes, companion cells, and a few parenchyma cells (Plate IV, G).

The protoxylem elements of the exarch xylem are small and spirally thickened. The metaxylem cells are larger and pitted. A cambium layer lies between the xylem and the phloem.

The pericycle consists of one layer of cells opposite the phloem, but several rows opposite the xylem. A single row of endodermal cells separates the vascular cylinder from the cortex. The cortex consists of fifteen or sixteen rows of parenchyma cells, among which are intercellular spaces. This is bounded on the outside by the root epidermis, which sloughs off early.

Stem

Since the transition region at the base of the hypocotyl will be taken up in detail later, only the portion of the hypocotyl which shows a typical stem structure will be described here. In this region, below the cotyledons, a ring of collateral bundles surrounds a large central pith (Plate I, G). The xylem of these bundles has a tangential arrangement rather than a radial such as occurs in the stem above the cotyledons (Plate VII, A, B). The xylem is endarch. A fascicular cambium separates it from the phloem, which is marked by large, darkly staining tannin sacs, which are not found in the root. These sacs are elongated cells with transverse cross walls. Surrounding each is a ring of parenchyma cells. Sieve tubes and companion cells make up the remaining tissue of the phloem. The sieve tubes are cylindrical cells with transverse end walls. The entire transverse wall consists of a sieve plate (Plate III, D). They are found also in the longitudinal walls (Plate III, F). Although sieve plates occur in the primary sieve tubes, they are much more noticeable in secondary tissue. This is probably due to the greater number of secondary sieve tubes in relation to other phloem cells.

In addition to the bundles composed of primary xylem and primary phloem, there occur between the larger ones, small bundles which consist of primary phloem only (Plate V, C).

The pericycle, in the form of a cap over the phloem of each bundle, consists of several rows of fibers, whose walls are not lignified until secondary thickening occurs. Between the bundles the pericycle consists of parenchyma cells which are continuous with those of the rays and the pith.

The cortex, as in the root, consists of several rows of large parenchyma cells, and from the epidermis arise hairs. The cells of the epidermis of the stem are elongated in the direction of the long axis of the stem, and their walls in surface view are not undulate. Stomata occur in the epidermis of the stem.

Above the cotyledons the vascular bundles are collateral, and the xylem extends toward the center of the stem parallel to the radius instead of tangential to the radius as in the region below the cotyledons (Plate I, H). In the internode between the cotyledons and the primary leaves, there are always twelve bundles. The six larger bundles occupy the six ridges or angles of the stem, and alternate with six small bundles. The tissues are similar to those in the hypocotyl, but the pith is considerably smaller. The six large bundles form the leaf traces to the primary leaves (Plate V, D). Above the primary leaves, the stem is marked by five more or less distinct ridges, which mark the position of the five large bundles that form the leaf traces to the compound leaves (Plate I, C). The number of bundles is somewhat variable at this point.

The branch traces originate in the axils of the leaves as branches of the individual bundles on either side of the gap left by the median leaf trace (Plate I, D). The vascular system of the branch is, then, connected to that of the main stem by these two bundles.

Leaf

In a cross section of the pulvinus (Plate II, D), it is evident that the vascular cylinder consists of a united ring of tissues compressed into a small space in the center, with only a very small pith. The cortex is very thick, and consists of eight or more rows of parenchyma cells. When

the leaf traces first enter the pulvinus, the vascular elements have an amphicribal arrangement (Plate II, B, C), but shortly, after some anastomosing, they assume a collateral position with the phloem toward the outside. The endodermis surrounds the united circle of conducting tissue, and delimits it from the cortex.

As the top of the pulvinus is reached, toward the narrowing of the petiole, the circle of vascular tissue breaks up into definite, separate, vascular bundles. A furrow gradually develops on the ventral surface of the petiole, and a narrow wing develops on either side. Thus sections from the middle of the petiole show a ring of separate vascular bundles, eleven in number in the compound leaf. The circle is not complete on the ventral side, opposite the furrow, but is separated by a gap. Two of the eleven bundles lie in the wings, each forming a trace to one of the stipels; these traces are amphicribal. The other bundles of the petiole are similar in structure to those of the stem. Their xylem consists of small protoxylem elements, metaxylem, and a few secondary vessels and tracheids. In the phloem are sieve tubes, companion cells, and large tannin sacs. Each bundle is capped by a group of pericycle fibers. Only a narrow cortex of one or two rows of cells surrounds the stele, except on the wings and to the outside of the five large bundles. The collenchyma tissue opposite the bundles consists of several rows of cells; in other parts it consists of but one layer. An epidermis with stomata surrounds the petiole.

The structure of the petiole of the simple leaf is similar to that of the compound leaf, except that there are but nine bundles instead of eleven.

The mesophyll of the blade of the leaf consists of a palisade layer and a spongy layer (Plate VI, C). The palisade tissue is in the form of a single layer of elongated cells arranged perpendicular to the epidermis, and separated by only a few intercellular spaces. These cells are in contact with the spongy parenchyma tissue, whose cells are irregular in shape and arrangement, and which has large intercellular spaces and chambers. There are usually not more than four layers of cells in this spongy tissue, and the chloroplasts are not as numerous as in the palisade tissue.

The cells of both upper and lower epidermis appear deeply undulate in shape in surface view (Plate VI, J). The thickness of the upper epidermis is about one and one-half times greater than that of the lower epidermis. Some of the epidermal cells are modified in several ways, and so show variation from the typical shape and arrangement.

A pair of guard cells containing chlorophyll surrounds each stoma, but no accessory cells are present. Over the veins the epidermal cells are much elongated parallel to the longitudinal axis of the veins, and their radial walls are mostly straight. The cells in contact with an epidermal cell which has given rise to a hair differ from adjacent ones. These surrounding cells are elongated, have straight walls, and radiate from the hair cell (Plate VI, I). No chloroplasts are found in the epidermal cells, aside from the guard cells of the stomata.

There is considerable variation in the number of stomata occurring in the leaf epidermis. They are more numerous on the lower surface, averaging there, in nature leaves, about eighty-five stomata per square millimeter. On very young leaves, two hundred and fifty stomata may occur per

square millimeter, but as the epidermal tissue increases in size, the stomata are pushed farther apart. Thus in still young leaves, but older than the former, there will be but one hundred stomata per square millimeter.

Hairs of several kinds are common, especially on the younger plants. Aside from the root hairs, three main types may be distinguished, occurring on the stems, leaves, stipules, and other parts (Plate VI, R). The longest hairs which are found are straight, taper to a point, and sometimes are 400 microns in length. They consist of three cells, two of which are basal and short, the third being long and terminal. Then there are the hooked hairs, similar to the first, but whose end curves; these are the "Klinzner" hairs of de Bold. The glandular hairs are short and club-shaped, consisting of a number of cells; and usually are about 60 microns long. No hairs are found on the cotyledons or corolla, but they are common on all other parts of the plant, especially along the veins of the leaves.

The vascular tissue of the blade is a continuation of that of the petiole into the midrib. The midrib projects prominently on the lower surface of the blade, but less so on the upper surface. The vascular tissue has the same general arrangement as in a bundle in the petiole. In cross section it has a semicircular form with the open part toward the upper surface. The vascular elements consist of xylem and phloem with a cap of fibers over the latter. The structure of the branch veins is essentially like that of the midrib, from which they have arisen. As the veins get smaller, the amount of xylem and phloem decreases accordingly until finally all the phloem disappears, and only one or two spiral elements of the xylem remain surrounded by conducting parenchyma.

Stipules

Since the stipules may be considered as a part of the leaf, their structure should be treated here. As has been stated previously, the stipules at the base of the petiole of the simple leaf are two-toothed at the apex and united at the base. The vascular supply consists of two traces which originate as branches of the two lateral leaf traces as they pass into the petiole of the leaf. Since in the compound leaves there is a pair of stipules for each leaf, it is probable that those at the base of the simple leaves represent two which have become united.

The stipules of the simple leaf have a mesophyll tissue which consists of spongy parenchyma, with no palisade cells (Plate VI, F). Usually it is under the stomata that most of the air spaces occur. The veins are similar to those of the leaf, but the amount of each tissue is reduced. There are two main veins, each running out to the apex, and a smaller vein along each margin. The stipules of the compound leaf also consist of spongy parenchyma, but it is more loosely arranged than in the stipules of the simple leaf. Four main veins furnish the vascular supply, with a smaller vein on each margin.

The stipules are covered with an epidermis, the cells of which differ from those of the leaf blade. They are slightly elongated parallel to the long axis of the stipule, and their radial walls are not undulate. Stomata are more abundant in the lower epidermis than in the upper.

Cotyledons

A cross section of a cotyledon shows that it consists of large parenchyma cells with thickened walls and numerous pits. (Plate VI, D, E). The intercellular spaces are small in comparison with those present in the

leaves. The cells of the epidermis have straight radial walls (Plate VI, E). The cells of the upper epidermis are much flattened, while those of the lower epidermis are almost isodiametric. Stomata occur only on the lower epidermis. The vascular tissue is similar to that of the leaves, and is derived from two traces from the hypocotyl. It is interesting to note the larger number of starch grains and of aleurone grains in the immediate vicinity of the veins in the storage parenchyma cells. No hairs of any kind project from the cotyledons.

Ontogeny

Root

A longitudinal section through a young root shows that it is composed of very definite parts. At its tip is the root cap, of more or less loosely arranged cells, and directly behind this lies the region of rapidly dividing promeristem. From this region the cells show a gradual elongation and enlargement until finally the mature condition is evident at the base of the root.

Behind the root cap, three regions are distinct (Plate IV, B), the dermatogen, a single layer of cells at the outside; the periblem within, which later forms the cortex; and finally the central region of slightly elongated cells, the plerome. About one and a half millimeters behind the root tip in the plerome, the central cells have increased in diameter and have elongated to five times their diameter. Outside of these pith initials, lie four strands of long, narrow, densely protoplasmic cells. These are the cells of the procambium which give rise to the phloem. They are seven to ten times as long as wide. In cross section these strands appear as groups in the four corners of a square (Plate IV, A). Between these groups or

strands are larger cells which differentiate into the first xylem. At this stage, the endodermis and pericycle cannot be very readily distinguished from the surrounding cells of the periblem. The dermatogen is fairly well marked off from the other layers, its cells having divided by anticlinal walls only.

Although the phloem is the first of the vascular tissues to differentiate, it is extremely difficult to follow the steps, due to the inconspicuous differences between the protophloem and the procambium. However, in sections where it is evident, one or two cells next to the pericycle in each of the four procambium strands show slightly thicker walls.

Simultaneous with the formation of the first protophloem elements, the first xylem cells differentiate (Plate IV, C). The protoxylem can be recognized by the noticeable thickening of the cell walls, and by their spiral thickenings (Plate III, E). By the time the protoxylem forms, the pericycle and the endodermis are more definite. In the region of the phloem, the pericycle consists of but one layer of cells, one and a half to two times as long as wide. The cells of the endodermis in longitudinal sections appear slightly longer than those of the pericycle.

The remaining protoxylem cells rapidly differentiate centripetally, thus making the xylem exarch. These later formed cells are larger in diameter than the first to differentiate, with spiral thickenings more closely arranged, and pass over into the reticulate types. Meanwhile, more sieve tubes and companion cells of the protophloem form (Plate IV, D). Then some of the procambium cells of the phloem region elongate, their end walls become oblique, and their walls thicken to form the first metaphloem

fibers, which lie adjacent to the protophloem (Plate IV, E). Metaphloem, consisting of sieve tubes, companion cells, and parenchyma cells differentiates to the inside of the fibers. The parenchyma cells between the xylem and the phloem strands increase in number.

Along with the development of metaphloem occurs the differentiation of the metaxylem, whose cells have a much larger diameter than those of the protoxylem and have numerous simple pits (Plate IV, F). At this time, a cross section of a root shows four well developed arms of xylem, with four alternating groups of phloem, the latter well marked by the thick walled fibers. Then the walls of the cells occupying the central portion of the root thicken, lignify, and become pitted, thus forming a solid center of conducting tissue (Plate IV, G). As a result of the increase in size of the cells of the vascular cylinder, the few rows of protophloem cells lying between the pericycle and the fibers become crushed and the cells in some cases are entirely obliterated, even before secondary growth has taken place.

The cells in other portions of the root have undergone little change except in size. Intercellular spaces have appeared in the cortex.

At this stage of development some of the parenchyma cells between the phloem and metaxylem divide longitudinally by tangential walls. A row of the cells of the pericycle just outside of the protoxylem likewise divides, and thus the cambium layer develops by the reversion to meristem of these parenchyma cells.

Secondary Growth in the Root

Most of the tissue of the mature root is secondary. In contrast to the small vascular cylinder of the primary root surrounded by the thick

cortex, the mature root consists of a very narrow cortex surrounding a great amount of vascular tissue.

The secondary xylem of the root consists mainly of tracheids and fibers arranged in radial rows. As in the stem, several tangential rows of these have thicker walls, and give an appearance of annular rings. Besides this tissue, large vessels differentiate from the cambium. These are well provided with simple pits. Parenchyma is formed especially in the vicinity of the vessels, but also to some extent among the tracheids. Four broad rays of parenchyma cells are cut off by the cambium opposite the four groups of protoxylem, and extend out through the phloem. As a result, the conducting tissues are not continuous around the root. The walls of the parenchyma cells eventually thicken and become lignified.

Most of the phloem is secondary, and much less is formed than xylem. The protophloem is so crushed that it is no longer recognizable. The characteristic group of primary fibers is unchanged. The secondary phloem consists mainly of sieve tubes, companion cells, and only a few parenchyma cells. Sieve plates are common.

The cells of the cortex, as well as those of the pericycle and endodermis, are crushed and flattened due to the enormous increase in size of the vascular cylinder. The outermost die and are sloughed off. The epidermis sloughs off soon after secondary growth begins and nothing remains of the cortex except three or four rows of cells.

Stem

The tip of the stem is comparable to the root tip only in the fact that it consists of meristem which differentiates into the primary tissues; their arrangement differs from that in the root. A root cap is

entirely lacking at the stem tip. As in the root, the apex consists of thin-walled, densely protoplasmic cells, which, directly behind the tip, begin to differentiate into more or less definite regions. These regions consist of the dermatogen, the ground meristem, and the isolated strands of procambium. The cells of the procambium differ greatly from all others in being elongated longitudinally, and in having a smaller diameter than the surrounding tissue. They also have denser protoplasm than the surrounding ground meristem.

Almost simultaneously with the setting off of these regions, the first conducting tissue differentiates from that part of the procambium strand toward the center of the stem (Plate V, A). This is the protoxylem. These elements are longer than the surrounding procambium cells and are characterized by secondary wall thickening in the form of loose rings. The walls are not yet lignified. Additional protoxylem cells differentiate centrifugally, and thus the xylem of the stem is endarch in contrast to the exarch xylem of the root. The successive protoxylem cells that form are larger than the first, and their wall thickenings are in the form of closer spirals, spiral-nets, and nets (Plate III, B).

At the same time, or probably a little before the appearance of the protoxylem, the protophloem differentiates from the procambium. The protophloem cells are so like the procambium that it is almost impossible to recognize them, and they soon disappear. The metaphloem is the first to be differentiated clearly. In the formation of a sieve tube, a procambium cell enlarges, elongates, and either directly forms a sieve tube or it may divide to form a sieve tube and adjacent companion cell. The first sieve tubes are differentiated from the procambium cells toward

the outside of the stem and so further development is centripetal. The most noticeable cells to develop in the primary phloem are the tannin sacs (Plate V, B). Their formation is initiated by the enormous enlargement of certain procambium cells, both in length and in diameter. Such cells very soon become filled with material which stains deeply with Delafield's haematoxylin. These tannin sacs appear very early in the development of the phloem. A single row of procambium cells surrounding a tannin sac usually enlarges, and may divide longitudinally parallel to the walls of the sac. The inner row forms a ring of parenchyma cells around the sac. Isolated parenchyma cells may differentiate from the procambium, and thus lie scattered through the phloem. By the time the phloem has developed to this stage, the walls of the protoxylem have become slightly lignified.

The ground meristem has almost ceased to divide and has assumed the appearance of parenchyma cells. A few intercellular spaces have developed. The dermatogen divides only by anticlinal walls to form the epidermis. The hairs appear from the epidermal cells very early. The single row of endodermal cells is evident at this time, and they are recognized by their greater diameter, especially in a radial direction, and by a greater length than the adjacent cortical cells. The pericycle cells of several rows are clearly marked off where they form a cap over the phloem just under the endodermis. In comparison with the cortical cells, these cells have thicker walls and less dense protoplasm. In addition, they are longer and narrower.

This period of differentiation is followed by one of great cell enlargement in all tissues. The appearance of a fascicular cambium characterizes the next step in development (Plate V, C). It is formed

by the tangential division of a row of undifferentiated procambium cells between the xylem and the phloem. Longitudinally the cambium cells are long and narrow with slightly pointed ends. Soon after the differentiation of this fascicular cambium, an inter fascicular cambium arises. It originates by the reversion to meristem of a row of parenchyma cells between the bundles.

In the xylem region at this stage, the metaxylem completes its differentiation as larger cells which are characterized by their pitted and reticulate walls. Although most of the cells of the metaxylem consist of large pitted vessels, some parenchyma differentiates, especially around the vessels. Lignification of the walls of the vessels soon follows their differentiation. The protoxylem elements, now lignified also, are becoming stretched, and the annular thickenings are farther apart.

In the phloem, all the cells have now differentiated from the procambium (Plate V, C). These groups are the "soft bast" of Dodel. Groups of sieve tubes and companion cells occur, among a few parenchyma cells. The large tannin sacs, surrounded by the layer of parenchyma, are conspicuous. The end walls of the sieve tubes have developed into sieve plates.

The cells of the pericycle have enlarged considerably, but the walls of those which cap the phloem are still only slightly thickened. They are packed close together and are angular. No intercellular spaces are evident. In longitudinal sections, these cells have increased in length, and the ends of adjacent cells have shoved past each other. The cells of the endodermal layer have increased in size, but no other change is evident. The cortical cells are much larger than in the previous

stage, and many intercellular spaces have developed.

The last stages of primary growth are completed at the same time that secondary growth is initiated, and so to a certain extent the two stages overlap. Primary differentiation ends with the complete differentiation, enlargement, and maturation of the proto- and meta- xylem and phloem elements. The walls of the pericycle fibers which cap the phloem are not yet lignified. That portion of the pericycle opposite the rays consists of parenchyma cells which are continuous with the rays between the bundles. The epidermis is a single layer of cells, with fully developed stomata. It bears numerous hairs. The endodermal cells in cross section are elongated in a tangential direction rather than in a radial direction as in younger stages. In longitudinal section, they are slightly longer than the parenchyma cells of the cortex.

Secondary Growth in the Stem

With the differentiation of the fascicular and the interfascicular cambium, further increase in size of the stem is brought about by the formation of secondary tissues by these cambia.

The first xylem cells formed by the cambium ring are two or three rows of thick-walled fibers which form a continuous ring around the stem (Plate V, E). Most of the cells outside these fibers consist of radially arranged rows of tracheids. Only a few pitted vessels are formed. Fibers may occur among the tracheids. Often a second layer of fibers is formed as the last layer of secondary xylem. This results in giving the appearance of an annual ring. The secondary parenchyma cells have a diffuse arrangement.

Besides the longitudinal conducting system of secondary xylem and phloem, the fascicular and interfascicular cambiums form a transverse system consisting of vascular rays. In the xylem, the parenchyma cells of these rays are radially elongated. Both uniseriate and multiseriate rays are formed. In height or vertical extent, they are six or more cells, and their radial extent varies. Some of the rays are continuous through the xylem and phloem. The multiseriate rays formed by the interfascicular cambium are continuous with the cortex.

The cambium associated with the groups of primary phloem which have no accompanying xylem, first forms the three layered ring of thick walled fibers toward the inside of the stem. The secondary xylem, later formed, like that of the primary bundles having both xylem and phloem, consists of large pitted vessels and tracheids. Thus these bundles have no primary xylem elements projecting into the pith (Plate V, F).

As the secondary xylem forms, great stress and pressure are exerted on the first formed xylem lying adjacent to the pith, finally causing the protoxylem to entirely disappear. Remnants of the cells may be seen, especially in longitudinal sections, where they are crushed and distorted, and the ring and spiral thickenings are scattered. The parenchyma in this region of the vascular bundle is likewise crushed and the walls crumpled. The parenchyma cells of the pith are especially affected, finally resulting in the disappearance of most of the pith and thus causing the mature stem to be hollow. Usually one or two rows of parenchyma cells of the pith which lie adjacent to the innermost xylem remain intact.

The secondary phloem consists of groups of sieve tubes and cal-

panion cells, and a few parenchyma cells (Plate V, E). In the formation of sieve tubes and companion cells a cambium cell enlarges slightly and then undergoes several longitudinal divisions. The first division is usually in a radial direction, forming two sieve tube mother cells. Of these, each may then cut off a small companion cell by another longitudinal division. Sieve plates in the transverse walls of the sieve tubes are conspicuous and numerous, and they occur also in the longitudinal walls. No secondary tannin sacs are formed. Like the protoxylem the protophloem becomes crushed and absorbed, and as the secondary tissues increase in amount, much of the primary becomes an unrecognizable mass, pressed against the cap of pericycle fibers.

The fibrous tissue of the pericycle, whose cells were only slightly thickened at the end of primary growth, bear thick lignified walls with minute lumens at the end of secondary thickening. They never form a continuous ring of tissue around the stem, being interrupted by the parenchyma tissue opposite the rays.

The endodermal cells during secondary growth flatten out and are crushed, due to the increase in thickness of the stem, and at other times are almost indistinguishable from the cells of the cortex. These cortical cells, as a result of the stress of the enlarging tissues, lose their shape, and are much flattened in a radial direction.

Secondary Roots

Secondary roots arise very early in the differentiation of the primary root. In some cases, these roots become much more conspicuous than the primary root. They arise in the usual manner, endogenously, by the reversion to meristem of the pericycle cells opposite the protoxylem.

Thus the organization of the primary structure of the main root predetermines the arrangement of the secondary roots into four longitudinal rows. Their structure is similar to that of the main root, although the amount of each tissue is less, as for instance, the number ^{of} rows of parenchyma cells of the cortex is much reduced, often to two or three rows.

Since the various tissues in the main root first develop behind the root tip, the differentiating vascular elements of the young secondary root are continuous soon with those of the main root. The four phloem strands of the secondary root join at different levels with adjacent parts of two strands of the main root. The xylem is continuous with but the one group of the primary root (Plate I, F).

Adventitious Roots

Adventitious roots are commonly found on the lower part of the hypocotyl. They are similar in structure to the true secondary roots (those originating from the root), and arise endogenously from the pericycle. Likewise, the region from which each comes is always opposite one of the four groups of protoxylem cells, which in the hypocotyl are endarch.

Transition Region

The change in the arrangement of the vascular tissues from that which occurs in the root to that in the stem takes place in the lower part of the hypocotyl. The typical stem arrangement of collateral vascular tissues is not completed until after the passing off of the cotyledonary bundles.

The four protoxylem groups in the root fork gradually, due to the lateral differentiation of procambium cells into xylem, and the two forks

swing laterally, finally separating entirely. Thus are formed eight groups of xylem in cross section views, the elements not arranged parallel to the radius as in the typical stem structure, but tangentially (Plate I, G).

The phloem, during these xylem changes, at first broadens out tangentially from the four groups alternating with the xylem in the root, to four bands of tissue to the outside of the xylem in the lower portion of the hypocotyl. Finally, at the time the eight groups of xylem form, each of the phloem bands becomes divided, thus forming eight groups which lie over the eight xylem groups, with the collateral arrangement of tissues.

Although the tissues in the hypocotyl actually have a collateral arrangement, it is not similar to that of the stem because the xylem has a tangential arrangement, not radial.

Leaf

In a young primary leaf, still folded between the cotyledons, differentiation in the meristem tissue has already begun (Plate VI, A). In a cross section, the upper and lower epidermis are distinct, and the cells beneath the upper epidermis are slightly elongated perpendicular to the surface. The cells of the future spongy mesophyll are still tightly packed together, with no intercellular spaces. The procambium strands are evident and beginning to differentiate into the initials of the vascular tissue. Only very few hairs have developed.

At a later stage, when the leaves are beginning to unfold above ground, the palisade layer has elongated to three times its length in the previous stage (Plate VI, B). Stomata have developed, but the spongy mesophyll, although its cells have assumed various shapes, have as yet no intercellular spaces. Hairs of the three types previously mentioned are well developed.

The development of the stomata from meristem is evident. Surface views of the epidermal tissue from the plumule while it is yet enclosed within the seed, shows it to be composed of small isodiametric cells, eight to twelve microns square with no indication of even the initial stages in the formation of stomata (Plate VI, G). However, as soon as germination takes place and the primary leaves emerge from between the cotyledons, early stages in the development of the stomata occur (Plate VI, H). A meristem cell enlarges to about twenty micronsⁿ tangential extent, and it is cut by an anticlinal wall (1), curved toward the center of the cell. In this cut-off cell, another curved anticlinal wall (2) appears. Then a cell arises within the last formed cell by the formation of still another anticlinal wall (3), which curves out noticeably from the previous wall. This last cell is the mother cell proper of the guard cell, and it is elliptical in shape. The mother cell divides by a longitudinal radial wall (4) into the two guard cells, between which the stomatal slit later appears. The guard cells and surrounding epidermal cells increase in size. (Plate VI, I and J).

The structure of the mature leaf has been described already in the discussion of the anatomy.

Course of the Vascular Bundles

This description of the course of the vascular bundles will be taken up under several headings, and will be followed by a summary to emphasize certain features. Since the root and transition region are the organs where the tissues are first differentiated, they will be taken up first.

Root, Transition Region, and First Node

The course of the bundles in the root is similar throughout its length, four strands of xylem alternating with four of phloem (Plate VIII, A). The first evidence of a change occurs in the lower part of the hypocotyl, when each of these strands divides, thus forming eight strands of xylem and eight, eventually, of phloem. Only the eight xylem groups, which will be referred to as primary bundles, 1, 2, 3, 4, 5, 6, 7, and 8, are shown in the figure. At the point where this division takes place, there appear the "Zwischensstränge", or intercalary bundles of Dodel and other investigators (Plate VIII, A, 9 and 10). These bundles, consisting of several metaxylem cells, but no protoxylem, and a few phloem cells, seem to have a "blind" origin, there being no connection between them and the primary bundles. Their number varies; sometimes there are as many as three, usually, however, only one or two, and in many cases, none. These intercalary bundles unite with the primary bundles which pass out into the cotyledons, and never continue above the first node.

Just below the first node, the greater part of two primary bundles, 1b and 2b, and 5b and 6b, passes out into each of the nearly opposite cotyledons. These, just before they turn into the cotyledons, each form branch bundles, 1a, 2a, 5a, and 6a, which unite with adjacent bundles and continue into the internode above. The cotyledonary traces, after traversing the cortex, unite, and then, at the base of the cotyledons divide to form three bundles, which continue into the cotyledons.

The four remaining primary bundles, 3, 4, 7, and 8 continue their passage through the hypocotyl unchanged until several millimeters below the cotyledonary node. There each splits into two parts, for example, 7

into 7a and 7b, and 3 into 3a and 3b, and the halves 7a and 3a nearest the cotyledonary traces, swing over until they are adnate with the cotyledonary traces 1b and 2b. After the passing off of the traces into the cotyledons, these bundles turn back into position and continue into the next internode, united with 1a and 2a, the branches of the cotyledonary traces, and are now designated as 17a, 23a, 86a, and 45a. These four bundles form the lateral traces to the simple leaf at the second node. The remaining halves of the primary bundles 7b, 8b, 3b, and 4b, unite at the node to form the large bundles 73b and 34b. These two large bundles form the median trace of the three which pass out into the opposite simple leaves of the second node. At the node and immediately above it, six small bundles alternating with the six large ones, arise as branches from the large ones. The most frequent manner of this branching consists of the following: 23b and 45b branch from bundles 23a and 45a; 17c and 86c from bundles 17a and 86a; and 17b and 86b from 17a and 86a. There is some variation in this, due to the fact that 17b and 86b seem to have the ability to appear as branches from either 23a or 17a, and 86a or 45a. These twelve bundles, then, are those found in the internode above the cotyledons.

The hypocotyls of many plants that were examined show a vascular system slightly different from that described above. The bundle course of such hypocotyls is not identical on the two sides of the stem below the cotyledons. The primary bundles 7 and 8 branch to form 7a, 7b, 8a, and 8b sooner and consequently farther below the cotyledons than do the primary bundles 3 and 4 on the opposite side of the hypocotyl. The second point of difference lies in the fact that the small bundles 17c and 86c, on this same side of the hypocotyl, arise as branches of 73b and not from 17a

and 36a.

Dodel, working with Phaseolus vulgaris, considered the cotyledonary trace to consist of two entire hypocotyl bundles, and in addition one branch from each of two other bundles. In the present study, such a condition never was found; in every case the cotyledonary trace consisted only of the greater portion of two hypocotyl bundles, in addition to the intercalary bundles.

Harris (1921) described the cotyledonary trace as made up of but two bundles of the hypocotyl, the whole of which bundles forms the trace. This investigation shows that a small branch from each of these two bundles unites with the two adjacent bundles.

Second Node

The twelve bundles pass unchanged from the first node to the second node where the opposite single leaves are found (Plate VIII, B). Several millimeters below the latter node the median bundles 78b and 34b begin to swing out through the cortex, and at the node pass into the basal part of the petiole. The lateral traces 33a, 45a, 17a, and 25a each branch, and form a complete girdle around the node. For instance, 45a divides into 45u and 45x; 45u passes under the bundle 33x, and forms one-half of the lateral leaf trace, 80x forming the other half. The bundle 45x passes to the opposite leaf and forms half of the lateral leaf trace there. The other three lateral traces branch in a similar manner. Thus the vascular supply to each single leaf actually consists of a median bundle and two lateral bundles, each formed in the manner just described.

On either side of the stem at the second node, a stipule occurs. The vascular supply of each of these has its origin in two bundles which

branch from the lateral leaf traces as they are migrating through the cortex.

The six smaller bundles which have not entered into the formation of the vascular supply of the leaves at the second node, and which alternate with the six large leaf trace bundles, each fork, thus making twelve bundles above the second node. However, this number changes very soon, for four of the bundles divide once more, into 17g, 17h, 17c, 17d, and 86f, 86g, 86h, and 86i, forming a total of sixteen bundles in the stem between the second and third nodes. The sixteen bundles often do not appear until directly below the third node, since frequently the four bundles branch at various heights in different plants.

The writer's studies on the derivation of the vascular traces to the primary leaves do not agree with those of Nägeli.

Third Node

Of the sixteen bundles usually found below the third node, five are larger and act as traces to the compound leaf (Plate VIII, E). Bundle 45c is the median bundle which passes into the petiole, and 86f, 86i, 17h, and 23b are the four lateral traces. As these five bundles pass into the petiole, an incomplete girdle is formed around half the stem.

The stipules on either side of the stem obtain their vascular supply from the lateral bundles of the leaf traces in the form of branches from them as they pass into the petiole.

Directly above the third node, eleven bundles are found. Very soon, however, bundles 45b and 23c divide to form 45d and 45e, and 23d and 23e. Then, 45e and 23e again divide. Thus above the third node, there are 15 bundles in a cross section of the stem.

The nodes above the third, at which compound leaves originate, have the same general structure, and into each leaf pass five bundles, just as into the leaf at the third node. There is considerable variation in the number of bundles in the internodes at different heights.

Several cases have been found in material investigated, where, instead of the normal five bundles passing into the petiole of a compound leaf, there are six. In such cases, the presence of the extra bundle seems to be correlated with a variation in the external morphology of the leaf. In these cases it consists of the appearance of an extra leaflet, reduced in size, just at the base of the petiolules of one of the lateral leaflets.

Although the compound leaves are normally alternately arranged on the stem, two plants have been found, which at the fifth node bore a pair of opposite compound leaves. Sections of the node showed that seven bundles in the stem formed the traces to these leaves, three and a half bundles passing into each petiole.

Nägeli reported that either four or five bundles formed the traces to the compound leaf. The four bundle condition has not been found in this investigation.

Branches

The vascular supply of the branches which arise in the axils of the leaves, is derived from branches of the two bundles of the stem which border the gap made by the median trace of the leaf (Plate VIII, E). These two bundles, which always originate at or immediately below the node that bears the shoot, divide to form a ring of vascular bundles (Plate I, D).

Simple leaf

As the five bundles forming the trace to the simple leaf pass into the basal portion of the pulvinus of the petiole, the two members of each lateral pair become united into one; the xylem lies in the center, with the phloem surrounding it. Above this point, there is anastomosing among the bundles, and they then become rearranged and form a circle of tissue in the center of the pulvinus, only a small pith remaining. At the upper portion of the pulvinus, the pith increases in size, and the ring of vascular tissue gradually separates into more or less distinct bundles.

Above the pulvinus, five bundles are distinct, arranged in a circle which is open on the ventral side (Plate VIII, D, C). There is a median dorsal bundle 3, with two lateral ones on either side, 1, 2, 4, and 5. The petiole in cross section at this point is round with a groove on the ventral side. The flange or wing present on either side of this groove runs the full length of the petiole, up to the point of attachment of the stipels.

Bundles 1 and 5, above the pulvinus, send off small branch bundles, 1a and 5a, which form the stipellar traces. These traces, at the point where they pass out into the stipels at the base of the blade, branch, one part forming the trace to the stipel and the other reuniting with the bundles 1 and 5 from which they originally came.

Two small bundles, 3a and 3b, consisting of only a few conducting cells, branch from the adjacent bundles a few millimeters above the pulvinus. At the base of the blade, these two bundles unite with the median dorsal bundle and go to form the midrib of the blade.

Above the attachment of the stipels just below the blade, the bundles of the petiole draw close together, and 1, 2, and 3a become adnate to each other. The same union occurs with 5, 4, and 3b. Thus the petiole at this point in cross section has the appearance of possessing a contracted, crescent-shaped mass of conducting tissue, actually consisting of united bundles. As this enters the blade, bundle 3, united with 3a and 3b, form the midrib of the leaf blade together with a branch from 1 and 5. Bundles 2 and 4 soon separate from 1 and 3, and form the lateral veins on either side of the midrib. The remaining portion of 1 and 5 form the veins of the simple leaf which follow closely the margin of the blade.

Sections of the midrib at various places from the base of the blade to the apex were studied to determine the formation of the branch veins. It was found that whenever a vein branched from the midrib, a small patch of xylem and phloem cells separated from the midrib bundle. Thus as the consecutive veins are formed, the amount of tissue in the midrib decreases, until finally at the apex it consists of only a few xylem and phloem cells.

Compound Leaf

The course of the vascular tissue in the pulvinus of the compound leaf is essentially the same as in that of the simple leaf, with the exception that there are more bundles involved. In fact, except for the greater number of bundles, the structure of the entire petiole up to the point where the lateral leaflets originate, is similar to that of the simple leaf (Plate VIII, F, G). Thus the nine bundles plus the two small ones forming the stipellar traces, pass upward unchanged until

just below the opposite lateral leaflets. Here the traces to the stipels divide, one-half passing into the stipels and the other reuniting with the adjacent petiole bundle. Just above the stipels, there is a complicated arrangement and anastomosing of the remaining bundles of the petiole, as some of them pass off as traces to the lateral leaflets.

Bundles 2 and 8 of the petiole form the median bundles of the five which pass into each lateral leaflet. Bundles 1 and 9 each divide into three parts, the middle portion of which passes upward into the petiole above the attachment of the leaflets. The branch nearest the one leaflet forms part of the trace into it; the other branch passes around to the other side, where it forms part of the trace to the other leaflet. The same occurs in the case of bundle 1. Bundles 7 and 3 similarly each divide into three parts, and behave as in the previous case. Thus the two pairs of lateral bundles of each trace to the leaflets consists of two bundles derived from adjacent bundles of the petiole, and two from bundles from the other side. There is some anastomosing between bundles 3 and 4, and 6 and 7.

The five bundles making up each trace to the lateral leaflets remain as a compact tissue in the center of the petiolule to the leaflet and do not appear as separate bundles as shown in the diagram.

Above the attachment of the leaflets, seven bundles continue, arranged in the same manner as in the petiole below, although less in number. Their further course is similar to that of the corresponding region of the petiole of the simple leaf.

Flower

The pedicel in cross section shows twelve vascular bundles, which tend to be grouped in a circle, in four clusters of three bundles each (Plate II, F). At the insertion of the pair of bracts which are attached to the pedicel just below the calyx, one bundle on either side of the pedicel divides, and the outer parts pass through the cortex and into the bracts (Plate VII, C). Each trace at the base of the bract divides into three bundles, which are the principle ones of the bract. Thus each bract is furnished with a trace consisting of the larger part of a bundle of the pedicel.

As these traces pass into the bracts, ten bundles branch from the vascular bundle in the pedicel, and migrate into the cortex, where they form a broken ring (Plate VII, D). It is these ten cortical bundles which furnish the vascular supply of the calyx, corolla, and stamens. The remaining bundles in the stele form the traces to the pistil. The zygomorphy of the flower is noticeable from the first, for the vascular supply to the ^{anterior}~~posterior~~ parts always passes from the stele before that to the ^{posterior}~~anterior~~.

The three ^{anterior}~~posterior~~ bundles of the ten in the cortex, 1, 2, and 10, the two lateral ones of which furnish the traces to the keel of the corolla, have a somewhat different origin than the other seven. These three are merely three branches from one bundle in the stele. The other seven consist each of a single one. Therefore, the ten bundles are not exactly similar as to their origin.

The traces to the calyx and corolla branch from the ten bundles at practically the same time. By referring to Plate VII, E, the origin

of the traces to the united calyx can be followed. From five bundles, 1a, 3a, 5a, 7a, and 9a, three small bundles branch, and from the remaining five which alternate with the first five, two bundles branch. These two bundles unite with adjacent members of the group of three. For instance, 1a forms branches 1b, 1c, and 1d. Bundle 3a has but two branches, 3c and 3d, and bundle 10a forms 10c and 10d. In the base of the calyx, 1d unites with 3c to form 1d, 3c, and 1b with 10d to form 10d 1b. 1c continues as a single bundle. In this way, fifteen bundles pass into the calyx, these being more or less united at its base. Only a distance of about one hundred and twenty-five microns lies between the points from which the traces to the bracts pass.

Alternating with the five bundles each of which sends three traces to the calyx, are the five, 2a, 4a, 6a, 8a, and 10a, which at the same time pinch off portions which form the traces to the corolla, 2b, 4b, 6b, 8b, and 10b. The remaining 10 bundles 1a, 2a, 3a, etc., form the traces to the stamens. When the traces to the sepals have migrated to the outer portion of the cortex, a cleavage furrow begins in the cortex, separating the corolla and the calyx from the pistil and the stamens. This begins at the ^{anterior} ~~posterior~~ side, noticeable first at the outside of the two bundles which form the traces to the keel.

A little higher, the calyx is completely separated from the remaining floral parts (Plate VII, F), and it consists of a narrow circle of parenchyma cells, about twelve cells in thickness. The two members of the keel are separated from the staminal ring, but the wings and the standard are still united with it. The stamen traces, although they appear to be arranged in a single whorl, actually are in two, those opposite the

sepals arising first and forming the outermost row and those alternating with the sepals arising later. The former bundles lie a little farther toward the outside of the ring. The bundle of the stamen opposite the standard, which soon becomes separated from the nine united ones, at this stage, is surrounded laterally by more cortical tissue than the other staminal bundles.

The two wings soon are separated from the staminal ring, leaving the standard only attached to the posterior stamen, which is now separated from the remaining nine stamens. Then the standard and single stamen are separated and all three outermost whorls are distinct (Plate VII, G). The vascular tissues in the stamens have an amphicribal arrangement.

The traces to the pistil consist of the portions of the bundles of the central stele which do not pass out as traces to the bracts and to the other three whorls of floral parts. These divide and form a more or less continuous circle in the stele. At the base of the pistil, these divide into twelve bundles; six move toward the posterior side and six toward the anterior. Thus, by the time the pistil is separated from the staminal ring, the vascular supply consists of one large, crescent-shaped bundle in the anterior side of the carpel, representing the dorsal suture or midrib, and two posterior bundles at the ventral suture, equivalent to the marginal veins of the leaf whose margins can be seen meeting (Plate VII, F). These bundles, until the pistil separates from the staminal ring, are adherent to the bundle of the single posterior stamen.

The ovules are attached to the placentas by the funiculus, and it is through this that the vascular tissue passes to the integuments, where it branches into two bundles. The two ventral bundles of the ovary then

alternately give off traces to the ovules, as Nelson (1932) has shown (Plate II, E). Thus the first ovule is supplied by one bundle, the second ovule by the other, etc. At the point where the last ovule has been formed, the vascular tissues continue into the style arranged in the same manner, two ventral traces and the crescent shaped dorsal trace. The tissue becomes very much reduced in the style.

Most of the bundles in the ovary walls are formed as branches of the large dorsal bundle in a manner similar to that in which the lateral veins branch from the midrib of the leaf. Each of the ventral bundles gives off only a few branches to the ovary wall. These correspond to the branches of the marginal veins of the leaf.

Summary

Phaseolus vulgaris L. var. Black Valentine is a dwarf bean with epigeal cotyledons. The first leaves are opposite and simple; the following ones that develop are compound and alternately arranged on the stem.

The primary vascular tissues of the root have a tetrach arrangement. The primary phloem consists of sieve tubes, companion cells, parenchyma, and a very noticeable group of thick-walled fibers. The first vascular cells to differentiate are the protophloem. At about the same time, the first spiral xylem elements appear. Most of the mature root, like the stem, consists of secondary tissues formed by the cambium ring. The xylem is composed mainly of tracheids, some vessels and fibers, and parenchyma. No tannin sacs occur in the root.

The structure of the hypocotyl is similar to that of the stem, except that the xylem cells project tangentially into the pith instead of

radially. There are eight bundles formed by the division of the four groups of phloem and xylem in the root. In the stem above the cotyledons, there are twelve distinct vascular bundles arranged in a circle. Six large bundles, the leaf traces to the primary leaves, alternate with six smaller bundles. The primary phloem is characterized by the presence of large tannin sacs, which are found only in the primary tissues. The first protoxylem cells have thickenings on their walls in the form of rings and spirals. Secondary thickening is brought about by the activity of the fascicular and interfascicular cambiums which form a complete ring of xylem and phloem except where broken by the rays.

The pith cells, except for several rows next to the xylem, disappear as secondary growth continues, leaving the stem hollow. The pericycle opposite the vascular bundles consists of fibers. An endodermis surrounds the vascular cylinder. The epidermis bears three types of hairs.

The leaves have but one layer of palisade cells and several rows of spongy mesophyll. Both the upper and the lower epidermis bear stomata. The stipules have no palisade cells. The stipules at the base of each single leaf probably can be considered as two which have become united. The cotyledons consist of parenchyma cells in which are stored starch and aleurone grains. Only the lower epidermis bears stomata.

The united calyx of five sepals is supplied with fifteen bundles. Each petal and stamen has but one trace, but the pistil has three. The vascular tissue of the stamens has an amphicritral arrangement. The ovules attached to the placenta of the ovary at the ventral suture derive their vascular supply from the two ventral bundles of the

ovary.

The transition of the vascular tissue from the arrangement in the root to the collateral arrangement of the stem takes place in the basal portion of the hypocotyl. This results in the formation of eight bundles in the hypocotyl. The larger part of two of these forms the trace to each of the cotyledons. The course of the bundles at the cotyledonary^{node}, as worked out in this study, does not agree with that of Dodel and Harris. Portions of all eight hypocotyl bundles pass out into the simple leaves at the second node as the five traces which go into each petiole. Of these five traces, one consists of an entire bundle, the other four being only half-bundles. At the third node, five whole bundles leave the stele and pass as traces to the compound leaf. These traces are branches of bundles at the second node, and they are derived from five of the hypocotyl bundles. Branches of the stem are derived from two bundles of the stem on either side of the leaf gap.

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Explanation of Plates

Anatomy of Phaseolus vulgaris L. var. Black Valentine.

Plates I-III are photomicrographs reduced 2 x. Plates IV-VII drawn with camera lucida; reduced 4 x. Plate VIII reconstructed from transverse sections drawn with camera lucida; reduced 4 x.

The following abbreviations are used: AL, aleurone; B, bract; BC, basal cell of hair; BR, branch; C, cortex; CA, cambium; CF, cleavage furrow; CU, cuticle; CX, Calyx; CO, collechyma; D, dermatome; DO, dorsal bundle of ovary; EN, endodermis; EP, epidermis; F, fibers; FC, fascicular cambium; FPE, pericycle fibers; FS, free stamen; G, guard cell; GL, glandular hair; H, hooked hair; F, funiculus; IFC, interfascicular cambium; K, keel; L, trace to corolla, stamen, calyx; LT, leaf trace; MPH, metaphloem; MX, metaxylem; O, ovule; P, parenchyma; PA, palisade cells; PED, pedicel bundles; PE, pericycle; PLR, periblem; PL, plerome; PH, phloem; PI, pith; PPH, protophloem; PRPH, primary phloem; PRO, procambium; PX, protoxylem; PRX, primary xylem; RC, root cap; SEC Ph. secondary phloem; S, stoma; SEC X, secondary xylem; SH, straight hair; SI, sieve plate; SP, spongy mesophyll; ST, starch grain; STA, standard; STI, stipule trace; T, tannin sac; TB, trace to bract; TCX, trace to calyx; TF, trace to pistil; TS, trace to stamen; TX, tangential xylem; UEP, upper epidermis; US, united stamens, V, vein; VLB, ventral bundle of ovary; W, wing; X, xylem.

Plate I.

- A. Cross section of midrib at base of leaf (x 120).
- B. Cross section of stem at second node, showing traces to opposite single leaves, and secondary tissues (x20).
- C. Cross section of stem at third node, with six leaf traces instead of normal five (x 20).
- D. Cross section of stem to show origin of vascular supply to branch (x 30).
- E. Cross section of stem above third node (x 30).
- F. Cross section of primary root, showing four xylem arms, and origin of branch root (x 30).
- G. Cross section of hypocotyl, showing arrangement of vascular tissues (x 15).
- H. Cross section of stem below second node (x 30).

Plate II.

- A. Cross section of flower bud, showing the floral whorls (x 40).
- B. Cross section of base of pulvinus of compound leaf, showing the five leaf traces (x 30).
- C. Cross section of pulvinus, showing rearrangement of tissues (x 30).
- D. Cross section of upper portion of pulvinus, showing arrangement of vascular tissues before they become separate bundles (x 30).
- E. Cross section young root, showing vascular supply of ovule (x 45).
- F. Cross section of pedicel below bracts (x 100).

Plate III.

- A. Longitudinal section of phloem in petiole, showing tannin sacs (x 35).
- B. Longitudinal section of root to show xylem and cambium (x 30).
- C. Longitudinal section through phloem of stem (x 300).
- D. Cross section of sieve tube, showing sieve plate (x 1500).
- E. Longitudinal section of protoxylem in root (x 500).

- F. Longitudinal section of sieve tube, showing sieve plates (x 1500).
- G. Longitudinal section of large ray (x 800).

Plate IV.

Development of tissues in the root (x 700).

- A. Cross section of young root, showing four procambium strands.
- B. Longitudinal section of root tip.
- C. - G. Cross sections of vascular cylinder of root, to show differentiation of tissues.

Plate V.

- A - C. Cross sections of stem to show development of tissues. (B - x 1500) (A, C - x 700).
- D. Cross section of vascular bundle of stem which forms a trace to the primary leaf (x 700).
- E. Cross section of stem at end of secondary growth (x 700).
- F. Cross section of bundle in which no primary xylem occurs after secondary thickening (x 700).
- G. Cross section of bundle in which only primary phloem occurs; primary growth (x 700).

Plate VI.

- A - C. Development of tissues in the leaf (x 700).
 - A. Cross section of plumule.
 - B. Cross section of young leaf.
 - C. Cross section of mature leaf.
- D. Cross section cotyledon (x 150).
- E. Single cell from cotyledon (x 700).
- F. Cross section of stipule (x 700).
- G - J. Development of epidermal tissue, showing differentiation of stomata (x 700).
- K. Epidermis of radicle (x 700).

- L. Epidermis of old stem (x 700).
- M. Lower epidermis of cotyledon (x 700).
- N. Epidermis of old root (x 700).
- O. Epidermis of corolla (x 700).
- P. Cross section of epidermal and collenchyma tissue in stem (x 700).
- Q. Longitudinal radial section of epidermis and collenchyma (x 700).
- R. Three types of hairs (x 700).

H Hooked hair

SH Straight hair

GL Glandular hair

Plate VII.

- A. Cross section of primary bundle of hypocotyl, showing tangential arrangement of xylem (x 700).
- B. Cross section of bundle of the hypocotyl after secondary thickening (x 700).
- C - C. Course of vascular bundles in the flower (x 50).

Plate VIII.

- Diagrams of the course of the vascular bundles (x 50).
- A. Root, transition region, first node.
 - B. Second node.
 - C. Habit sketch of simple leaf to show portions diagrammed in D.
 - D. Petiole of simple leaf above the pulvinus.
 - E. Third node.
 - F. Habit sketch of compound leaf to show portion diagrammed in G.
 - G. Petiole of compound leaf below terminal leaflet.

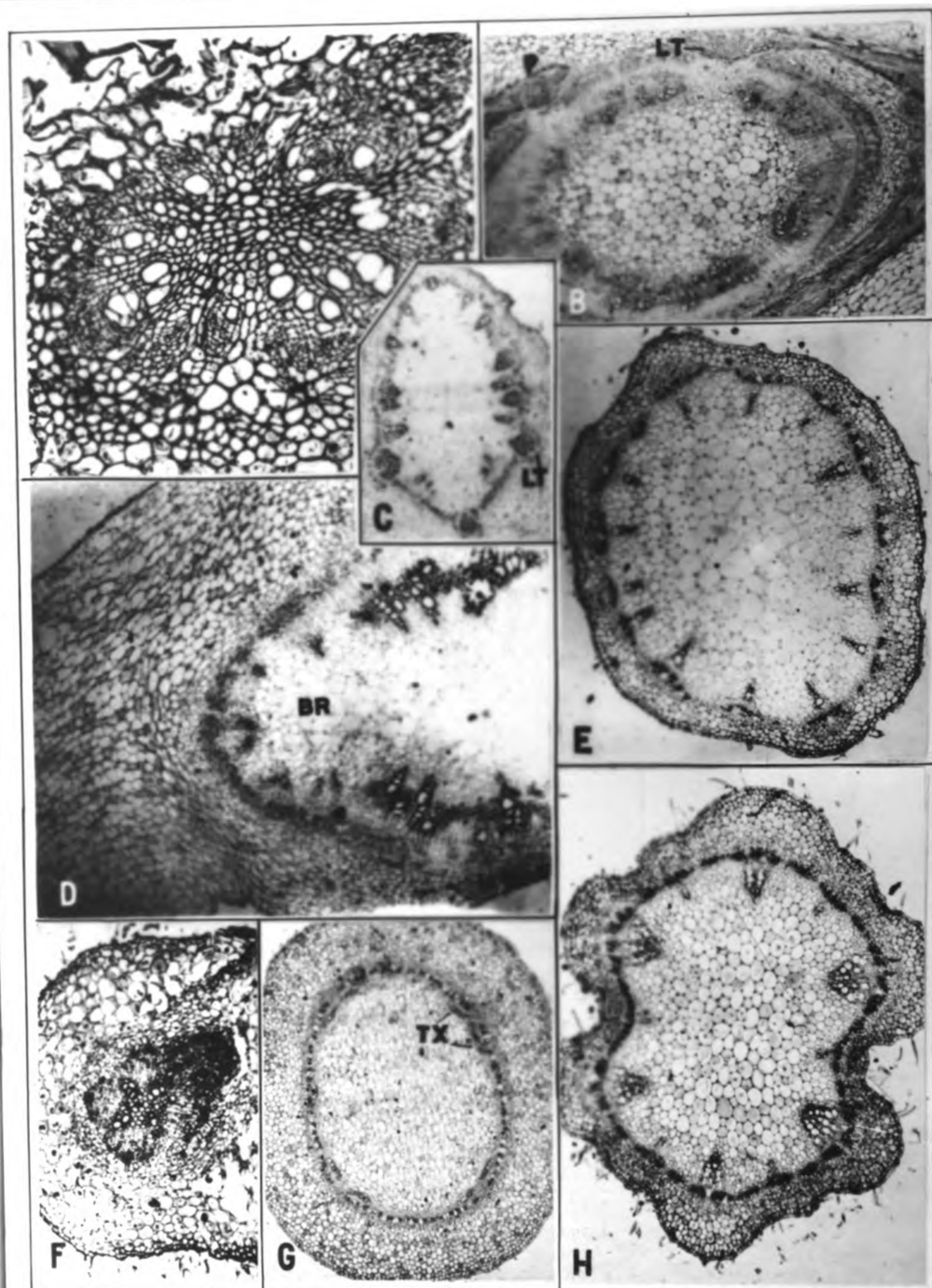


PLATE I

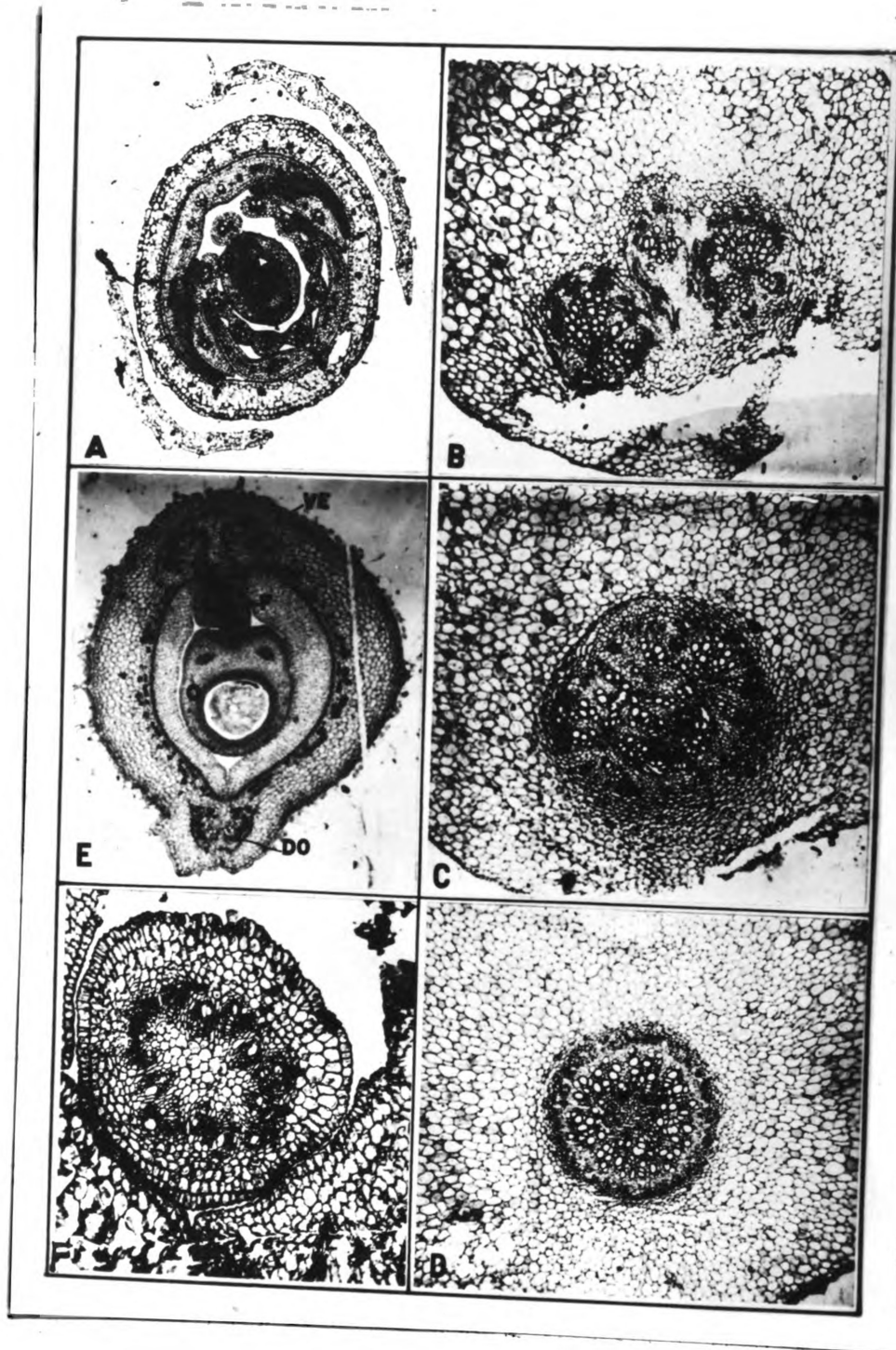


PLATE II

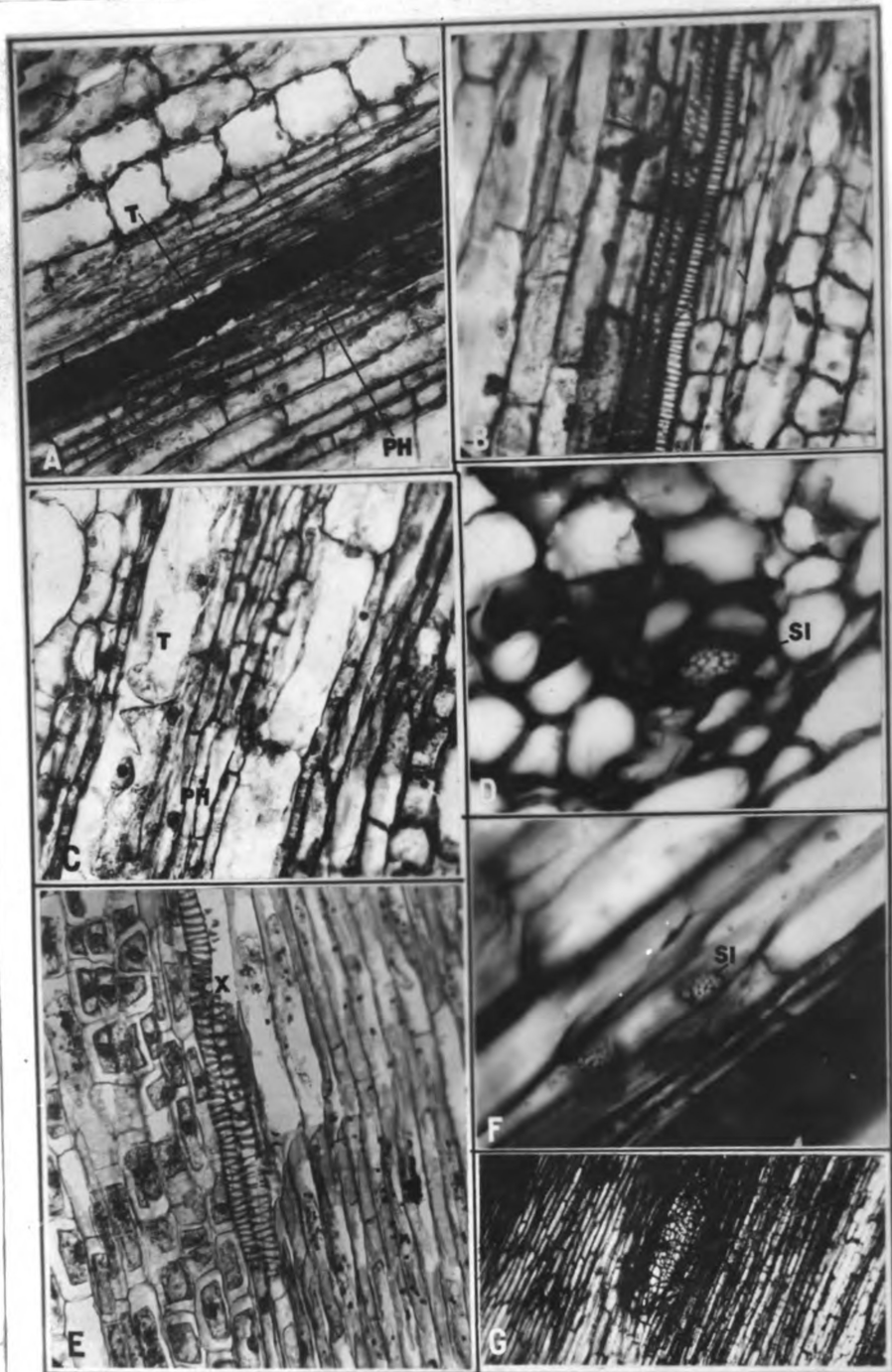


PLATE III

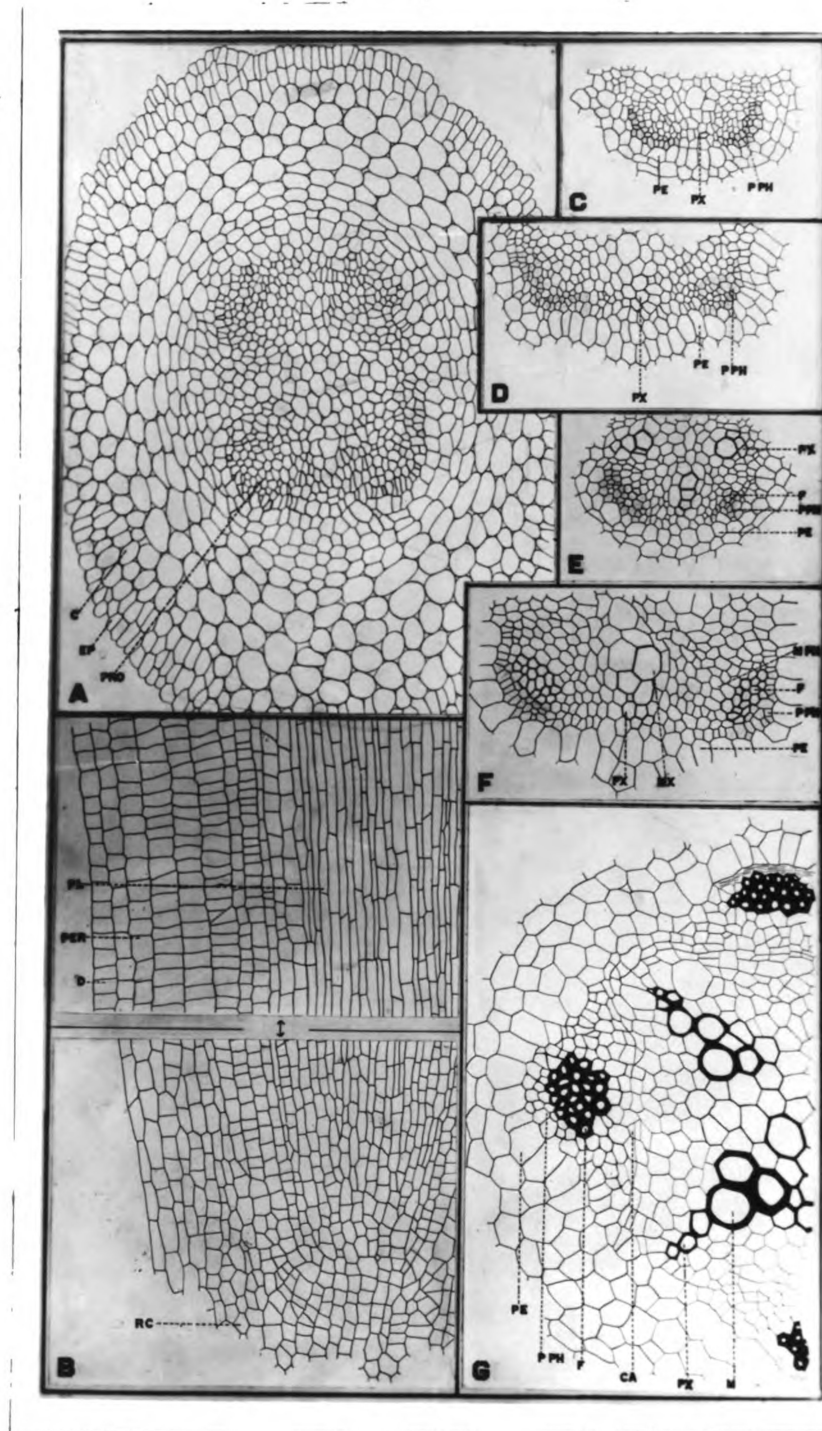


PLATE IV

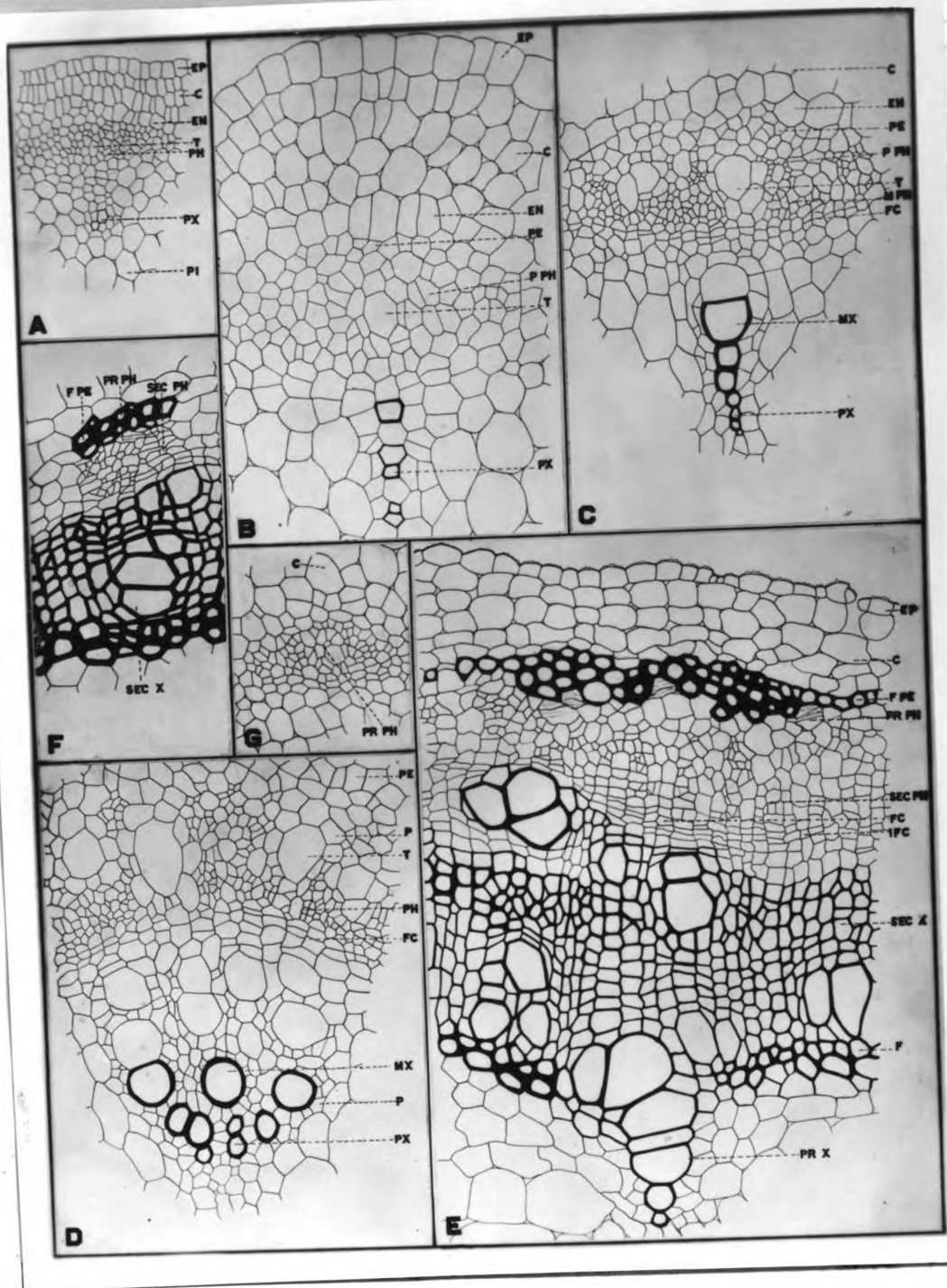


PLATE V

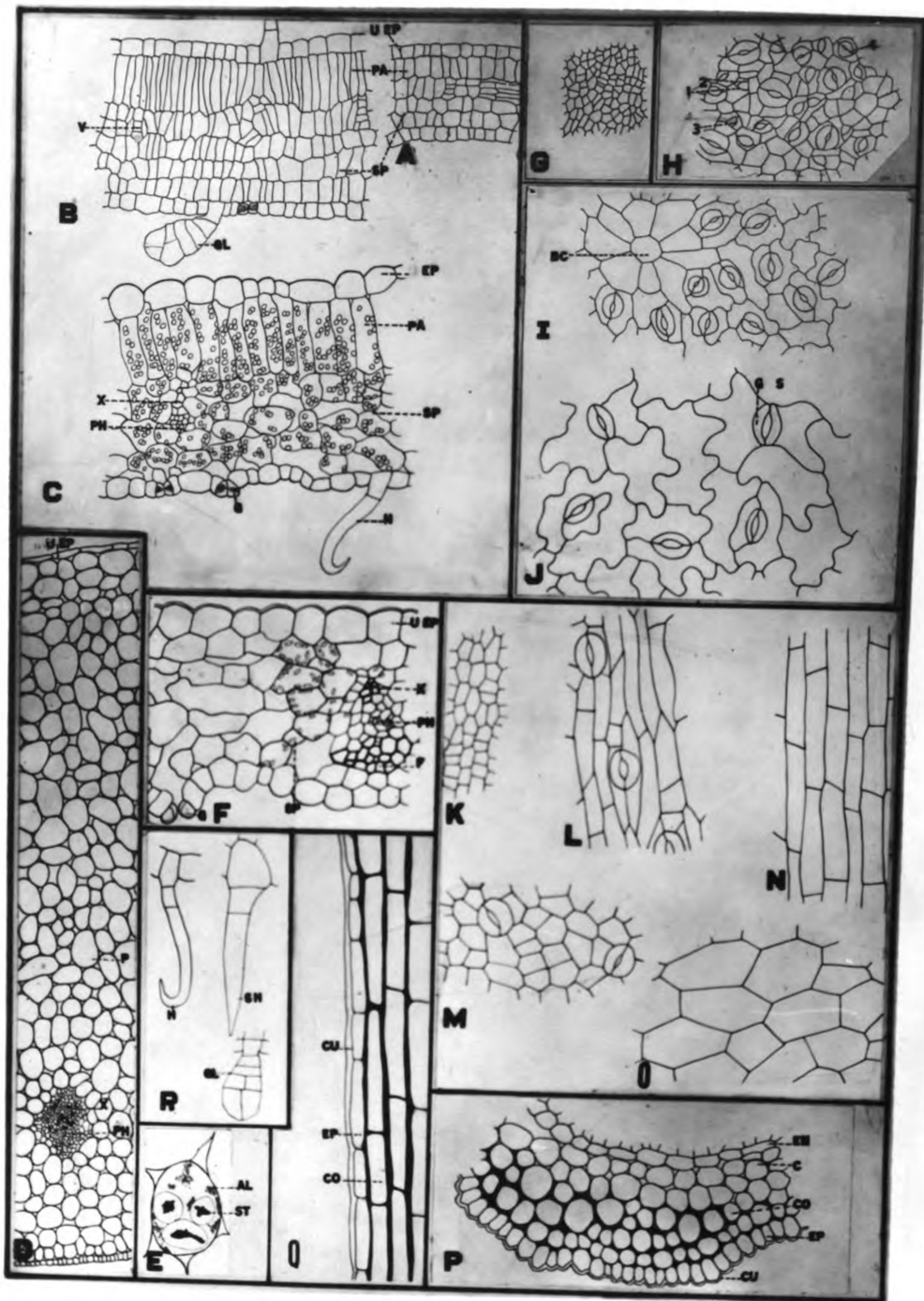


PLATE VI

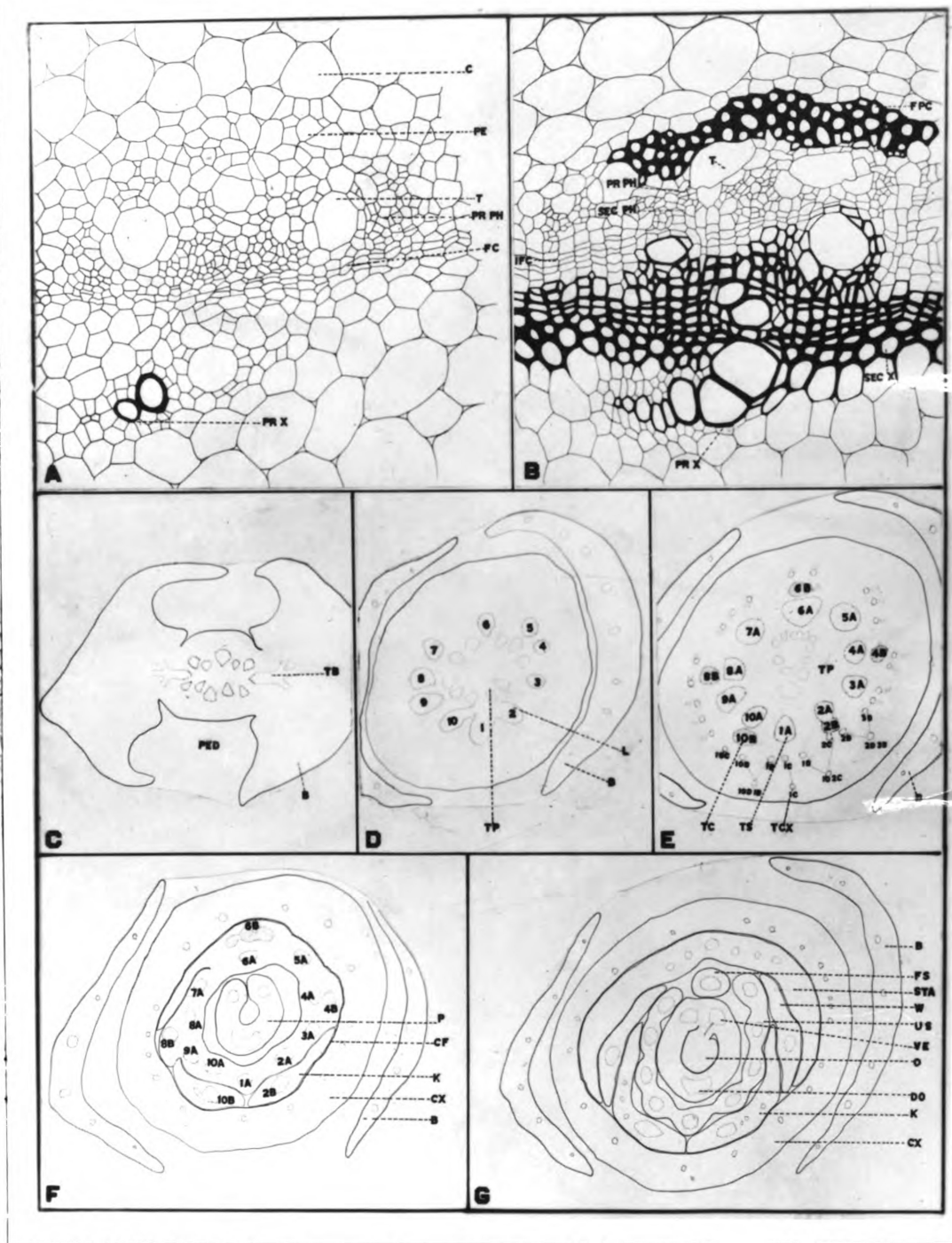


PLATE VII

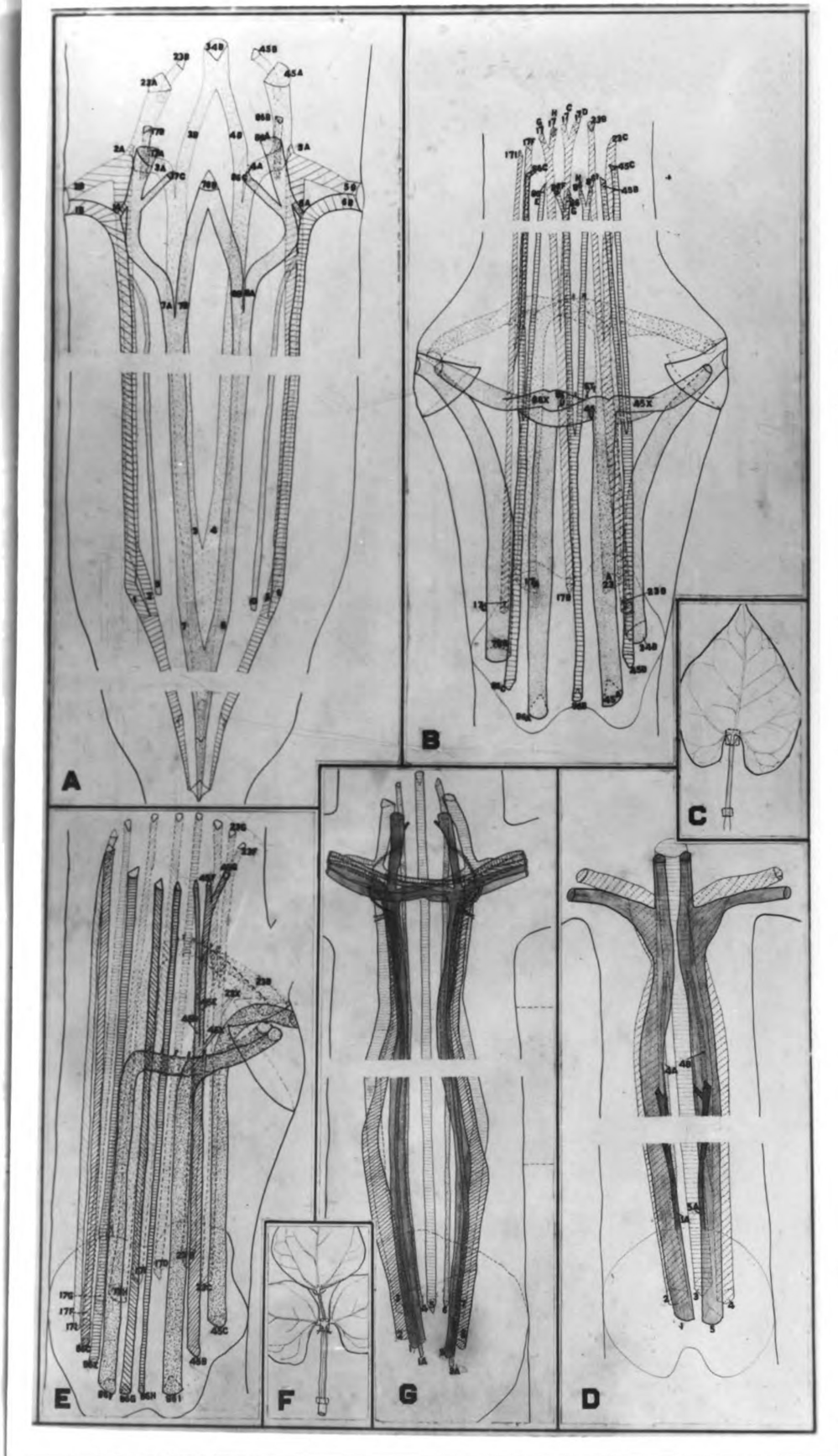


PLATE VIII

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