

# BURRKNOT FORMATIONS IN RELATION TO THE VASCULAR SYSTEM OF THE APPLE STEM<sup>1</sup>

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## INTRODUCTION

Knight (8)<sup>3</sup> in 1809 mentioned the occurrence on the stems of certain varieties of apples of "rough excrescences, formed by congeries of points which would have become roots under favourable circumstances." Recently the writer (11, 12, 13) has called attention to the work of Knight and of others and has shown that many of our present commercial varieties of apples can be grown from cuttings containing burrknots, as Knight called these rough excrescences. The present paper deals with the anatomy of burrknot formation, a study undertaken in order to throw more light upon the physiological problem of the formation of adventitious roots on stems.

Kissa (7) in 1900 briefly described a case of "goiter gnarl" on *Malus chinensis* (*Malus spectabilis* Borkh.?), which was undoubtedly burrknot and which involved the production of adventitious roots. He showed that such roots arise as swellings at the outer edges of medullary rays, that growth in length of the tips is stopped by dryness, and that a lateral, basal branching takes place within the protecting cortex of the stem. Kissa made no reference to any definite location of these roots in relation to the primary vascular structure of the stem.

Borthwick (2) in 1905 published descriptions and photographs of adventitious roots in the apple and the maple, as well as in *Pyrus aucuparia*, *Ulmus campestris*, *Thuja gigantea*, and *Cupressus pisifera* (*Chamaecyparis pisifera*?). He shows that such roots arise at the outer edges of medullary rays, and that the cambium of the stem is connected with the cambium of the root, but he makes no mention of the relation of these roots to the primary vascular system.

Van der Lek (9) seems to have been the first to recognize the relation between the primary vascular system and the distribution of "root germs" on woody plants. Working with willow, poplar, and black currant, he found that most of the numerous root germs—he found 36 in one internode—arise in definite relation to the primary vascular system. He distinguishes between nodal roots—those which actually arise on the leaf traces, or branch traces themselves—and internodal roots—those which arise on the medullary rays. In some species the root germs are largely internodal, in others chiefly nodal.

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<sup>3</sup> Reference is made by number (italic) to "Literature cited," p. 544.

## METHODS AND MATERIALS

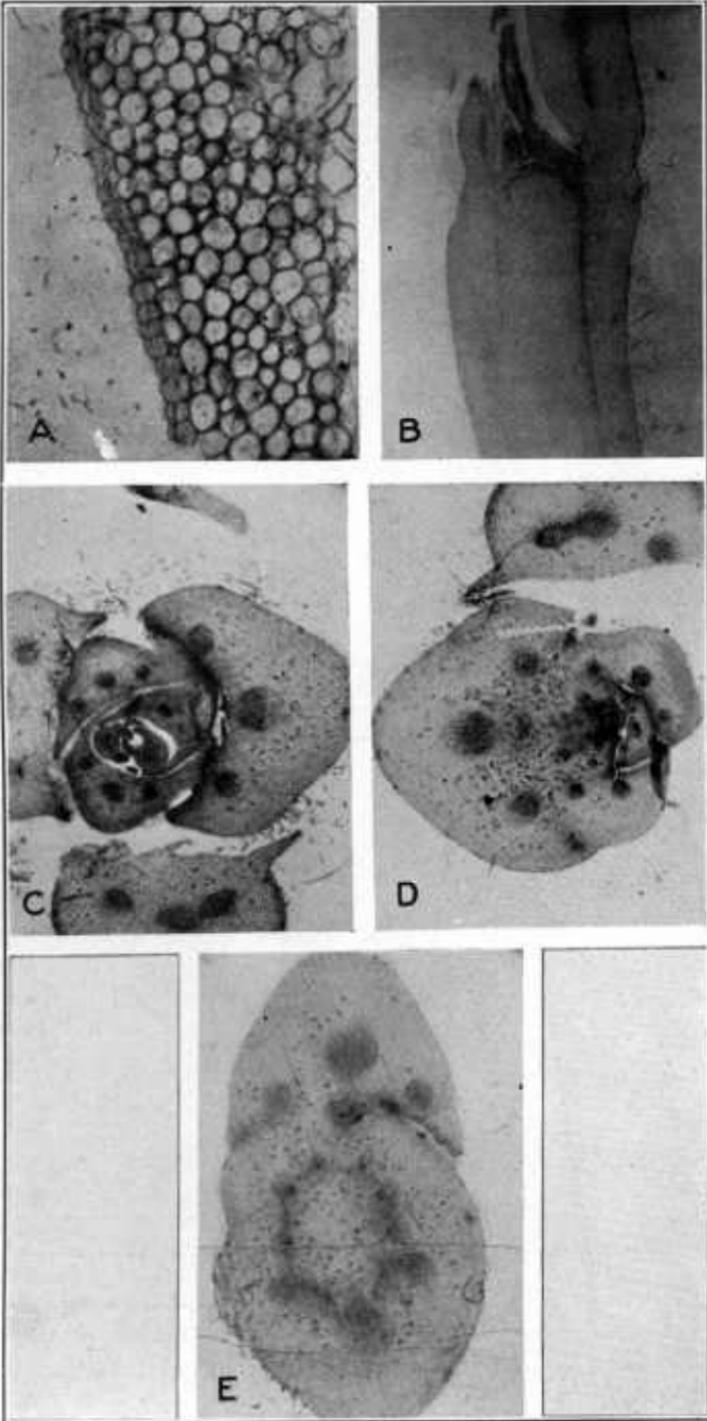
The work here reported was done in the botanical laboratory of Johns Hopkins University, Baltimore, Md. For the study of root anatomy, material of the apple varieties Buckskin, Jersey Sweet, Rambo, Wagener, and Springdale was used. The material was removed from 25-year-old trees in the orchard at Arlington Experiment Farm, Rosslyn, Va., cut into  $\frac{3}{4}$ -inch lengths, and placed in Bouin's picric acid-formalin-alcohol killing fluid. The air was removed under vacuum to insure the penetration of the killing fluid. After 24 hours the material was washed in 40 per cent alcohol, which was changed several times during two or three days. The material was then kept in 60 per cent commercial hydrofluoric acid for two to four days, or until it was soft enough to cut easily with a knife. It was next washed in water until no hydrofluoric acid taste could be detected. The material was next run up through the alcohol. Since it was desired to show cell walls rather than cell contents, a more rapid transition was used than is desirable for cytological work. It was necessary to thoroughly remove all water by changing the absolute alcohol several times. The total time in the various alcohols was usually about five days.

The hydrofluoric-acid treatment necessary to soften 5 to 10 year-old wood made the material so brittle that it was necessary to embed it in celloidin. Plowman's method, as given by Chamberlain (4), was used. However, in order to determine the exact position of the root germs in relation to the leaf and branch traces, it was absolutely necessary to have serial sections. To get these a modification of Wilhelm's (14, p. 17) method was used. After the celloidin-embedded material had been hardened in chloroform it was put into xylol (which was changed several times) and then embedded in paraffin. This made it possible to cut serial sections on a rotary microtome and to get sections of 8 to 10 microns in thickness of apple stems 10 years old. By putting the ribbons containing the sections on the slide and keeping them in place with mosquito netting, tied on with thread, it was possible to stain in series on the slide. Safranin and gentian violet proved the best stains. Some study was made of free-hand sections of fresh material. But for securing complete thin sections of wood the double embedded method was found to be necessary.

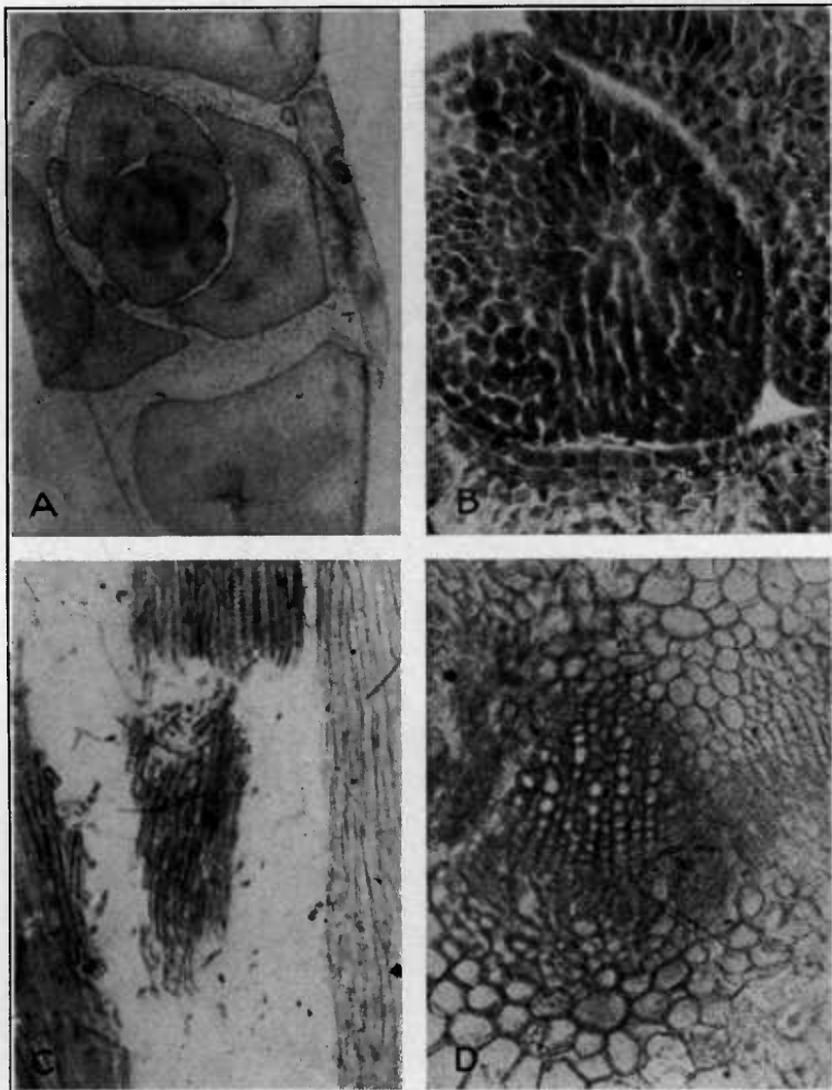
The structure of the primary vascular system was studied in new growth taken from the varieties listed above and also from the varieties Delicious and Tolman. Paraffin sections and free-hand sections were used. In the latter case the bundles were traced by haematoxylin which had been allowed to enter the twigs used, either at the cut end of one of the petioles or through the cut base of the twig. In both instances the evaporation from the leaves furnished a pull which drew the stain into the stem. The haematoxylin was found to follow closely the leaf-trace bundles, showing very little lateral diffusion.

## THE PRIMARY VASCULAR SYSTEM OF THE APPLE

Except for the short hypocotyl, the entire stem of the apple tree is the product, primarily or secondarily, of the terminal growing point of the embryo. This apical growing point of the stem is quite



A.—Origin of cork cambium in epidermis. ( $\times$  about 150)  
 B.—Longitudinal section through stem growing point. ( $\times$  15)  
 C.—Cross section of stem of Buckskin apple, just above the growing point. ( $\times$  15)  
 D.—Another cross section through the stem growing point. ( $\times$  15)  
 E.—Just below the growing point of the stem shown in C and D. ( $\times$  15)



- A.—Cross section of the growing point of stem of Wagener apple. Note the procambial strands in the leaves near the center and the vascular bundles, which arose as procambial strands, in the outer leaves. Notice also the protecting hairs. ( $\times$  about 20)
- B.—A higher magnification of part of the stem growing point shown in A. ( $\times$  150)
- C.—Spiral thickening of primary xylem elements. ( $\times$  100)
- D.—Origin of cambium within the bundle. Note the metaxylem in radial rows. ( $\times$  100)

effectively protected from drying out by the leaves recently formed by the growing point. These leaves grow very rapidly and soon push up and entirely surround the growing point. As will be noticed in Plate 1, B, C, and D, and Plate 2, A, the young leaves bear many hairs.

From this terminal growing point are differentiated the promeristems, from which the tissues of the main stem itself are derived. It also forms the leaves and the lateral branch rudiments or axillary buds. Before primary growth has entirely ceased there has been formed a cambium ring which is to give rise to all secondary vascular tissues. At about this same time the cork cambium, from which the outer portion of the bark is derived, is formed in the epidermis (pl. 1, A). The first cork cambium in most woody dicotyledons is derived from the outer layer of the primary cortex, although not a few genera have a cork cambium initiated in the epidermis, as does the apple.

The terminal growing point of the apple is broad and depressed (pl. 1, B), so that within a few millimeters of the tip the hollow central cylinder or siphonostele, characteristic of most woody dicotyledons, is recognizable. A cross section taken immediately behind the growing point (pl. 1, E) shows pith in the center with the vascular bundles grouped in a ring between a central pith and the cortex. Connecting the central pith and the cortex, and separating the bundles from each other, are the medullary rays. The cells of the central pith, the medullary rays, and the cortex differ from each other chiefly in position. Practically all cells of the stem for several centimeters back of the growing point, even cells of the central pith, contain chlorophyll.

Each bundle of the stem consists of a longitudinal strand of cells. The bundles have no direct connection with the growing point, but as they run upward each passes out of the stele and then on through to the outer cortex, where, coming close to two other similar bundles, it enters the base of the petiole. Here the two outer bundles divide, the inner half of each continuing out into the leaf, the outer half going into a stipule. Followed downward, each stem bundle becomes smaller and smaller in the tangential dimension until—several internodes below the point of its entrance—it merges with a neighboring bundle derived from another leaf. The following description of the leaf traces of woody dicotyledons in general, given by Eames and MacDaniels (6), is applicable to the special case of the apple.

Since the trace is merely an extension of the vascular system of the stem—either as a definite, abruptly separated branch of that system, or as a strand gradually set off as a distinct part—there is not usually a definite point of origin of a trace. The trace, as an identifiable, protoxylem-containing strand may, indeed, often be followed down the stem for some distance below the level at which it begins to swing outward, and there found to merge with other traces or with the xylem of the primary cylinder. . . . Below the point where the trace is separated from the cylinder it is in many cases evident for some distance as a distinct, though not isolated, strand, chiefly of protoxylem. This distinctness of the strand in the xylem cylinder is due to the type and size of cells composing it, these being different from those of the adjacent xylem. . . . Such a downward extension of the trace may be very short or lacking, or may be several internodes in length.

Figure 1 shows diagrammatically the path of the bundles from 9 leaves in a stem of Delicious apple. It will be noted from the diagrams that the general arrangement is such that at any given cross section of the stem the 9 most distinct bundles are the 3 sets

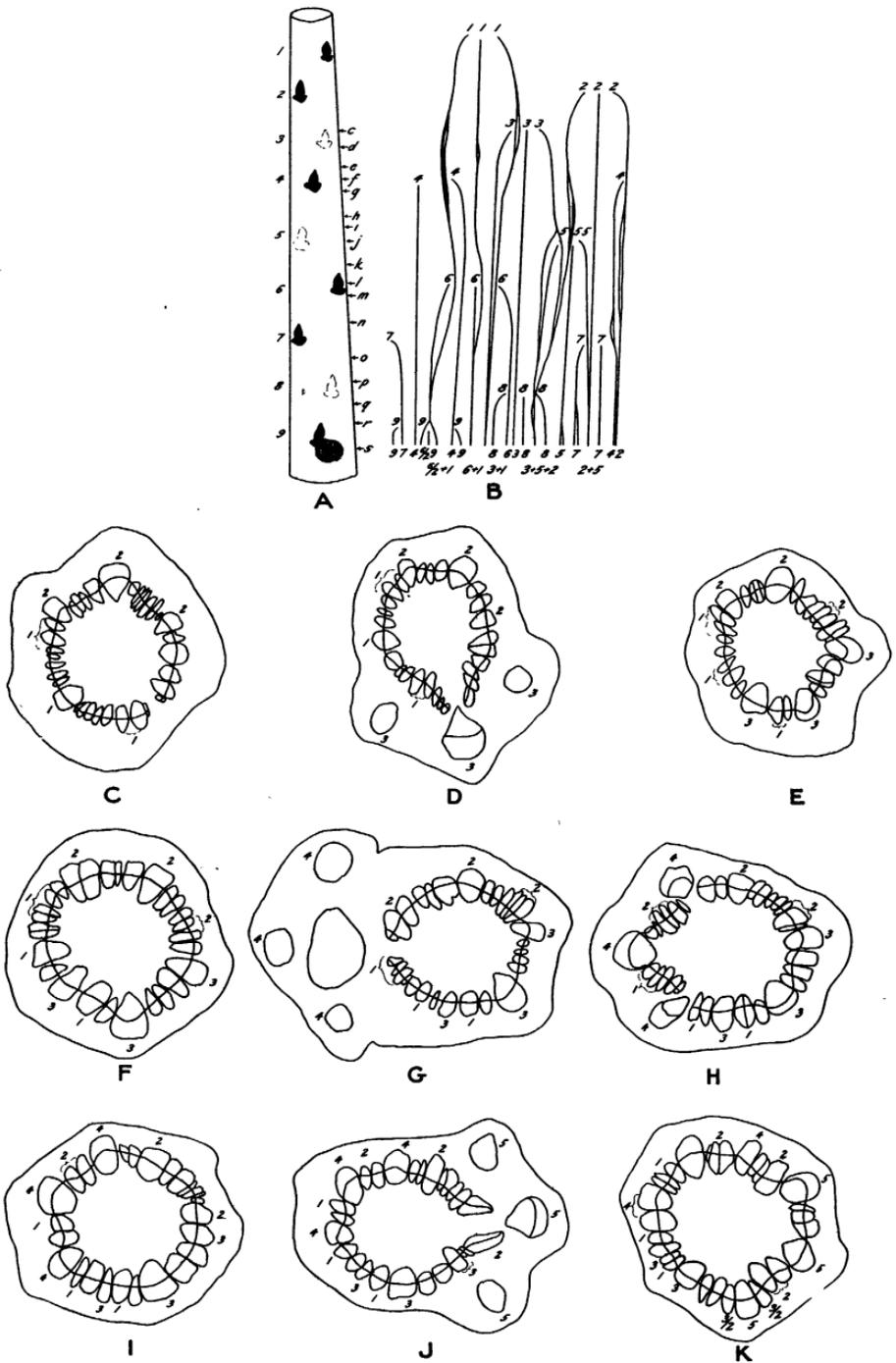


FIG. 1.—Diagrammatic representation of the courses taken by leaf traces in a stem of Delicious apple. A, external appearance of the stem. The numbers refer to the numbers of the buds, the letters to the points at which cross sections having the corresponding letters were cut. B, diagrammatic representation of the paths of the bundles. C to S, camera-lucida sketches of cross sections taken at points indicated by the corresponding letters in A

of 3 each which lead to the 3 leaves next above the section. These bundles are so distributed that one of the side bundles of the uppermost of the 3 leaves (numbered 1 in fig. 1, D) lies between a lateral bundle and the median bundle of the leaf immediately above the section (numbered 3 in fig. 1, D). From the successively lower sections (E to S) it will be seen that the bundles become less and less prominent and that each will ultimately lose its individuality by fusing with a neighboring bundle. This can be clearly seen by following two of the bundles of leaf 2 in diagram B, and in sections C to S. (The third bundle of leaf 2 fused still lower down.)

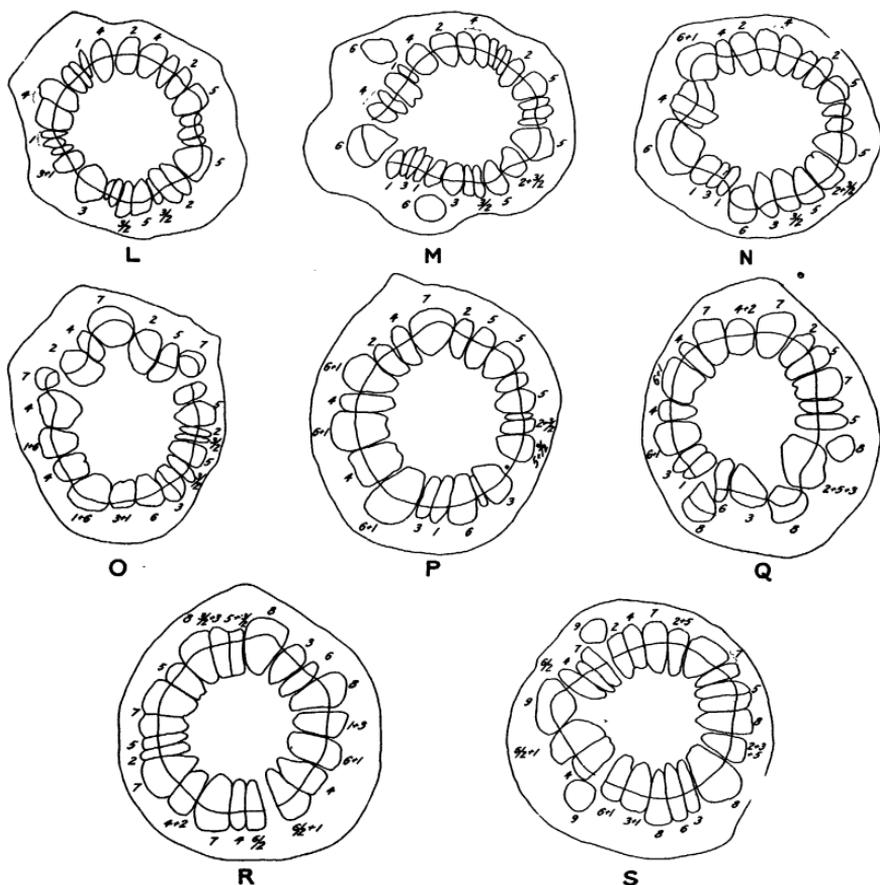


FIG. 1—Continued

Figure 2 shows a series of sections through a Delicious apple stem in which interposition of bundles does not always occur. In rare cases the three traces from each of the three leaves immediately above the section lie next each other in the stele. The laterals of one set do not cross over to become interposed between the laterals and medians of the adjoining set. (See trace 3 at right in diagram B, fig. 2, and sections C to K.)

In other cases, the upper bundle divides, half going on each side of the lateral bundle from the second leaf below. (See trace 2 in fig. 2, B.) In both these sets of diagrams (figs. 1 and 2) it will be

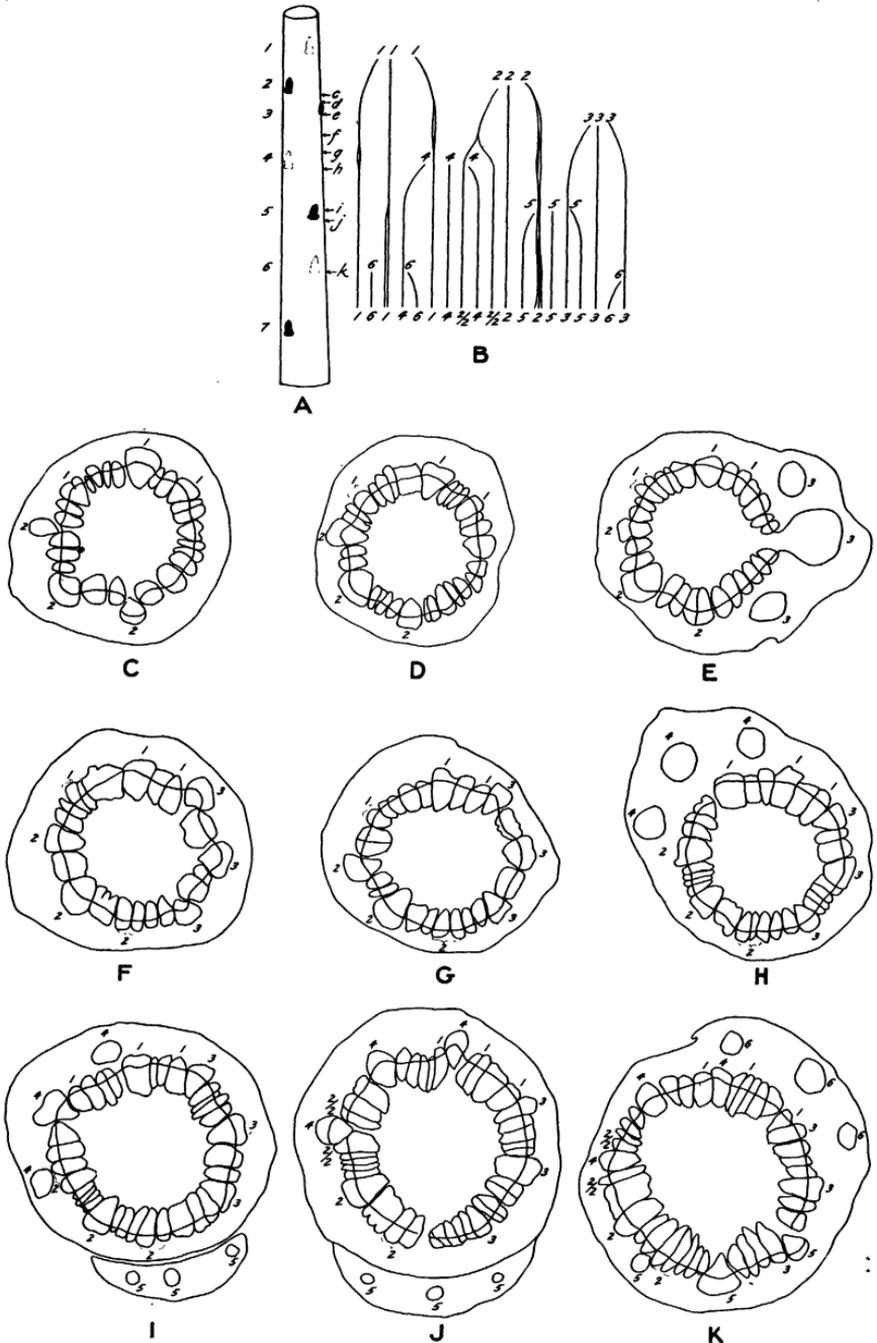


FIG. 2.—Diagrammatic representation of the three types of arrangement of leaf traces found in the stem of a Delicious apple. A, external appearance of the stem. The numbers refer to the numbers of the buds, the letters to the points at which cross sections having the corresponding letters were cut. B, leaf-trace courses. Note that between 3 and 1 there is no interposition such as occurs between 3 and 5. Note also that one of the laterals of leaf 2 divides and goes on both sides of the lateral of leaf 4. C to K, camera-lucida sketches of cross sections taken at points indicated by the corresponding letters in A.

noticed that there seems to be little regularity in the way the bundles divide and merge. These irregularities seem surprising in view of the fact that only a primary vascular structure is under consideration and that supposedly it is the genetic constitution, rather than any controllable outside factor, that determines the primary arrangement peculiar to any given species.

As is mentioned below, in connection with the spiral arrangement of leaves on the stem, these irregularities in the courses of the bundles may possibly be significant in regard to the root formation or fruit-bud differentiation or to other factors, though of this nothing is known at present. Nägeli (10) noted and diagrammed similar irregularities of the bundle courses in *Ribes*, *Prunus*, and in other plants, without commenting on their significance.

The fact that each bundle takes an almost direct longitudinal course and the further fact that merging takes place only after the bundle has become much reduced in tangential width would seem to offer at least a partial anatomical explanation for the physiological results obtained by Auchter (1), which led him to conclude that there was normally little or no transverse movement of materials in the apple stem.

After the first differentiation of the leaf rudiment beside the growing point, the bundles of the leaf are laid down as procambial strands. Each procambial strand consists of a group of meristematic cells, each of which divides so that most of the cells are much smaller than those of the undifferentiated part of the growing point. Plate 2, A and B, shows procambial strands formed near the growing point.

By continued division and growth of cells the procambium forms the first water-conducting cells, the protoxylem. These are next to the pith and are closely followed in position and time of development by the metaxylem. Both the protoxylem and the metaxylem persist throughout the life of the plant or until decay sets in at the center of the trunk. These primary xylem elements probably function for many years, although it is only a few weeks before they are in large measure replaced by larger and more efficient tracheids and vessels formed by the cambium. In Plate 2, C, is shown the spiral thickening of the primary xylem with extremely thin walls between the thickened spirals where the thickening bands of some of the elements have been pulled out in sectioning, and resemble very small springs. The larger elements of the metaxylem are pitted and are indistinguishable from secondary tracheids. The apple, unlike most woody dicotyledons, has the primary xylem elements lined up in definite rows, with rows of parenchyma between them. This arrangement makes it difficult, in the stem, to distinguish the metaxylem from the secondary xylem. In the leaf, where no cambium is found, one sees that these same radial rows of metaxylem occur entirely independently of the secondary xylem although they look very much like it.

At about the same time that the protoxylem and metaxylem are being differentiated there arise on the outside of the bundle the prothloem and metaphloem. These differ in appearance from the other cells of the procambium chiefly in being of much smaller diameter. They are living cells, with the function, supposedly, of conducting elaborated food, although this function of the phloem has never been definitely proved, and Dixon (5) and others have raised

serious doubts concerning the conduction of elaborated food by the phloem. The primary phloem cells are soon crushed by the outward growth of secondary phloem, cut off by the cambium which arises between the metaxylem and the metaphloem.

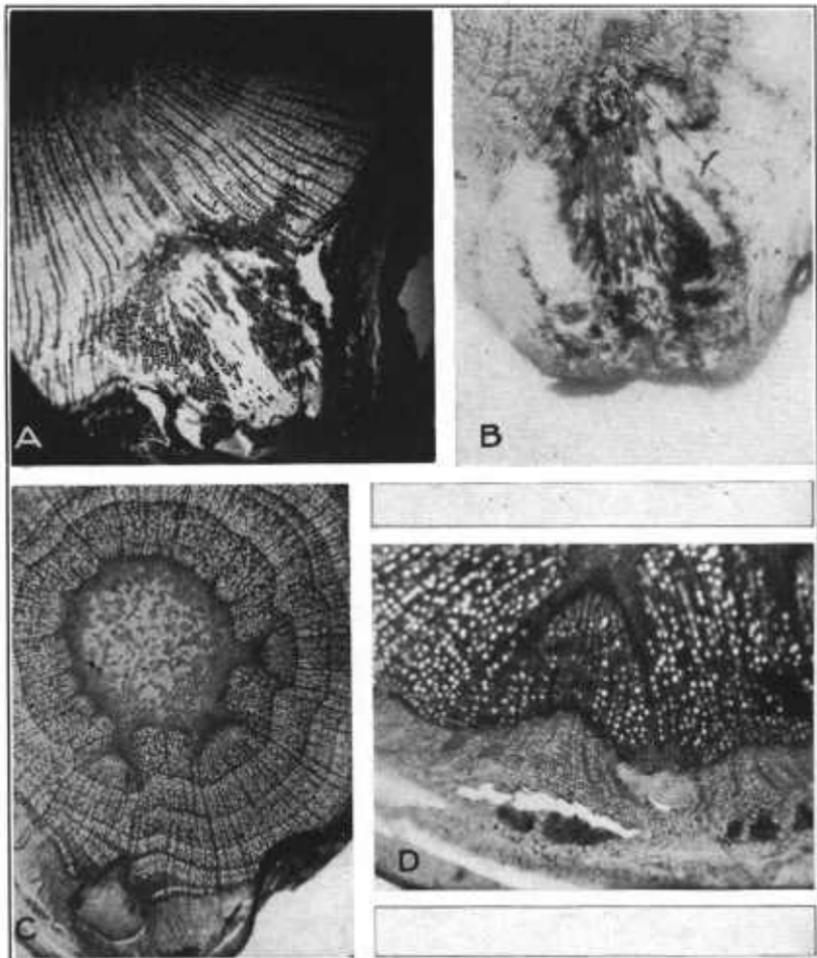
In the axil of each leaf either a fruit bud or a branch bud is formed by the growing point. This bud is connected with the pith by a broad band of parenchymatous cells. In contrast to the leaf gaps, the branch gaps extend downward only a short distance. The lateral bud is in all essential respects a duplicate of the terminal bud, but it may or may not have the same leaf spiral that the terminal bud has. If one examines a branched shoot of the apple he will see that all the buds and leaves formed by any one growing point stand in definite relation to one another. Starting at any given leaf and going up the stem through the leaf bases in the order of their origin, one makes two revolutions around the stem, and passes four leaves, before arriving at the sixth leaf, which is directly over the first leaf. Thus the apple is said to have a  $2/5$  phyllotaxis. It will be noticed, however, that in part of the stems the twist—i. e., the direction of the genetic spiral—is clockwise, while in other stems this spiral joining the leaves in the order of their development runs counterclockwise. It seems improbable that any significant correlation exists between root germ or fruit-bud formation and the direction of the genetic spiral or the twist of the stem. However, it is possible that such a correlation exists, and this point should be investigated.

Between the metaxylem and the metaphloem is a region, at first undifferentiated, but which soon gives rise to the cambium in that portion of the bundle attached to the stele (pl. 2, D). A cambium exists as such for only a very short time, if at all, in that part of the bundle that passes out to the leaf. From the cambium, xylem cells are cut off on the inside and phloem on the outside. Between the vascular bundle strands there is formed the interfascicular cambium, which cuts off parenchymatous medullary ray cells on both sides. Thus, a cross section such as Plate 1, E, shows a complete cambium ring. The cambium layer as a whole forms a hollow, truncate cone, with short breaks at the leaf and branch gaps.

#### BURRKNOT FORMATION

The majority of burrknots swelling on apple twigs are shown by superficial examination to occur in the immediate vicinity of a bud. Probably this fact led Knight (8) to conclude that such burrknots had the power of giving rise to *either* roots or shoots. Since both root and stem growing points are present at the nodes, of course both may arise from almost the same place, although each rudiment has a distinct growing point that probably can develop into only one or the other.

As is shown by Figure 1, C to S, and Figure 2, C to K, the bands (or radial plates) of parenchyma connecting the cortex with the central pith, are, beginning with the broadest: (1) The branch gaps; (2) the leaf-trace gaps; (3) the pair of primary rays, one on each side of each leaf trace after it has entered the stele; (4) the secondary rays within the individual leaf trace bundles. Examination of thousands of sections has led to the conclusion that the order in which they are listed above is also the order of frequency of oc-



A.—Root germ at node. Note the broad band of parenchyma, characteristic of the branch gap, connecting the root germ with the central pith. (X about 25)  
 B.—Root germ, 5 years old, which has arisen on a leaf trace. (See also fig. 3.) (X 25)  
 C.—Photomicrograph of cross section shown in diagram in Figure 4, A. (X 10)  
 D.—Very young root germ on primary ray of stem of Buckskin apple. (X 25)

currence of root primordia on the four types of rays of apple stems. Figure 3 shows diagrammatically the four ways in which root germs may be placed. Not a single case has been observed on the apple in which roots arose from xylem cells or even phloem cells. Thus the root germs are always placed with definite relation to the primary vascular system, except when they occur on secondary rays.

In the initiation of a root germ, one of the cells in the vertical sheet of parenchyma making up the medullary ray, branch gap, or leaf gap increases its meristematic activity and cuts off a great many cells, such increased activity starting at the point in the ray where it crosses the cambium. No physiological explanation of this strict localization of the root rudiment can yet be suggested. The root germ is soon recognizable in sections as a knob of meristematic tissue. By the end of the second or third year these knobs have elongated and are then roots, with root cap, growing point, cambium, and primary xylem all discernible, as was pointed out by Kissa (7). Apparently the branching of the root is very slight until after the third year. Branching may continue indefinitely, so that on old trees most of the surface of large limbs may be covered with these burrknots. The age at which burrknots appear differs in different varieties. The size of individual root germs, the size of patches of burrknots, and the amount of callus around each root germ also differ.

Plate 3, A, shows a root germ which has arisen on the branch trace. Plate 3, B, shows a leaf-trace root germ several years after differentiation. The root germ has appropriated the vascular system of the leaf trace. This is shown in the diagram given in Figure 3. Figure 4 and Plate 4 show various stages in the differentiation of root germs in the medullary rays bounding the leaf traces and in secondary rays.

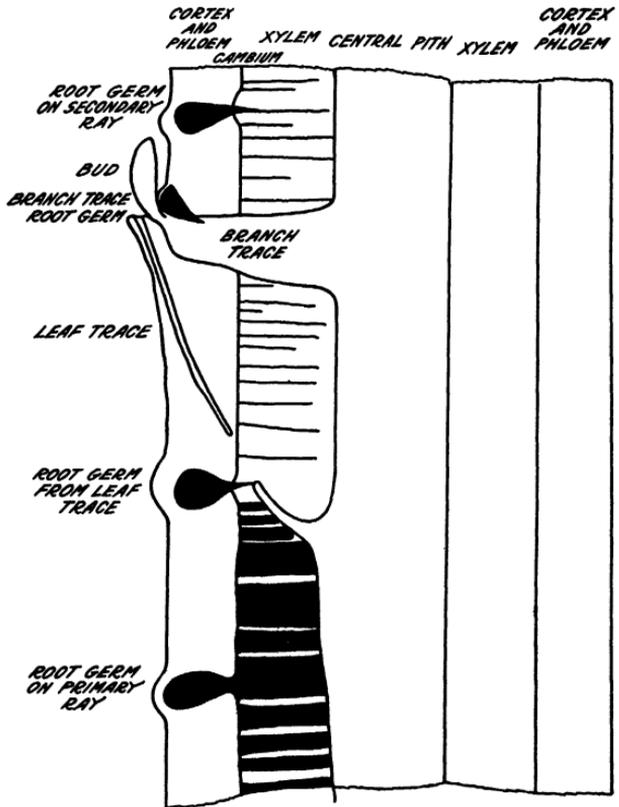


FIG. 3.—Diagrammatic representation of a radial section of apple stem showing the four ways by which root germs may arise

## WOOLLY APHIS GALLS

Brown (3) has called attention to the fact that burrknot swellings might possibly be caused by woolly aphid (*Erisoma lanigera* Hausmann). The writer (11) has already published some evidence against this view. His further anatomical work strengthens these objections. A study was made of sections of many twigs which showed superficially the characteristic woolly aphid swelling—a swell-

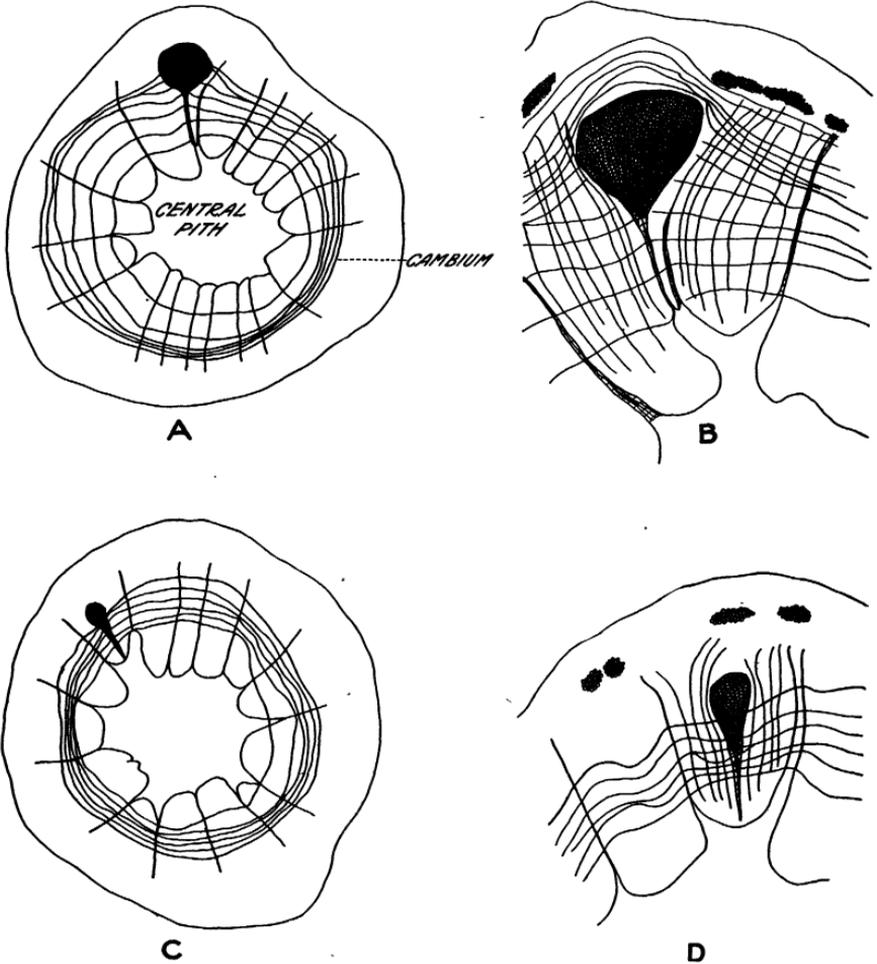
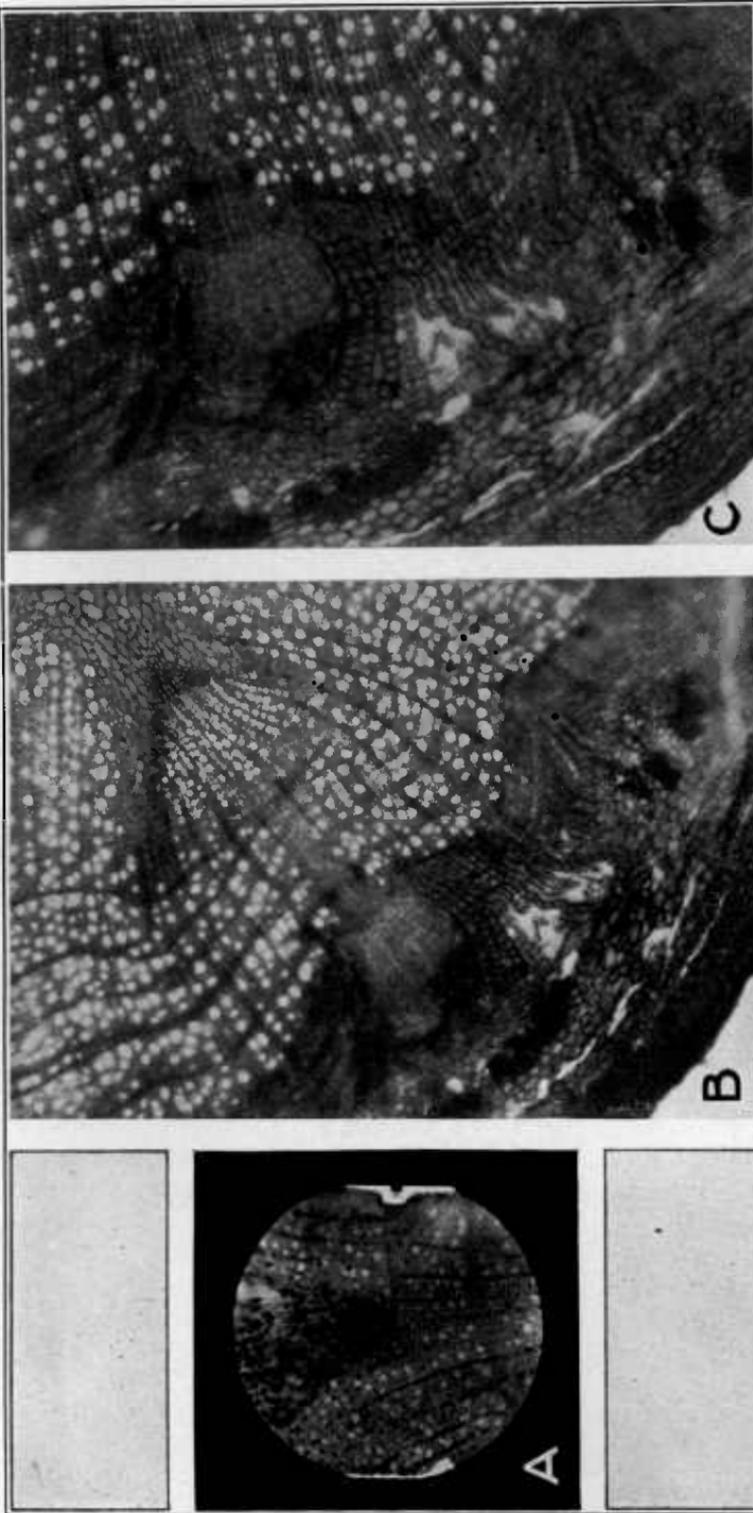
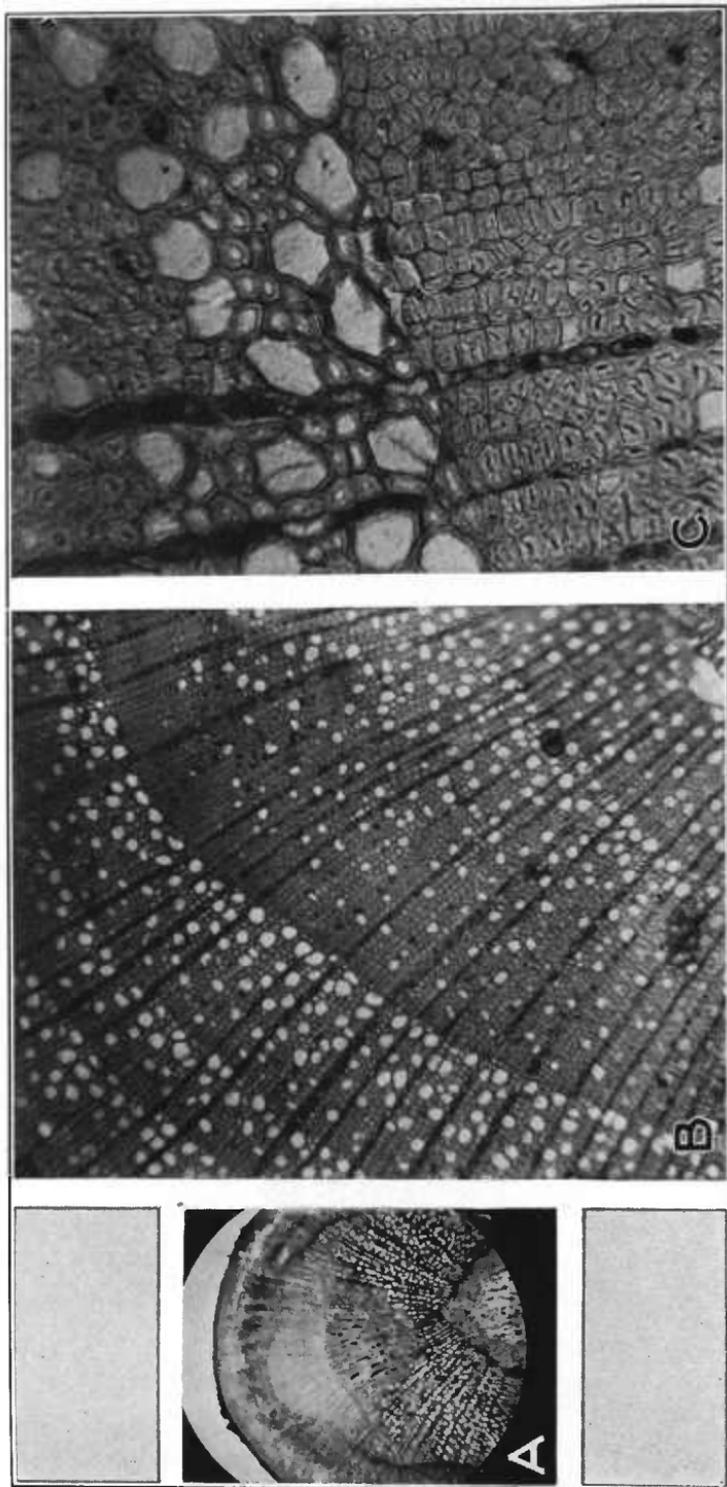


FIG. 4.—A, cross section of 6-year-old Buckskin apple stem, showing root germ which has arisen on a primary medullary ray; B, the same root germ as that shown in A and in Plate 3, C; C, cross section of 6-year-old stem of Buckskin apple, showing root germ which has arisen on a secondary medullary ray; D, the same root germ as that shown in C

ling of a type quite distinct from burrknot swellings. Such (assumed) woolly aphid swellings were taken from the stems of Buckskin, Tolman, and other varieties of apples. Among the varieties at Arlington Farm, the Buckskin showed the most pronounced burrknots, while Tolman has never shown them. The (assumed) woolly aphid galls were about equally numerous on both varieties. As is shown in Plate 5, anatomically the woolly aphid swellings have no points of close resemblance to burrknots. The peculiar anatomical charac-



A.—First cell division at base of old root germ. Note that the root arises from one cell of the right row of the primary medullary ray, the left row of cells being pushed aside by the more rapid growth of the root germ. (X about 50)  
 B.—Root germ arising on a secondary ray. (See fig. 4, C and D.) (X 30)  
 C.—Same cross section as that shown in B and in Figure 4, C and D. (X 50)



A.—Woolly aphid swelling on 1-year-old stem of Tuhman apple. (X about 15)

B.—Woolly aphid swelling on 6-year-old stem of Bucksin apple. Note the very great loosening of the stem caused by the great increase in the number of fiber tracheids at the close of the second year's growth. Note also the medullary rays that apparently were not changed (except in length) by the woolly aphid. (X 50)

C.—A higher magnification of part of B. (X 200)

teristic of the woolly aphid swellings is a great increase in the number of tracheid fibers produced in the region affected. Approximately the same number of vessels is formed as in the normal stem, but the great increase in the number of tracheids makes it appear that fewer vessels are formed. Nothing was seen which indicated that burrknots ever arise from these woolly aphid swellings.

### CONCLUSIONS

From the observations made in the study here reported and those made by other investigators it would seem that the formation of roots on stems has many points of similarity throughout the different plant groups in which it has been studied. Especially in apple and willow the same connection between root germs and the primary vascular system is found. Similar differences exist between different varieties of the same species in regard to the manner and amount of root formation (even apparently its entire absence in some varieties of both apple and willow). The chief differences between willow and apple in regard to the manner and amount of root formation are (1) speaking generally, the root germs on willow arise on younger wood and in greater numbers than those on apple, and (2) the apple root rudiments continue to elongate and to branch more than do those of the willow. With only these minor differences between apple and willow, it seems safe to conclude, in the absence of any contrary proof, either that in both apple and willow the formation of stem-borne roots is due to some pathogenic organism, or that no organism is concerned in either. The writer inclines to the latter view.

### SUMMARY

This paper reports a histological study of burrknots in the apple and of the relation of their rudiments to the primary vascular system.

A celloidin-paraffin method of microtechnic is described whereby it was possible to cut, on the rotary microtome, complete series of 8 to 10 micron sections of 10-year-old apple stems.

A method is described of injecting the vascular bundles with dyes, which makes it possible to study in free-hand sections the course of the vascular strands in young apple stems.

The primary vascular system of the apple consists entirely of common bundles, each bundle connected with, i. e., ending above in, a leaf.

Each of the three bundles from every leaf passes down the stem a greater or less distance, ultimately merging with a bundle from another leaf. Before merging, each leaf trace may or may not divide into two or more parts. In some cases the two parts may run down on either side of a bundle entering from a lower leaf.

The general course of the bundles is straight downward in the stem, with few lateral connections. This fact would tend to explain in part the physiological results obtained by Auchter, who found little or no lateral diffusion of material in the apple stem.

The causes for the different courses taken by bundles of successive nodes in the same branch is unknown.

Root germs in the apple may be initiated at the following points in the cambium ring: (1) At the branch gaps, (2) at the leaf gaps, (3) at the primary medullary rays, and (4) at the secondary medullary rays.

The histological structure of woolly aphis galls on the apple is entirely different from that of burrknots.

The origin and arrangement of the root germs of the apple is very similar to the arrangement of root germs in willow, poplar, and other plants. It is concluded that similar physiological and genetic factors (rather than pathological factors) are involved in the formation of root germs in the apple and in the willow.

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