

**THE VASCULAR ANATOMY OF THE FLORAL PARTS
OF SOME SOLANACEOUS PLANTS**

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THE VASCULAR ANATOMY OF THE FLORAL PARTS
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During the past few years it has become apparent that numerous physiological and pathological problems depend upon a knowledge of the vascular anatomy of the floral parts, especially the carpels, for their solution. This is especially true in physiological and pathological anatomy which must depend upon a knowledge of normal anatomy for interpretation. In addition to this, during the last decade, particularly in its latter half, there has been another very evident and widespread revival in pure anatomy and a recognition of the close correlation between vascular distribution and morphology. The present controversial theory of "carpel polymorphism" advanced by Saunders (22 to 40) is an example of this trend.

The present paper deals with the vascular anatomy of four species of the family Solanaceae, which was selected because of the great economic importance of certain members. It is contemplated to continue the study of other species of this family.

The four species described in this paper are Solanum nigrum L., S. carolinense L., S. pseudo-capsicum L. and Lycopersicon esculentum Mill., (Solanum Lycopersicum, Linn.) The first two species of Solanum are not economically important; S. pseudo-capsicum is widely grown as a house plant; L. esculentum is a valuable agricultural cash crop in Maryland, and many other sections of the United States, and is capable of being grown throughout tropical and temperate regions. The vascular

pattern for each species has been considered as an individual expression of the problem of vasculature, without an attempt to deal with morphological and ontogenetical interpretations, except as these may be pertinent to an analysis of vasculature.

In standard texts on general botany, morphology and anatomy general descriptions of the vascular supply to the floral organs will be found, which are helpful in a general sense, but in every branch of science there are so many "exceptions which prove the rule" that such account cannot be taken as an absolute guide in any particular species, especially in plants which have been developed for any commercial use.

Among the various anatomical studies which have appeared in the literature in recent years should be mentioned the very careful study made by Kraus and Ralston (18) of vasculature of flowers and fruit of apple, which may well be taken as a guide to similar studies; that of Harris, et al (14) (15) (16), on the vascular anatomy of seedlings of *Phaseolus vulgaris*; Shuhart (41) on the morphology and anatomy of *Hicoria pecan* fruit; Winter (46) on the vascular system of young *Medicago sativa* plants; Blasberg (7) on the anatomy of *Asparagus officinalis*; Doult (11) on the anatomy of *Phaseolus vulgaris*, containing a complete and well illustrated account of the vascular anatomy of the root, transition region, stem, leaf and flower; Jackson (17) on the morphology of the flowers of *Rosa* and some related genera; Artschwager (3) and (4) on the anatomy of the vegetative organs of sugar cane and sugar beet; Artschwager, et al (5) concerning the development of flower and seed of sugar cane and Avery (6) on the comparative anatomy and morphology of embryos and seedlings of maize, oats, and wheat. While the subjects of these studies indicate a trend

toward pure anatomy, it is significant that they all deal with economic plants.

In the family Solanaceae, Payer (20), 1857, gave the most detailed account that had been given up to that time, but his studies dealt with organogenesis rather than with anatomy. Van Tieghem (44), 1875, in his classical work on the structure of the pistil, in dealing with numerous families including the Solanaceae, states that the pistil in all cases is composed of one or several leaves, free or united, open or closed, which produce ovules upon their margins, or upon a greater or less extension of their surface. This conception, which is the foundation of the old morphology, is still held to be true by the great majority of workers.

There is probably no farm crop which has received more attention from the standpoint of experimentation than the tomato. Such work, and the literature resulting therefrom, has dealt with cultural practices, fertilization, hybridizing, etc. Probably the outstanding pioneer in the early improvement of this plant as an agricultural crop was Tracy, of the Bureau of Plant Industry, U. S. D. A., author of a practical treatise on the tomato (45). There is also a tremendous collection of Experiment Station bulletins on various phases of cultural work and disease and insect control.

Among the anatomical analyses which have been published on members of the Solanaceae should be mentioned the admirable work of Artschwager (1) on the anatomy of the potato plant and (2) potato tuber; Thiel, (42) (43) on the vascular anatomy of the transition region of seven species; Cooper (10) on macrosporogenesis and macrogametophyte development in *L. esculentum* and (9) on the anatomy and development of the tomato flower; and Kraus and Kraybill, (19) on vegetation and reproduction of tomato.

Materials and Methods.

The structures which have been used in the studies of each of the several species of plants mentioned have consisted of varying stages of development of the floral parts. S. nigrum and S. carolinense were found growing in the open. S. pseudo-capsicum material was taken from house plants and the material of L. esculentum was obtained partly from greenhouse plants and partly from field plants, the variety used being Marglobe, selected because of its commercial importance as a market and canning variety. The oldest structures examined have been fruits up to a diameter of 6 mm., as it was found practically impossible to satisfactorily infiltrate with paraffin, fruits of larger size intact. Such material was placed immediately in formalin-acetic-alcohol killing and fixing fluid, carried through the ordinary series of higher alcohols, and infiltrated and imbedded by the paraffin method. All sections, transverse and longitudinal, were cut 20 microns in thickness, mounted serially and stained by the combination safranin and fast green method, which was found to be most acceptable, after comparison with some sections stained in haematoxylin.

The diagrams used as illustrations are based on sections. The drawings were made with the aid of a B. & L. microprojector. Photomicrographs were taken with a 15X Zeiss compensating ocular and a B. & L. 40 mm. objective for Fig. 1, and a 10X Zeiss compensating ocular and B. & L. 4 mm. objective for Figs. 2, 3, and 4, Plate VI. The approximate magnification is given in explanation of plates.

Results.

The vascular supply of the stem, pedicel, sepals, petals and stamens is essentially the same in all four species. Consequently for a description of the vascular anatomy of these organs, the four species will be

treated as a group.

The stem in an amphiphloic siphonostele, and the structure of the pedicel is essentially like that of the stem. The transverse section diagrams (Plate I), show the important structures to be considered here. The cortex, external phloem, xylem, internal phloem, and pith regions of a young pedicel are indicated in Fig. 1.

As the apex of the pedicel (i.e., the base of the receptacle) is approached from below, the vascular tissue shows a looser, less compact arrangement, although distinct bundles are not observable. (Plate VI, Fig. 1). Whatever the condition of the vascular ring in the pedicel at the point of departure of traces supplying the several floral organs, the same condition is found at the base of the branch trace. A segment of the ring, consisting of the protophloem, external and internal, and protoxylem, swings outward and supplies the part for which it is destined.

Finally a point is reached where the five traces which supply the sepals are shown detached from the stelar ring leaving five distinct gaps, (Fig. 2). These gaps are short vertically and the ring soon becomes closed again, to be followed at a very slightly higher level by the indications of the five petal traces, shown as emergences from the stelar ring in Fig. 3, alternate with those to the sepals. Prompt closure of the ring results in another circle of vertically short gaps.

Later the sepal traces are seen well out toward the periphery with the calyx zone differentiated from the remainder of the receptacle. (Fig. 4). Here the first indications of stamen traces are apparent as slight projections from the vascular ring, alternate with the petal traces, which means that they are opposite the sepal traces.

A further advance in development and orientation of the traces supplying androecium members is shown in Fig. 5. Here the calyx zone

remains about as in the preceding figure. The stamen traces have taken an upward, outwardly diagonal course, so that they occupy a position, alternate with the petal bundles, which makes the two appear to form a circle of ten bundles, but close inspection shows that the five petal traces form an outer circle of slightly greater diameter than the inner circle of five stamen traces.

Since the structure of the pistil, while the same for the three species of Solanum, is markedly different from that of L. esculentum, it is necessary at this point to separate the descriptions. The remainder of the figures in Plate I apply to the Solanum spp.

Referring again to Fig. 5, there appear in the center of the diagram two crescent-shaped regions of vascular tissue with their concave sides toward the center of the axis and two smaller areas between adjacent extremities of the crescents. This is all that remains of the previously prominent stelar vascular ring, after the traces to calyx, corolla and androecium members have been identified. After the stamen traces, shown as small emergences from the ring in Fig. 4, leave their resulting gaps in the vascular ring, the remaining vascular tissue forms a complete circle again and very shortly above that the condition indicated in Fig. 5 is found. Passing upward through the receptacle (Fig. 6), the sepals are distinct from each other. This means that this diagram represents a level above the calyx tube and in later drawings the sepals are not shown. Inside the whorl of sepals will be noted the two circles of corolla and androecium traces. In the center of the diagram the two smaller areas of vascular tissue retain their same relative position as shown in the preceding figure. The two crescent-shaped areas have now become changed in shape, being greatly

shortened tangentially but increased in their radial diameters. These areas, occupying an equatorial position in the diagram, represent the fused adjacent ventral or adaxial bundles of the two carpels which make up the ovary. The smaller polar areas represent the dorsal or abaxial bundles.

An examination of a large number of sections of each of these three species shows that the behavior of adaxial bundles may vary greatly. While there is no definite proof that they have fused in the true sense of the word, since a large part of the procambium tissue in the specimens studied was still undifferentiated, oftentimes adjacent ventrals approach each other so closely as to give the effect of a single area.

Higher up in the central part of the diagram the abaxial (dorsal) and adaxial (ventral) traces occupy the same relative positions as previously shown, (Fig. 7). All of the stelar vascular tissue has been allocated so that there is no axis or stem tissue appearing in the diagrams later than in Fig. 5, the vascular tissue of the central ~~area~~^{area} going to supply the carpel traces. This means that the two carpels are terminal on the axis or practically so, and that the stem tissue (receptacle) does not extend beyond the point where the ventral traces are differentiated and consequently is not prolonged into the central axis of the ovary. This is important in comparison with tomato. This figure represents a section just above the base of the ovary, as the two locules appear here as very small ovals or ellipses between the fused ventrals in the center of the pistil and the dorsal bundles on each side.

The corolla and androecium traces later occupy one zone (Fig. 8), which has become separated from the central ovarian or carpellary region.

The petal traces are shown well out toward the periphery of this zone, while the stamen traces make a distinct inner circle. The locules are now much larger and the two placentae have each expanded unilaterally and protrude somewhat into the locules, with numerous ovules attached. The dorsal bundles, occupying the same relative position as in previous figures, are quite prominent. Throughout the ovary wall or carpel surface from base to apex of the ovary, there is a profuse supply of branching and anastomosing vascular tissue, which originated from the dorsal bundles. These are easily seen in all sections of the ovary wall, being cut either in strictly transverse or diagonal sections, but are not indicated in the diagrams. Toward the apex of the ovary these converge and anastomose with the dorsal bundles of their respective carpels. In the middle septum, caused by the infolding of the adjacent carpellary edges, there is found a single area of vascular tissue which represents the four ventrals of the two carpels which sometimes so closely approach each other as to appear as one area. The behavior of the ventral traces is quite different at different levels in the same pistil. At some levels they appear as four distinct traces. At others, two may be distinct, while the other two appear to coalesce, or all four may so approach each other as to appear as one region (Fig. 8). However, the multiple nature of such regions is shown by the fact that in various sections branches are given off to supply the ovules which are nearest to that particular area of the ventral vascular supply.

Later tangential cleavage takes place in the outer zone, dividing this zone into the corolla and androecium whorls and also radial divisions have separated each of these whorls into their component parts of petals and stamens respectively, (Fig. 9), showing that the section is

above the corolla tube. The ventral vascular tissue shows as three areas, two of which, at the left represent the two ventrals of adjacent carpels, while on the right the two ventrals form one continuous area. Following diagrams show only the pistil.

Fig. 10, represents a condition which was found only in buds and flowers of S. nigrum, due to incomplete infolding of margins of adjacent carpels, but not found in any of the other species of Solanum. The location of the two ventrals, of adjacent carpels, each pair fused or coalesced into one mass, is shown on each of the projections in the diagram. Here the locules are smaller than in previous drawings, and the diameter of the ovary is much smaller, since its apex is being approached.

At the apex of the ovary or the base of the style, the dorsal bundles are distinct and occupy the same relative positions as previously indicated, with an elliptical area between them, (Fig. 11). This same area, also seen in the style (Fig. 12), is the stylar canal and apparently is composed of procambium cells.

Plate II, Fig. 1, is a composite diagram of a longitudinal section through the middle of the flower showing the vasculature in Solanum spp. The lowermost traces laid down and connecting with the stellar ring, supply the sepals, next above these are the traces supplying the petals, and just above the petal traces and running parallel with them, but not joining them are the stamen traces which curve upward at a point below where the stamen becomes exerted from the corolla tube and one trace passes into each stamen.

Above the point where the stamen traces are attached, the vascular tissue orients itself once more into a ring. The dorsals (abaxial) traces are first given off, pass into the ovary wall and continue upward as well-differentiated traces, not only to the apex of the ovary, but

through the style to a point just below the stigmatic surface of the pistil. The remainder of the vascular tissue converges to a point at the summit of the receptacle and continues upward through the axis of the ovary as the four ventral traces of the two carpels. Only two of these four traces are shown in the diagram. Branches from these ventral traces are given off on each side to supply their adjacent placentae and the ovules attached thereto. The placentae are shown to be lateral protuberances of the septum into the locules. Above the placentae the ventral bundles are less mature and at the apex of the ovary converge into a single area. From their point of union up to and including the stigmatic surface, the stylar canal is found. The nature of this area has been described previously. A comparison of the series of cross section diagrams with this figure will give a conception of the arrangement of the various structures at different levels.

In L. esculentum there is a marked difference in the development of the ovary. Plate III, Series A, is made up of actual drawings of a series of transverse sections of the same pistil, beginning at the base of the ovary and taken at various intervals throughout the ovary region and continuing upward well into the style showing the distribution of the vascular tissue.

A detailed description of the structures essential to this study will make clear the progressive development from the base of the ovary to its apex as well as show the structure of the style. All drawings in this plate are of relative size at the various levels.

A comparison of Figs. 1, 2 and 3, shows the differentiation and distribution of the vascular tissue near the base of the ovary. The stelar vascular tissue, which forms a complete ring after the departure

of the stamen traces, becomes distorted into crescent-shaped loops, some of which are connected, others isolated. Such breaks represent gaps in the receptacular vascular ring made by the differentiation of the dorsal bundles.

The points of the crescents differentiate into the dorsal bundles and orient themselves toward the periphery of the ovary, through an upward, outwardly oblique course. The remainder of the crescents becomes more dispersed at higher levels. At first three locules and five dorsal bundles are seen. Next the same number of dorsals and four locules appear, while in the third figure there are six dorsals and five locules, the latter becoming larger as the sections progress upward.

The next drawing shows twelve dorsal traces and twelve locules, (Fig. 4). This number of peripheral dorsal traces remains constant and continues to be seen in all sections, even in the style, to just below the stigma. The central vascular tissue has taken on the form of separate, crescent-shaped areas, rather definitely arranged. The tips of adjacent crescents approach each other, interior to the locules, and opposite the dorsal traces. The two ventral traces of each carpel possibly occupy the tips of adjacent crescents, although in tomato these have not been found to differentiate at this stage. Later the locules are larger and some have developed well-defined placentae, with ovules attached, (Fig. 5). The regions of central vascular tissue are shown as supplying the placentae with some branches going to individual ovules. However, there is still visible in the center, a considerable amount of vascular tissue which does not take part in such supply and which should probably be considered as strictly stelar on account of its position.

In the following drawing the arrangement of the vascular tissue is much the same, but an important change has taken place in the central region, in that three additional locules have made their appearance, (Fig. 6). Since these are very small, the section passed near the lower limits of these cavities. It is impossible to identify dorsal traces for these central carpels in this section.

The drawing in Fig. 7 shows three additional interior locules and accompanying two of these six inner locules, well-defined, dorsal bundles are seen. There now appear a total of eighteen locules, indicating eighteen carpels. The twelve peripheral carpels are clearly delimited, throughout the greater part of their extent, by branches from the dorsal bundles, ramifying and anastomosing in the ovary wall and septa, shown throughout this series of drawings as small traces, cut either transversely or diagonally to their course. The arrangement of these in a more or less circular pattern, outlines the infolded nature of the carpels.

In the succeeding drawing six dorsal bundles accompanying the six inner locules are seen, (Fig. 8). The two locules, labeled a and b in Fig. 7 where they are separated by a complete septum, are now really one locule, due to lack of complete infolding of adjacent carpellary margins, a condition already mentioned as occurring in S. nigrum. The two dorsal traces for these carpels still persist and continue into the style.

The peripheral locules are shown to be smaller in extent in Fig. 9, while there is slight variation in the inner whorl, some being slightly larger than in the preceding drawing, while others are slightly smaller. Four of the inner locules show the production of ovules but the two most

central ones, c and d do not, either here or in sections higher up in the ovary, showing that they are sterile. The septum which at lower levels completely separated locules a and b is seen here as a slight projection from the outer ovary wall.

This series of drawings is completed on Plate IV, where Fig. 10 shows essentially the same condition as in the preceding drawing, except that some of the locules are smaller. There is a decrease in the diameter of the ovary as it approaches the base of the style. At this level the definition of dorsal bundles of the two central, barren carpels, c and d, is not clear.

A section where the ovary is merging into the style is shown in Fig. 11. Due to the fact that it is practically impossible to cut sections exactly at right angles to the vertical axis, the upper-left half of this drawing represents the stylar condition and the lower-right half, where locules are still apparent, is the condition at the apex of the ovary. The full number of eighteen dorsal bundles is present and the denser areas accompanying many of the dorsal bundles in this drawing represent the stylar canals.

About midway of the style the eighteen dorsal bundles are clearly defined, (Fig. 12). These persist throughout the style to the lower surface of the stigmatic area and do not branch after leaving the ovary. There is not always a single area of stylar canal tissue accompanying each dorsal trace, as adjacent areas of such tissue may coalesce, so that one of these united regions may be considered as accompanying several dorsal traces. No stylar canal tissue is so situated that it might be considered as accompanying the sterile carpels c and d shown in Fig. 11.

In another pistil of L. esculentum, Series B, sections at progressively higher levels from the base of the ovary, represented in Figs. 1, 2, and 3, show that this pistil has ten carpels and ten locules near the base which are clearly defined in Fig. 1. The dorsal bundles are easily seen but it is impossible to distinguish the ventrals as such. The placental vascular supply is extensive. The two central carpels evidently are attached to the stem axis (upper receptacle) at a higher level than the eight peripheral carpels, as indicated by the smaller size of the central locules in this section. Locules a and b are completely separated from each other by the intervening septum.

Two important changes have occurred at the level of Fig. 2. The two central locules now appear as one, due to lack of infolding of the carpellary edges to form a complete vertical septum. The same thing has occurred in the case of the two carpels forming locules a and b which now appear as one. Here the remains of the septum persists as a slight projection into the locule from the ovary wall. In each of these cases, however, the two original dorsal bundles persist throughout the ovary and into the style.

In a cross section of the style about midway of its length, (Fig. 3), the ten dorsal bundles stand out prominently and the accompanying stylar canal tissue, in some cases as single areas, in others coalesced, is evident.

Series C, is a six carpelled pistil and is much simpler in construction than those just described, because there is only a single set of carpels, inserted at practically the same level, but even here, it is likewise impossible to distinguish ventral bundles for any of the several carpels. The descriptions for drawings of the two previous series apply here in general. Vertical septa between locules are all complete throughout.

The appearance of the styler canal tissue is somewhat different, (Fig.3), in that it occurs in only two areas.

In studying progressively the drawings of Series A, B and C, it appears that the stelar vascular tissue becomes less and less, regardless of the number of carpels involved, as one proceeds from the base to the apex of the ovary. It supplies the placentae and gives rise to dorsal bundles of a first and sometimes second whorl of carpels, until a level is reached when there is no remaining vascular tissue in the central part of the floral structure. The only vascular tissue seen in sections above where carpellary supply, including placentae, has been provided, is dorsal bundles and cross and diagonal section views of their branches in the ovary wall.

Radial longitudinal sections verify the descriptions given for transverse sections in the foregoing pages. The first three drawings of Plate V are of such sections of three different pistils. A very young two carpelled pistil (Fig. 1), shows clearly the continuation of the stele into the central axis of the ovary and an abundant supply of stelar vascular tissue to each of the placentae. The two dorsal bundles are seen in the style, while extending well down into the ovary below, uniting above and spreading out over the distal end of the style to form the stigmatic surface, the two styler canals are apparent.

A multicarpellary ovary (Fig. 2), contains a whorl of inner carpels arising at a higher level on the axis than the basal whorl. Short portions of the dorsal veins for the two carpels of these two whorls, included in this section, are seen where they join the stelar plexus and small areas of vascular tissue, which are probably sections of smaller branches from the dorsals, may be seen in the ovary wall at the left.

The ovary wall of the lower carpel bends in toward the axis at the upper end of the locule which it surrounds, and is united with the outer wall of the upper carpel, making a greatly thickened wall in this region. Stelar vascular supply to the placenta of this carpel is very evident.

The section through the carpel at the right of this figure does not show the attachment of the placenta. The dorsal bundle is shown as a branch from the stelar plexus, extending a short distance into the ovary wall.

Just at the base of the style, only a very short portion of which is shown in this drawing, there is a region which has the same appearance as stelar canal tissue, mentioned elsewhere.

Another tomato ovary is represented in Fig. 3, which has two whorls of carpels. At the base of the figure the abundant stelar vascular tissue is shown, with a short attachment of the trace supplying the sepal at the left. Five locules show in this section. Of the carpels surrounding these locules, two apparently are attached at the lower level and three at the higher.

Composite diagrams of the vascular supply to the floral parts in L. esculentum are presented in Plate II, Figs. 2 and 3. In Fig. 2, for the sake of simplicity, only two locules are shown, both of which arise at the same level on the receptacle, but the number of basal carpels could be multiplied many times without changing the fundamental ground plan. The development of the whorls of sepals, petals and stamens and the connections of traces supplying them, is in acropetal succession, and the description of Fig. 1, for Solanum spp. for these exactly describes what is found here. Above the point where the stamen traces join the stele the behavior of the stelar vascular ring is quite

different. The dorsal traces which are the first to differentiate, pass into the ovary wall, where they branch profusely, and continue upward in the style, where they do not branch at all, to the lower boundary of the stigmatic area. The remainder of the stelar vascular tissue instead of all differentiating into the ventral bundles as in the longitudinal diagram of Solanum spp. (Fig. 1), all enters the central axis of the ovary, supplies the placental regions abundantly, while these same regions expand unilaterally and produce the ovules. A branch of vascular tissue supplies each ovule. The axial vascular tissue does not extend beyond the upper end of the placental region; from this point there extend into the style traces which very soon lose the typical appearance of vascular tissue as it is seen in parts of the ovary and gradually changes into the typical stylar canal tissue which extends as a central core (or as numerous cores or strands in multicarpellary pistils) to the apex of the style where it expands laterally in all directions, such lateral expansions capping the dorsal bundles and forming the stigmatic surface of the pistil. This diagram and Fig. 1, Plate V, show that the stem extends into the axis of the pistil.

A different appearance is presented where there are two whorls of carpels, one above the other, shown diagrammatically in Plate II, Fig. 3. Here the stelar tissue enters the axis of the ovary, supplies the dorsal bundles and placentae of the lower carpels and continues upward to next give off dorsals to the upper carpels and branches to their placentae. Here the stelar vascular tissue ends and from this point upward the stylar canal tissue appears. Reference to Figs. 2 and 3, Plate V, show the same condition as is represented diagrammatically here. It is evident that the stem extends to the upper limit of attachment of the placentae of the higher set of carpels.

Since the foregoing descriptions on multicarpellary ovaries of the Marglobe variety of tomatoes were written, the writer has had an opportunity to study numerous transverse and longitudinal sections of the floral parts of the variety Yellow Plum, representing the more primitive varieties, where the ovary is normally composed of only two carpels. The behavior of the vascular tissue in this case is the same as in specimens of the Marglobe variety, which usually have a considerably greater number of carpels. The ventral bundles enter the axis along with the large amount of stelar tissue and do not become differentiated as such.

In specimens of tomato buds and flowers examined, the vascular supply of the stamens shows an occasional variation. Such a condition was found in a series of sections represented in Plate V, Figs. 4 to 10. The first section shows the receptacular stele of a pistil with seven petal traces well out toward the margin, and seven stamen traces as emergences from the central vascular ring, alternate with those of the petals. Even at this point the bilobular appearance of one stamen trace at the right is evident. In a segment of the receptacle at a slightly higher level, this trace is entirely detached from the ring and the bilobed condition is very marked. A section through the filament shows two distinct traces, and a little later there is indication of division of the filament into two units. This becomes more apparent in the succeeding section through the anther region, where three pollen sacs are seen. As the tip of the stamen is approached, eventually a point is reached where the branching of the anther is complete, with two pollen chambers in each branch. In the last drawing there is seen what is very nearly the normal appearance of two distinct anthers, except that one of these has only three pollen sacs. This trace joined the stele as one trace, although even then there was evidence of its double composition. Very soon it branched into two distinct traces, which progressing upward along the stamen are found to precede the branching of the anther.

In every specimen examined there has not been found in floral parts any differentiation of vascular tissue from procambium beyond the protoxylem and protophloem stage, possibly due to age of material. While in the protoxylem there are a very few annular elements, it consists practically entirely of spiral elements, with relatively thick lignified walls, (Plate VI, Fig. 2). The protophloem parenchyma differs but slightly

from procambium tissue and from adjoining parenchyma cells chiefly by its smaller cell size.

One trace for each sepal leaves the central vascular cylinder each making one gap. Very soon this separates into three traces, even while there is still a lack of divergence of the individual sepals from the receptacular cylinder. One trace for each petal, with its resulting gap, leaves the cylinder and their subsequent behavior is like that of the sepal traces. There is normally only one trace for each stamen, which does not divide at all. Each of these makes a single gap in the central cylinder. There is no reason to believe that we have anything but the normal three traces usually found for each carpel. The dorsal traces differentiate first each leaving one gap. As already mentioned, the ventral traces never become distinguishable from the mass of stelar vascular tissue remaining after the dorsal bundles have been given off in tomato, while they are quite distinct in Solanum spp.

Discussion

This study deals with the vascular supply of the floral parts. However, since this is continuous with the vascular cylinder of the pedicel, which in turn traces back to the stelar vascular tissue, the condition in the stem should be considered. Kraus and Kraybill (20) give the following description of the tomato stem: "The tomato stem in cross section is made up of an epidermis from which arise glandular hairs, several layers of cortical cells, endodermis, a more or less interrupted layer of bast cells, the phloem with small patches of sieve cells, primary and secondary xylem, small patches of internal phloem and internal xylem separated from each other and the protoxylem by pith cells, and lastly the pith."

This corresponds with what has been noted by the writer except

that it is not possible to identify the endodermis and in Solanum spp. the internal xylem and phloem is not apparent as such.

While the primary vascular tissue in the pedicels of all four of the species studied, becomes less compact as the receptacle is approached, it is never possible to determine individual bundles. The development of the floral parts and of the vascular tissue supplying them is in acropetal succession. All the flowers are gamosepalous and gamopetalous at the base. The stamens are adnate to the corolla tube and alternate with the petal midribs. They leave the stelar ring as separate traces and while they run practically parallel with the petal traces, to the point where they curve upward to enter the filaments, they are never united with them, thus differing from *Tetracentron*, *Andromeda glaucophylla*, *Gaylussacia frondosa* and species of *Vaccinium*, as mentioned by Eames, (12, pp. 170-171).

This same author (pp. 150-151), mentions two types of behavior of the tip of the vascular cylinder in flowers, viz; one where the vascular cylinder of the stem extends upward into the axis of the flower, after the ventral traces to the carpels have been given off, as found in *Aquilegia* and the other where the vascular tissue remaining after the dorsal traces to carpels have been supplied, divides into the ventral traces, with no residual vascular tissue, as illustrated by *Scheuchzeria*.

The Solanum spp. illustrate the latter type. From the foregoing descriptions it is apparent that when the ventral traces are given off no other vascular tissue remains. Therefore, the entire flower axis and the placentae are strictly carpellary.

In tomato the first type mentioned by Eames is typified. Foregoing descriptions bring out the fact that after the dorsal traces to carpels

differentiate, the entire remaining stelar tissue continues upward in the axis, and only ceases to exist after the placentae have been supplied. This is not only well illustrated in a pistil of only two carpels, but is much more emphasized in the case of an upper, as well as a lower whorl of carpels in the same pistil. This inner (upper) whorl of carpels has been found to consist of as few as two and as many as six, arising from the stem at a higher level than the basal whorl, the outer (lower) and inner (higher) sets being united to form the multicarpellate ovary.

Cross sections of the several ovaries all bring out the fact that there is much more vascular tissue present in the lower part of the ovary than could possibly be considered as ventral traces alone. Also in transverse as well as longitudinal sections it is evident that the placental region of each carpel is supplied with vascular tissue direct from the stelar cylinder. This indicates that the placentae are, to a considerable extent at least, morphologically stem. While it is not the province of this paper to discuss the ontogeny of the placentae and ovules, it is essential to make some reference to the morphology of certain structures, because of the intimate relationship between their origin and their vascular supply.

Eames and MacDaniels (13, p. 292) mention that in many fruits, especially those of the fleshy type, enlarged placentae may form a considerable part of the fruit, as in the tomato and watermelon. They further state that "the placenta is, of course, a part of the carpel, though not usually considered a part of the pericarp. In histological structure it is similar to the pericarp."

It is quite evident that in fruits of the Solanum spp. studied, the appearances are exactly in accord with this statement, but in the

case of tomato some further explanation and description seems desirable. As pointed out above, the sections show by the vascular supply to the placental region, that much of this structure is morphologically stem. Perhaps the decision as to whether the placentae are stem or carpel tissue, depends on just how much of the knob-like structure protruding into the locule from its ventral side, should really be considered as placenta. It seems reasonable that in L. esculentum the entire structure might be considered as being derived from a combination of the two. According to this view the fleshy part of the placenta would be morphologically stem (branch) whose periphery is encased by the enfolded carpel (leaf), but unfortunately such differentiation is impossible to determine. This latter part would be considered the placenta proper, from which the ovules arise. This appears to be the only interpretation which would reconcile the generally accepted view that placentae are carpellary in origin, as expressed by Eames and MacDaniels, and at the same time have the structure agree with what appears from the sections studied.

Eames (12, p. 154) states that ovule traces are derived from the ventral bundles and on p. 163 mentions some species where the ventrals are very much reduced so that the ovule appears to be borne on the dorsal bundle, as found in some species of Ranunculus--"a condition never actually present in Angiosperms (though sometimes apparently existing)."

In descriptions of sections studied it has been mentioned that at no time in L. esculentum was it possible to distinguish the ventral traces, while in Solanum spp. it was easy to distinguish them and their branches supplying ovules in the placental regions. In the tomato then, in conformity with the above statement by Eames, the only deduction

possible is the one already mentioned in the descriptions, that these are so closely allied with the stelar plexus supplying the center of the placental structure that they are indistinguishable from such stelar traces and may be said to become distinguishable only as the ultimate branches supplying individual ovules.

In the descriptions it was mentioned that a condition was found in buds of several ages and in completely opened flowers of S. nigrum, where adjacent carpel edges do not form a complete septum from bottom to top of the ovary, so that at the apex there is really only one locule. In young fruits the septum is found to extend completely from bottom to top. This condition in S. nigrum has been duplicated in several instances in tomato, where what are two locules at the base of the ovary, become one locule higher up, because adjacent carpel edges do not meet throughout their vertical extent. Thus the number of locules is not always an index to the number of carpels that make up the ovary. But what does appear to be a criterion for deciding the number of carpels is the number of dorsal bundles, which are usually quite prominent in all sections throughout the ovary and also in the style. In every pistil studied the number of dorsal bundles in the style has been found to exactly correspond with the number of well-defined carpels at the base of the ovary.

All Solanum spp. are 5-merous, 5-androus and bicarpellate. The primitive forms of tomatoes are the same but the commercial varieties have been greatly improved by selection. A recent publication of the U. S. Dept. of Agriculture (8) describes the Marglobe variety, with the number of sepals as typically six and the number of locules as typically six or seven, somewhat irregular in shape and arrangement. A well-defined, solid, central, fleshy mass and large fleshy placentae are

described. The cells (locules) are characterized as small and well filled with pulp.

Specimens examined by the writer agree very well with this description. While the floral parts may be said to be typically six, they vary from five to nine. In every case examined, the number of sepals, petals and stamens has been found to correspond. The number of carpels has been found to vary from two to eighteen.

Very slight reference is made in the literature to what has usually been named the "conducting tissue" of the style. In preceding pages attention has been called to the tissue of the stylar canal, using the term in the sense to include both the solid and hollow types of styles. This tissue may occupy a segregated area, opposite each dorsal bundle or several such areas may coalesce, the aggregate region remaining in close proximity to several dorsal bundles. In the sections studied this tissue appears different from the lower part of the same trace where such is distinguishable and stains differently from the other tissues. The cells have the appearance of very young procambium cells in that they are elongated vertically, have a very dense cytoplasm and never develop protoxylem. While the procambium of other traces undergoes differentiation into protophloem and protoxylem elements, this tissue in the style never undergoes further differentiation beyond the procambium stage, as far as it has been possible to observe in any of the specimens studied. Since the style is shed soon after pollination in all of the four species under discussion, it might be inferred that if any further differentiation were ever to take place, it would occur certainly by the time the flower is fully open and pollen mature, a time at which protoxylem and protophloem differentiation has occurred in other traces, even in the dorsal traces of the style.

In some sections it is very difficult to tell just where ventral bundles end and stylar canal tissue begins. The former seem to be replaced by the latter as we go progressively upward through the pistil, above the placental level. This stylar canal tissue seems to occupy the position of the ventral traces toward the apex of the ovary.

A recent paper by Joshi (18) on the morphology of the stylar canal in Angiosperms has thrown much light on this seemingly long-neglected tissue and its relation to the vascular system. He has made studies of ten species in four different families, and also finds that in every case the stylar canals are either continuous with the ventral traces or make their appearance at and occupy exactly the situation of, such traces.

Joshi believes that the pollen tubes in order to reach the ovules in the lower part of the ovary, progress through some of its vascular bundles and that the ventral bundles would be the obvious channels since the ovules are borne on the ventral side. He concludes that the earliest stylar canals originated by a mere cessation of the differentiation of the ventral traces of the carpel at the procambial stage. In some cases there is apparently a gap or break between the two.

In the case of sterile carpels, no accompanying stylar canal tissue could be identified.

The stylar canal at the upper part of the style, expands to form the stigmatic surface of the pistil, so that this structure is continuous from the stigma to the ovary.

While the number of stamen traces is usually one, which does not branch, or anastomose with any other trace from the time it leaves the stelar ring until it ends near the tip of the anther, there are occasionally found stamens in which the trace bifurcates in the filament, to be

followed higher up by a branching of the anther itself. This corresponds to the condition found by Cooper (9, p. 406).

Whether the number of carpels is only two or as many as eighteen, there is nothing in their structure, arrangement and relation to each other, which does not conform to the well-established and generally accepted idea that the carpel is morphologically a folded sporophyll, producing megasporangia and ovules, along the region of union of its ventral margins. Thus each septum of the ovary is made up of the contiguous infolded portions of the lamina of two adjacent carpels and the outer ovary wall consists of united arcs of individual carpels, traversed by the dorsal bundles. None of the numerous cases cited by Saunders (22 to 40) in her theory of "carpel polymorphism" apply here and the interpretation of the complicated eighteen carpellate ovary of tomato has not required the employment of the principles of this newer morphology.

Summary

The several facts which have been brought out in the study of the four species of Solanaceae, namely S. nigrum, S. pseudo-capsicum, S. carolinense and L. esculentum, may be summarized as follows:

1. In all four species, the floral organs and their vascular supply arise in normal acropetal succession.
2. Traces to each sepal and petal leave the stelar ring as one but soon divide into three.
3. Stamen traces leave the stelar ring as one, remain distinct, usually do not divide, but occasionally separate into two.
4. In Solanum spp. all the stelar vascular tissue above the stamen traces, differentiates into the dorsal and ventral bundles of carpels. The floral axis is carpellary.

5. In L. esculentum the stelar vascular tissue above the level of stamen traces, first gives off dorsal traces; and the remaining vascular tissue with ventrals undifferentiated, enters the floral axis and supplies placentae.
6. In L. esculentum probably only the covering of the placenta, bearing ovules, is of carpel origin.
7. Only ultimate branches of the vascular plexus of the placentae, supplying ovules, can be considered as distinct ventral traces in the tomato.
8. A second whorl of carpels may occur in L. esculentum, attached to the axis (stem) at a higher level than the basal set, the two uniting to form the ovary.
9. The styler canal appears to be a part of the same procambium trace, which in its lower part forms the ventral bundles. It is continuous with the stigmatic surface, but appears to be lacking in the case of sterile carpels.
10. Septation between locules is sometimes incomplete, due to lack of complete union of carpel edges throughout their vertical length.
11. The number of carpels is two in Solanum spp. while in L. esculentum the number varies from two to eighteen.
12. The interpretation of the vascular supply and anatomy of the pistil conforms to the established theory of carpel morphology and the employment of the theory of "carpel polymorphism" has not been required for explanation.

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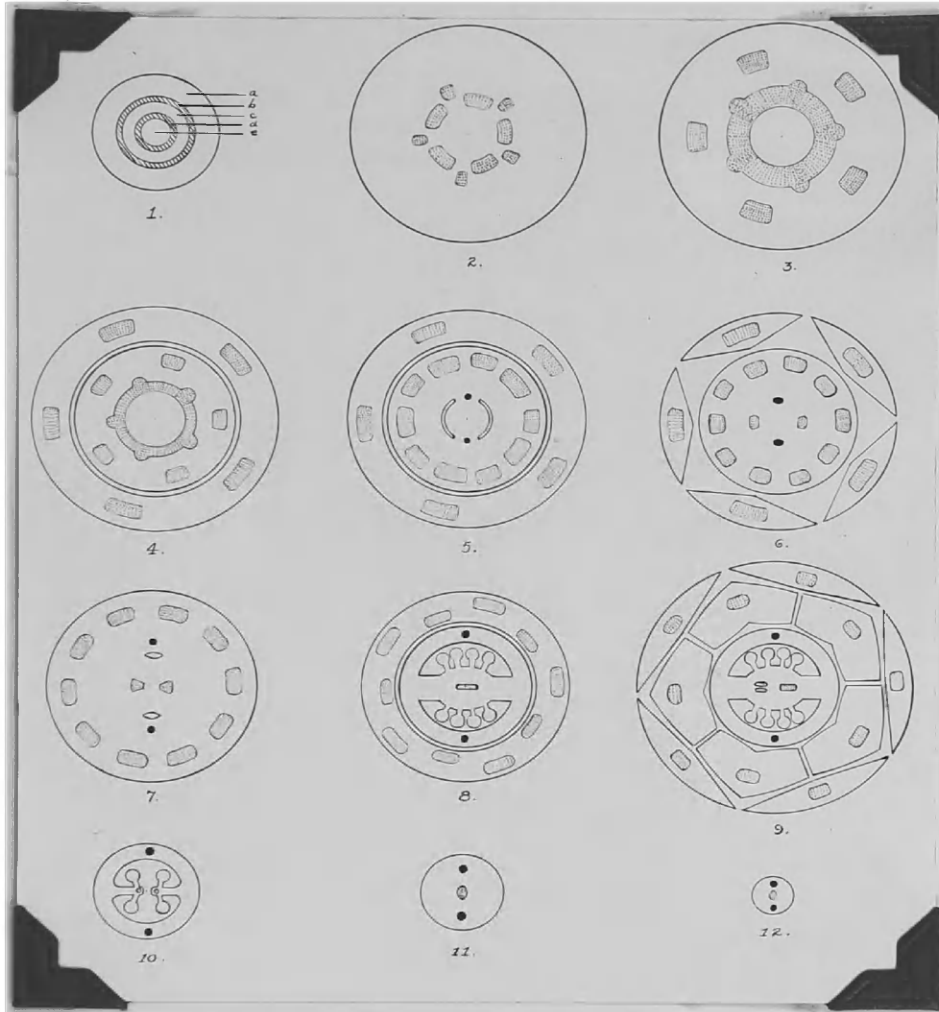
Acknowledgment

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Explanation of Plate I

Diagrams of progressive transverse sections from pedicel through ovary, into style. Figs. 1 to 4 apply to all four species. Figs. 5 to 12 apply to Solanum spp. only.

- Fig. 1. Upper pedicel:
a. - cortex; b. - external phloem; c. - xylem;
d. - internal phloem; e. - pith.
- Fig. 2. Five sepal traces, leaving five gaps in stelar ring.
- Fig. 3. Five sepal traces well out. Five petal traces emerging.
- Fig. 4. Calyx zone independent. Petal traces distinct. Five stamen traces emerging.
- Fig. 5. Petal and stamen traces forming two circles of five each. Dorsal traces distinct. Two crescents in center representing remainder of stelar tissue.
- Fig. 6. Sepals distinct. Fused ventrals of adjacent carpels seen in equatorial plane. Sepals not shown in later diagrams.
- Fig. 7. Two elliptical locules, between dorsal and ventral bundles.
- Fig. 8. Combined corolla and androecium zone diverges. Locules larger. Ovules attached to placentae. Ventral traces fused into one central area.
- Fig. 9. Petals and stamens independent. Ventral traces represented as three areas.
Later diagrams show only pistil.
- Fig. 10. In S. nigrum only - Incomplete septation at apex of ovary.
- Fig. 11. Base of style. Two dorsal bundles, one area of stylar canal tissue in center.
- Fig. 12. Well up toward distal end of style.

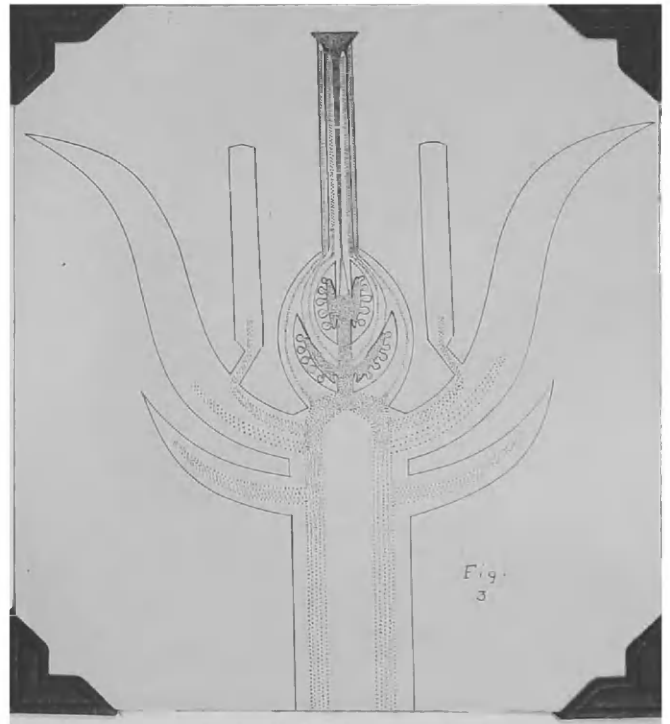
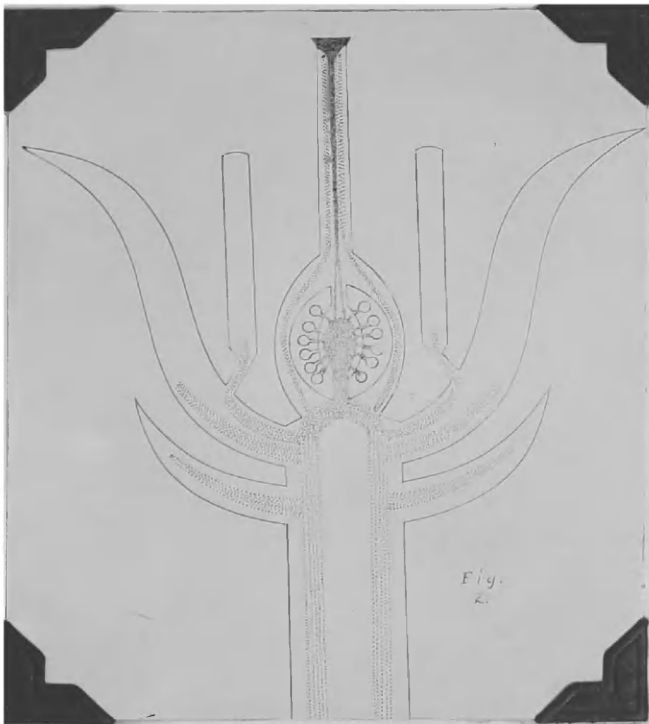
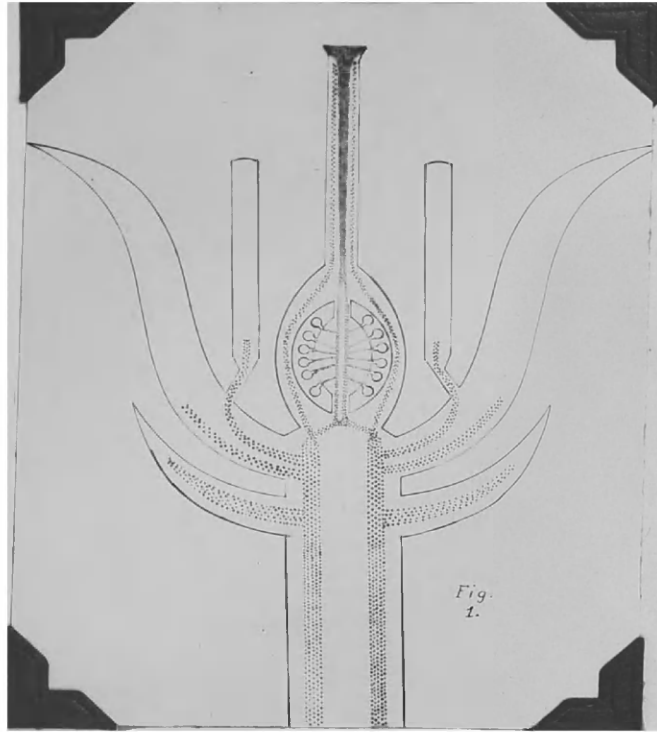


Explanation of Plate II

Longitudinal Radial Diagrams.

Sepal, petal and stamen traces in acropetal order.

- Fig. 1. Solanum spp. Dorsal bundles of carpels differentiate, traverse ovary wall and style. Remaining stelar tissue forms ventral traces, which traverse axis, connect with placentae and ovules. Styler canal tissue in upper part of ovary, extending throughout style and forming stigmatic surface.
- Fig. 2. L. esculentum with only a basal whorl of carpels. Ventral traces undifferentiated at base of ovary but enter floral axis along with a considerable amount of stelar tissue, which connects with placentae.
- Fig. 3. L. esculentum with an upper (inner) whorl of carpels and a lower (outer) whorl. Stelar tissue, ventral bundles undifferentiated, extends upward in floral axis to the level where it connects with the upper set of placentae. Ovary walls of the two sets of carpels united. Dorsal bundles extend upward through style independently.



Explanation of Plate III

L. esculentum - Series A.

Magnification X12.

Drawings from transverse sections through same ovary from base toward apex.

Fig. 1. Five dorsal bundles. Three locules. Stelar tissue in center arranged in crescent-shaped loops.

Fig. 2. Five dorsal bundles. Four locules.

Fig. 3. Six dorsal bundles. Five locules. Central stelar tissue more dispersed.

Fig. 4. Twelve dorsal bundles. Twelve locules. Most of central stelar tissue arranged in rather definite areas.

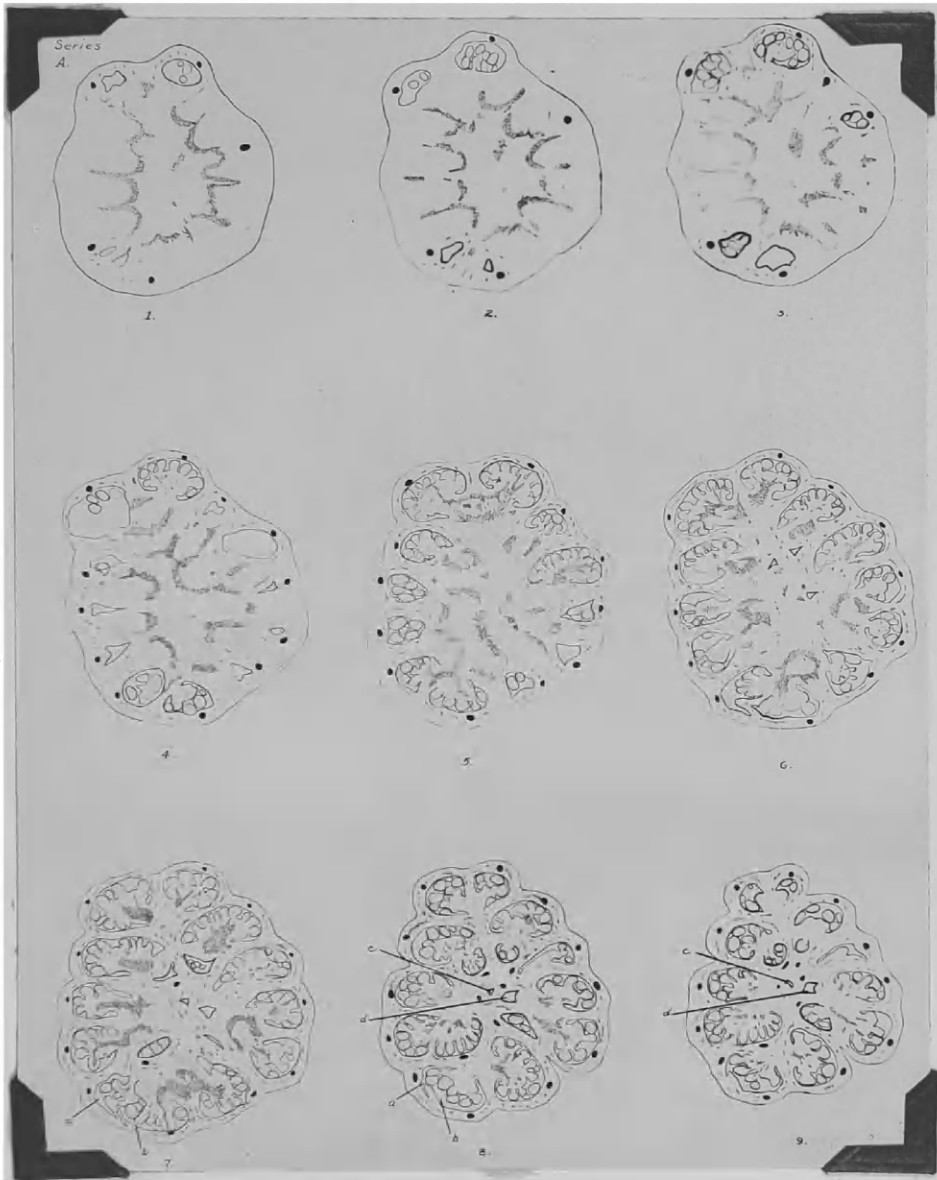
Fig. 5. Placental supply from stelar tissue. Several of most central areas of stelar tissue appear to have no relation to the peripheral locules.

Fig. 6. Three inner locules, indicated as triangular spaces.

Fig. 7. Three more inner locules, making a total of six. Locules a and b separated by intervening septum.

Fig. 8. Six inner locules, six distinct dorsal traces, indicating a total of eighteen carpels, a and b not separated, c and d contain no ovules.

Fig. 9. c and d, barren locules. Stelar tissue becoming progressively less prominent. Infolded nature of many carpels indicated by more or less circular pattern of sections through branches from dorsal bundles.



Explanation of Plate IV.

L. esculentum.

Magnification X 12.

Series A continued.

- Fig. 10. Locules c and d barren. All locules smaller.
- Fig. 11. Apex of ovary or base of style. Upper-left half represents stylar condition. Lower-right half shows ovary condition.
- Fig. 12. Section through style. Eighteen distinct dorsal bundles. Denser areas represent stylar canal tissue.

Series B.

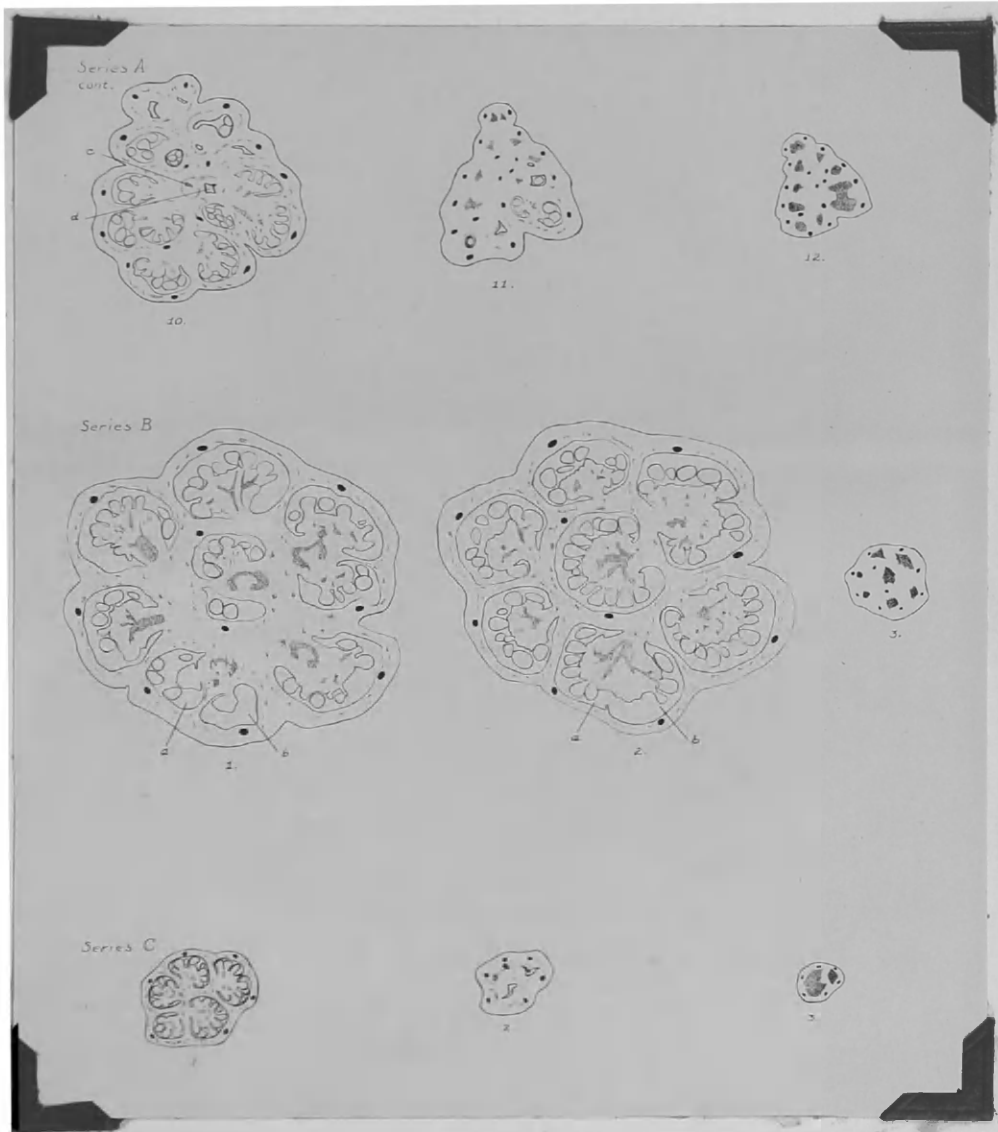
Transverse sections of another pistil, base to apex.

- Fig. 1. Eight peripheral, two central locules. Ten dorsal bundles. Locules a and b completely separated. Stelar tissue supplying placentae.
- Fig. 2. a and b are now one locule, as are original two central locules.
- Fig. 3. Section through style. Ten distinct dorsal bundles and stylar canal tissue.

Series C.

Transverse sections of a third pistil, base to apex.

- Fig. 1. Basal whorl of six carpels, six dorsal bundles, six locules. No central stelar tissue except that supplying placentae.
- Fig. 2. Section where ovary and style join. Only two locules seen. Six dorsal bundles. Stylar canal tissue areas apparent opposite four dorsals.
- Fig. 3. Section through style. Six distinct dorsal bundles. Stylar canal tissue coalesced into two areas.



Explanation of Plate V.

L. esculentum.

Magnification X12.

Fig. 1. Radial longitudinal section of a two carpelled ovary.

Note stelar vascular tissue in the floral axis. Stylar canal tissue well down into ovary.

Figs. 2 and 3. Radial longitudinal sections of two ovaries with two whorls of carpels.

a. base of carpel of lower whorl.

b. base of carpel of upper whorl.

c. stelar vascular tissue supplying placenta.

d. stylar canal tissue.

Fig. 4. Transverse section of receptacle. Seven petal traces toward periphery. Seven stamen emergences from ring.

a. Bilobular stamen trace emerging from ring.

Succeeding figures are at progressively higher levels.

Fig. 5. Segment of Fig. 4. Same stamen trace, distinctly bilobed.

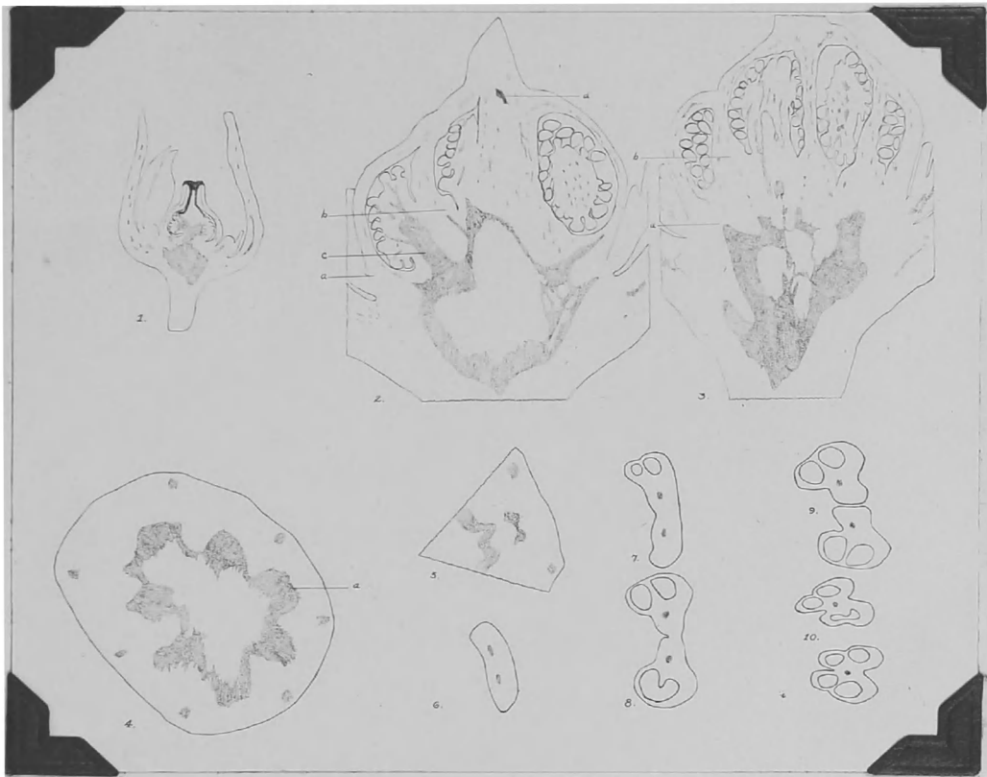
Fig. 6. Section through filament. Two distinct traces.

Fig. 7. Lower part of anther.

Fig. 8. Anther shows evidence of dividing.

Fig. 9. Anther divided. One trace in each branch.

Fig. 10. Anther branches more widely diverged.



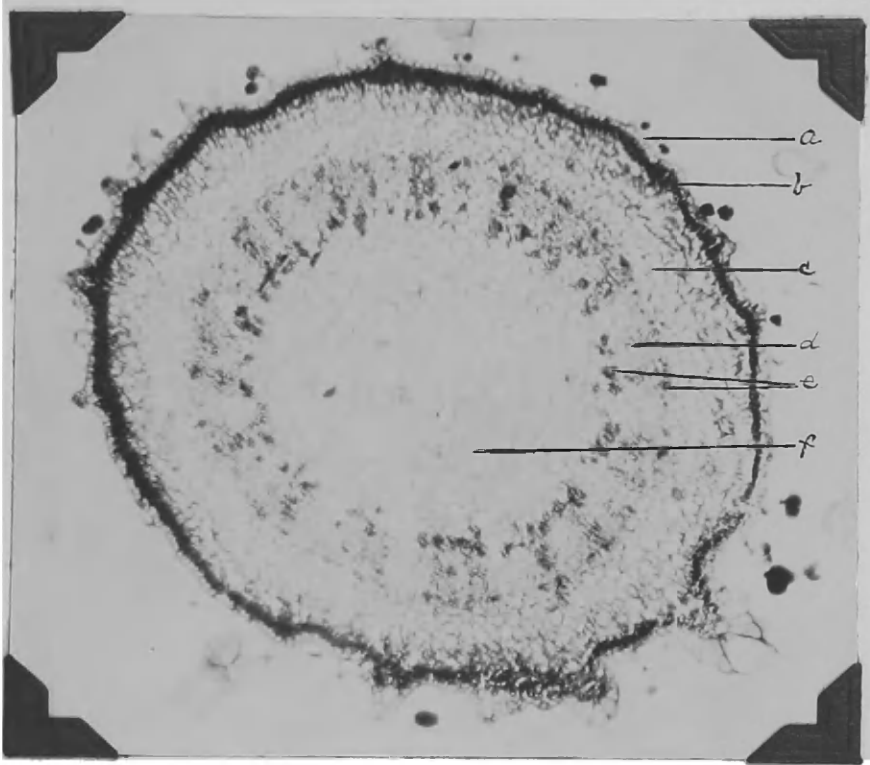
Explanation of Plate VI.

Photomicrographs.

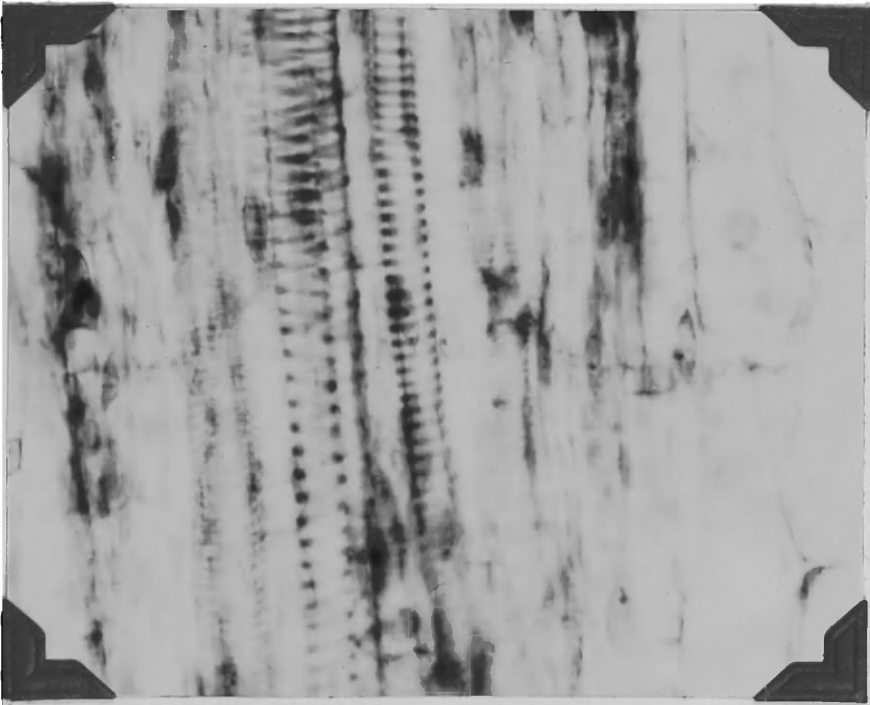
L. esculentum.

Fig. 1. Transverse section of pedicel near apex. Epidermal layer (a); collenchyma cells (b); cortex (c); protoxylem (d); protophloem parenchyma cells (e); pith (f). X64.

Fig. 2. Longitudinal section of spiral elements of protoxylem, with protophloem parenchyma cells on either side and pith cells at extreme right. X590.



1



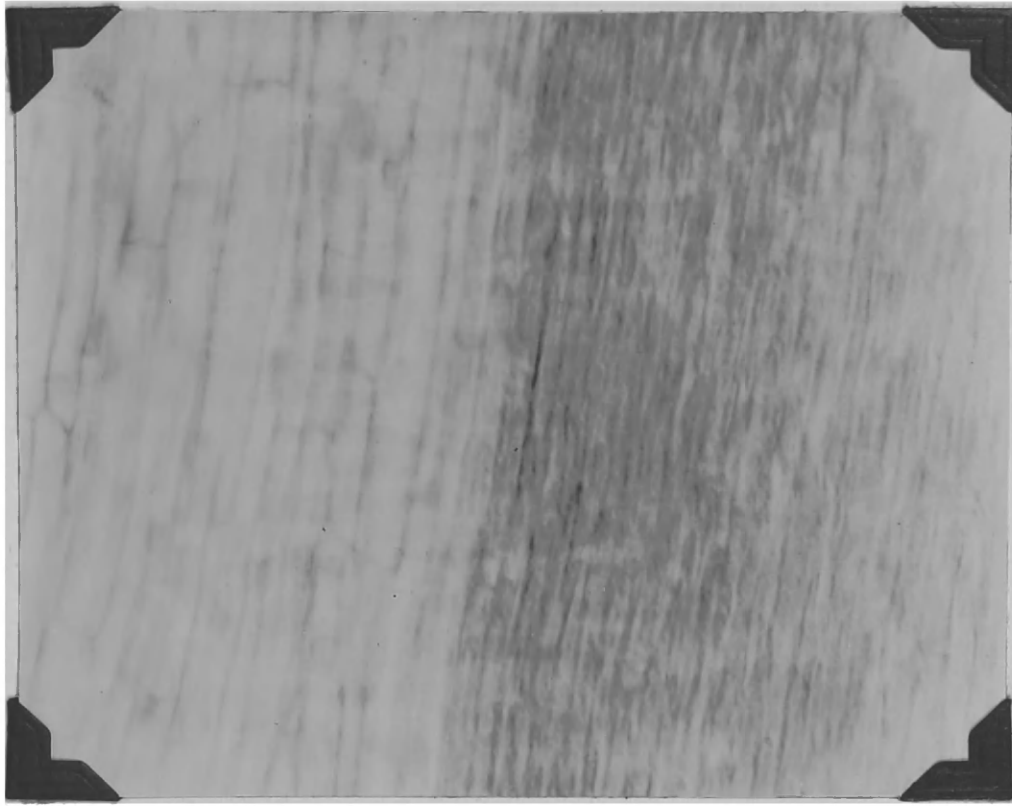
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Explanation of Plate VII.

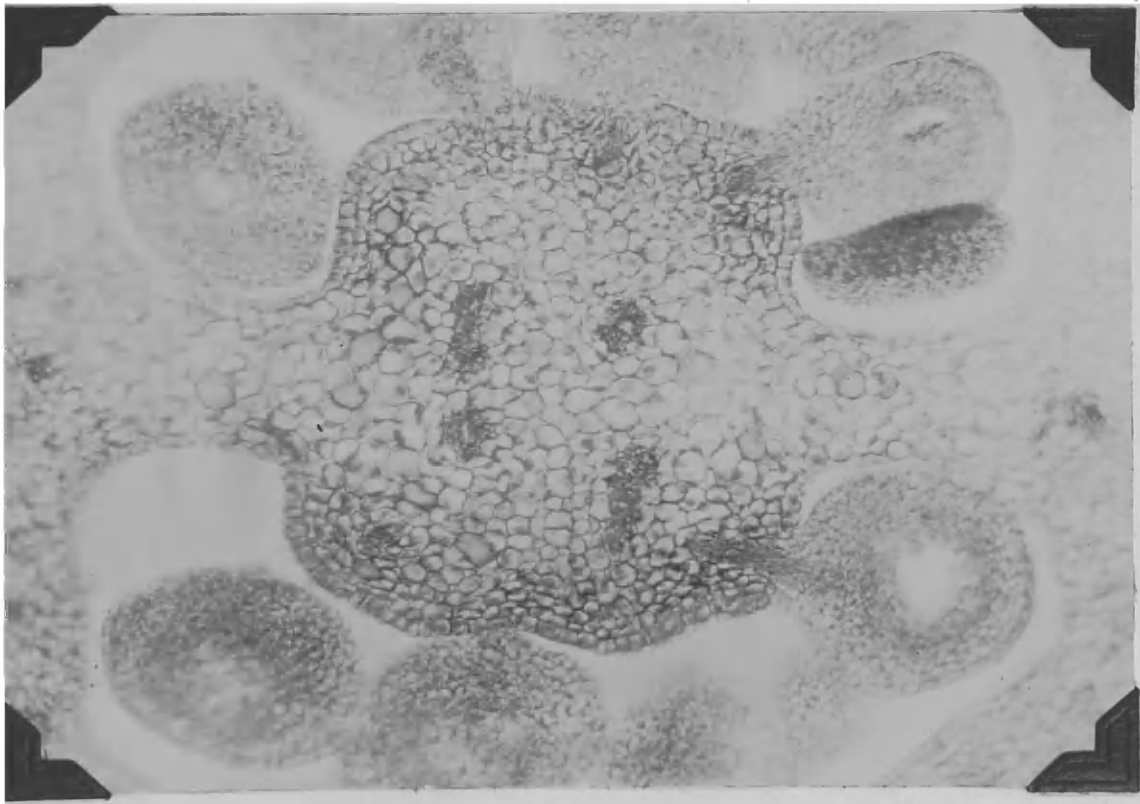
Photomicrographs.

Fig. 3 of L. esculentum. Fig. 4 of S. nigrum.

- Fig. 3. Longitudinal section of style showing smaller cells of stylar canal tissue at right, with dense cytoplasm and larger parenchyma cells of style at left. X700.
- Fig. 4. Cross section of ovary of S. nigrum, showing septum, placentae and ovules, four ventral traces of the two carpels in center. The attachment of several ovules to the placentae is shown, with individual branches of vascular tissue supplying them. X635.



3



4