THE ORIGIN AND DEVELOPMENT OF THE PERIDERM IN SOME WOODY STEMS

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A C K N O W L E D G E M E N T S

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INTRODUCTION

The origin and development of the periderm in woody stems has but infrequently been the subject of investigation. Some of the early workers described minutely the anatomical features of periderm tissue, but did comparatively little work to determine its mode of generation. Even in the few comprehensive works on plant anatomy extant, the authors have simply described the morphological identity of periderm by classifying the tissues of which it is constructed. Most of the early work was done in Europe during the period between 1860 and the beginning of the twentieth century. In fact, these publications remain the criteria on the anatomy of the periderm and constitute practically our entire knowledge of the subject. On the other hand a number of more recent and contemporary authors, both in this country and abroad, have indicated the importance of periderm from the standpoint of its role and function as a protective tissue. Their conclusions are that periderm may act in three different ways, namely, (1) retarding evaporation by suberization of phellem, (2) insulating and minimizing the effects of temperature changes, and (3) acting as a barrier to fungal infection.

In recent years only two investigators have attempted to determine the time-position-environment relationships of periderm formation. Thus the amount of specific information on the subject is quite limited even though it is considered basic to a course in general botany. Since a careful search of the literature on periderm revealed so little, it seemed desirable to extend the previous work done by the author in this field in which he determined, in four woody stems, the point and time of origin of the primary periderm and the cortical region in which inception was first noted. The present investigation

deals with a number of additional woody stems which were available in a sufficient number of stages of growth to determine periderm ontogeny. A list of those studied, named according to Gray's New Manual of Botany, Seventh Edition, follows:

Genus and Species	Common Name	Family	Order
Acer negundo L.	Ash-leaved Maple	Aceraceae	Sapindales
Acer rubrum L.	Red Maple	Aceraceae	Sapindales
Alnus maritima (Marsh.) Muhl.	Sea-side Alder	Betulaceae	Fagales
Diospcros virginiana L.	Common Persimmon	Sapotaceae	Ebenales
Fagus grandifolia Ehrh.	American Beech	Fagaceae	Fagales
Liriodendron tulipifera L.	Tulip Tree	Magnoliaceae	Ranunculales
Platanus occidentalis L.	Sycamore	Platanaceae	Rosales
Prunus virginiana L.	Common Chokecherry	Rosaceae	Rosales
Quercus falcata Michx.	Spanish Oak	Fagaceae	Fagales
Rhus copallina L.	Dwarf Sumac	Anacardiaceae	Sapindales
Sambucus canadensis L.	Common Elder	Valerianaceae	Rubiales
Ulmus americana L.	American Elm	Urticaceae	Urticales

REVIEW OF LITERATURE

Perhaps no review of the literature of periderm formation would be complete without mention of the fact that the cell theory, as propounded by Robert Hooke in 1665 was based on his observation of cells which he observed in thin slices of cork. His was the first recorded description of cork tissue as seen through a microscope.

A long period of time, in fact nearly two hundred years, elapsed before further recorded references were made to cork development. These appeared in European journals. Sanio's work (17) in 1860 is practically the only prime source material available today. His descriptions of cork structure and development were made with particular reference to primary periderm formation.

The next important work was that of Joseph Möller (9), which was partially translated by Kreuger (8). Möller's detailed observations on a great many species of woody stems, in which he attempted to generalize the classification of the cork structure for several whole genera, failed because he found that bark characters were not sufficiently distinct to make a workable key for identification. His work, however, remains as an important general work on cortex anatomy. Further, he was the first to recognize that the formation of scales and plates of bark on the outside of a tree is not governed entirely by a certain stage of development, but rather by outside mechanical and physiological factors.

In 1884, DeBary (2) compiled the then existing information on periderm, into a monumental work in which he made a correlation of the comparative anatomy of vascular plants. This was closely followed in 1889 by Douliot's (4) researches on periderm. Almost twenty-five years elapsed before Mylius (10) in 1913 made a comparative study of various cortex tissues.

During the 1920's, the extensive contributions of Priestly and his coworkers (11-16) brought to light some rather significant data on the physiological aspects of the problem in which they determined some of the causal factors in meristem and cork formation, particularly in wound tissue.

Within the last decade two workers have contributed work of more specific significance. The first was de Zeeuw (3) who was interested in the causal

factors in deep cork formation, particularly as influenced by exposure conditions. The pertinency of this work is relatively important.

The second, Brown (1), in a preliminary study of four species representing the genera, Evonymous, Liquidambar, Tilia and Fraxinus, observed two common types of cork, each of which was generated in a manner unique for the species examined. Wing-type cork was formed in Evonymous and Liquidambar while the annulose-type was formed in Tilia and Fraxinus. In Liquidambar and Tilia, periderm formation was early associated with stomatal and lenticular development which in the former was especially pronounced. Phellogen was localized beneath wing cork and of stomatal origin in Evonymous; it was derived from the epidermis and extended in a ring beneath lenticels, and later extended circumferentially around the stem in Tilia, while it was derived sub-epidermally and formed uniform annulose rings in Fraxinus. Periderm was observed to arise during the first year in all cases except Tilia which developed its first cork during the second year. In every case observed only one layer of phelloderm had been formed. It was characterized as being the inner layer of cells next to the parenchyma of the cortex and distinguished from that tissue by the radial arrangement of its cells.

It is probably true that recent authors have drawn heavily upon the writings of the early workers, particularly those of Sanio, Möller, and DeBary, in compiling their general works on plant anatomy. It is particularly significant, however, that there is a sparcity of fundamental data concerning the development of periderm tissues. For this reason, then, an extension of the work of Brown (1) appeared desirable.

MATERIALS AND METHODS

Field collections began in 1948 and continued through the spring of 1950. Samples were taken monthly which were considered representative of normal growth, that is, selected during different periods of the growing season from twigs which were of average internodal lengths. Occasionally, unusually long or short twigs were taken to determine relative periderm activity. Some species were collected one year, some another, and some for several years in succession. Segments, each one centimeter in length, were cut from successive annual growth increments and numbered consecutively from the apex. Thus, it was possible to indicate with a reasonable degree of accuracy, the approximate location of periderm initiation.

The stem segments were killed and fixed in formalin-aceto-alcohol (FAA) modified as recommended by Johansen (7). Accordingly the proportions used were:

70% ethyl alcohol	90 cc
Glacial acetic acid	4 cc
formalin, U. S. P.	6 cc

The twig and stem specimens were aspirated, allowed to stand at least thirty hours in the FAA and washed for two hours in seventy percent alcohol. It was found that thin microtome sections could be removed from some segments taken directly out of the seventy percent alcohol. The sections were cut serially between eight and thirty microns in thickness. The more limber segments were successfully sectioned by hand while held between slabs of elder pith. These were judged to be comparable in size but varied individually since each hand section was cut on a slant in such a manner as to obtain the thinnest part of the wedge on one of the outside edges. Those samples which

were to be embedded were dehydrated by the standard tertiary butyl alcohol technique and embedded in tissuemat. The older embedded woody stems were allowed to stand in a mixture of hydrofluoric acid, glycerine and alcohol according to a technique perfected by Foster and Gifford (6), to facilitate cutting. All slides were differentially stained with safranin and fast-green. Screening methods and experience simplified the selection of segments in which the periderm origin was shown.

RESULTS

The following descriptions of cork initiation in twelve species were obtained from approximately eighteen hundred transverse sections. In sections prepared from twenty-five additional species insufficient evidence was found concerning periderm origin to warrant inclusion in these data. The twig and bark descriptions were compiled by macroscopic examination of several twigs of each species and of the trees from which they were taken.

ACER NEGUNDO

Twigs. Stout, green to purplish green, smooth, polished or often with a glaucus bloom which readily rubs off. Lenticels conspicuously absent.

Bark. On second year and older stems lenticels somewhat longitudinally elongated, appeared as scattered, raised, buff dots. Stems up to three and four years remained green to purplish green and smooth with occasional thin grayish patches of cork extending from a lenticel until in the older stems it became extensive enough to give a continuous thin, pale gray, or light brown covering. Later, the bark developed a light brown color, broken by narrow rather shallow fissures into narrow, irregular, flat-topped anastomosing ridges

which were further cracked horizontally. On old trees the bark is more deeply furrowed.

Cork initiation. In the early meristematic stem the epidermis is formed of cells somewhat columnar in shape and covered with a thick cuticle (Fig. 1). As the twig elongates and enlarges the epidermal cells appear to elongate laterally while a few layers of hypodermal cells divide radially to increase the circumference of the twig (Fig. 2).

All during the first year the cells adjacent to the epidermis and for several layers beneath, remain larger than those of the inner cortex. These somewhat larger cells assume a granular appearance which seems to be indicative of an incipient cork cambium formation but none forms during the first year. During the second year the cuticle cracks, the hypodermal cells become more granular, and finally divide forming several sectors of phellogen around the stem (Fig. 3). The hypodermis at this time appears to have divided radially and tangentially simultaneously. This is contrary to the conventional manner in which phellogen was observed in other stems, namely, in newly divided cells laid down in radial rows. In A. negundo, further division forms lenticular swellings which at the end of the second year may be found here and there on the surface (Fig. 4). As the lenticels become more numerous, patches of cork may be seen extending from lenticel to lenticel. These patches correspond to those seen upon a superficial examination of the surface of the stem. In some cases the circumference was observed to be free of lenticels with a half dozen layers of annulose cork formed uniformly around the stem. As soon as phellogen has formed, the adjacent epidermal cells become heavily suberized (Fig. 5), while additional layers of phellem are laid down. When as many as a half-dozen layers of cork have formed, the epidermis usually cracks and,

together with the cuticle, sloughs off. Only one layer of phelloderm forms at any time during this period.

The age at which the stem becomes completely ringed with cork varies for different environments. Some specimens were observed which appeared to be completely covered early in the second year while others still showed green patches in four-year-old stems. At no time was more than one layer of phelloderm observed.

ACER RUBRUM

Twigs. Slender, smooth, bright or dark red, lustrous with sparce downy hair in early twigs and covered with numerous conspicuous lenticels.

Bark. Smooth and light gray on young branches, very dark gray on older trunks, roughened into long narrow ridges, occasionally somewhat shaggy and separating in long plates by shallow fissures. In some localities the bark remains smooth until the trunk is a foot or more in diameter.

Cork initiation. In the meristematic stem the epidermis is irregular on the surface (Fig. 6), the cells soon becoming radially elongated and covered with a heavy cuticle (Fig. 7). The subepidermal cells divide radially as the twig expands laterally, while the hypodermis may be seen divided beneath stomata (Fig. 8), in various sections within a short distance of the terminal bud. Toward the latter part of the first year, the divided hypodermis can be seen where scattered stomata have developed into rather large lenticels (Fig. 9). This is repeated under near-by stomata and cork is proliferated rapidly as the lenticel expands. Laterally the cork cambium extends to join that from another lenticel and the surface is gradually dotted with small areas of cork (Fig. 10). Exfoliation of the young bark tissue from the lenticel openings forms irregular

raised places on the surface which gives the twig a speckled appearance. Cork on second year and older stems increases until the third to the sixth year depending upon the environment, when it may be observed extended around the entire perimeter of the stem. Until this phase is reached the twig has a decidedly greenish appearance with ashy gray and brown patches of cork.

ALNUS MARITIMA

Twigs. Rather slender, more or less zigzag, finely downy, light green at first, very lustrous, marked with occasional small orange-colored lenticels and minute glandular dots during the first summer, becoming dull light orange or reddish brown in the winter and turning ashy gray, often slightly tinged with red, the following season.

Bark. Thin, smooth, light brown or brown tinged with gray.

Cork initiation. Soon after the growing season begins, numerous stomata can be observed close to the terminal bud. Within a short distance of many stomata, about five or six centimeters behind the apex, hypodermal cells can be found divided forming phellogen (Fig. 11). This stage is quickly followed by more extensive division of the phellogen to form long layers of cork which join each other around the stem (Fig. 12). As many as ten or twelve layers of cork were observed in first year twigs. Further proliferation is indicated by jagged openings in the lenticel areas which occur early in the first year, approximately eleven centimeters in back of the twig apex. During the second year, lenticular development is marked by numerous layers of phellem which become heavily suberized and bulge outward at the center (Fig. 13). As more and more phellem is laid down the lenticel bursts open giving the typical flare at its sides (Fig. 14). The first year cork was observed to remain intact in

some sections of the circumference while in others it became separated. Only one layer of phelloderm was observed at any time.

DIOSPOROS VIRGINIANA

Twigs. Slightly zigzag, hairy, greenish, becoming ashy gray or brown, marked with occasional orange-colored lenticels at the end of the first year.

Bark. Smooth at first, dark reddish brown, cracking into thick, squarish blocks.

Cork initiation. Before the growing stem tip shows complete organization of the various cortical tissues, the epidermis is covered with a heavy cuticle. While the cells are still irregularly shaped the hypodermis divides to cut off phellem (Fig. 15), which builds up to several layers (Fig. 16). Contrary to the manner of development of most stems, the phellem does not become heavily suberized or form regularly shaped cells. Considerable distortion results from compression of the multiple layers of phellem. After staining, the phellogen with two or three adjacent layers is sharply delineated and appears to form a closed ring around the stem cutting deeply under lenticels (Figs. 16 and 17). Only one layer of phelloderm was observed.

FAGUS GRANDIFOLIA

Twigs. Slender, somewhat zigzag, light green, hairy, becoming smooth, yellow, and finally changing to reddish brown and gray during the first summer. During the second year conspicuously marked with bright orange lenticels which turn, through reddish brown, dark brown and finally ashy gray.

Bark. Close, smooth, steel-gray with more or less dark mottled surface.

Cork initiation. Meristematic stems are characterized by an orderly arrangement of the outer cortical cells. The epidermis is composed of more or

less irregularly shaped cells without a thick cuticle which shows signs of shriveling by the end of the first year. The hypodermis soon divides forming the phellogen and lays down phellem which becomes partly suberized (Fig. 18). Usually but one layer of phellem and one of phelloderm is formed beneath the epidermis during the first year. A few lenticels, however, can be observed here and there. Second year stems at the same stage of growth have formed five or six layers of phellem while the epidermis has shriveled completely. The outer circumference is now conspicuous with lenticels, many of which show flaring (Fig. 19).

LIRIODENDRON TULIPIFERA

Twigs. Slender to somewhat stout, light yellow-green with more or less glaucous bloom during the first summer, becoming reddish brown, lustrous and finally gray, marked with conspicuous gray lenticels during the first winter.

Bark. Dark green and smooth when young with white spots becoming dark and cracked into a regular network of shallow, firm ridges which on old trunks becomes deeply furrowed, brown and rough.

Cork initiation. The epidermis of early growth twigs is covered with a thick cuticle. The cells are thicker radially than they are long and are quite irregular in size. The cortex is composed of several layers of small cells on the outside giving way to larger cells toward the center. Interspersed are many circular intercellular openings which resemble oil glands. As the growing season progresses, the epidermal cells become elongated and divide anticlinally to increase the circumference. Toward the end of the first growing season the hypodermis shows divided cells at intervals around the stem (Fig. 20). Partial areas of the circumference expand as the phellem forms lenticulate areas some

of which develop into large lenticels, while others form cork two or three layers thick (Fig. 21), not uniformly distributed around the stem. The phelloderm is not sharply defined and can be found only here and there around the stem.

PLATANUS OCCIDENTALIS

Twigs. Conspicuously zigzag, slender, dark green at first, becoming orange-brown, smooth and finally gray. Lenticels pale, minute.

Bark. Creamy white on young branches soon turning reddish brown or gray and forming characteristically mottled patches on the upper trunk by the exfoliation of the outer bark exposing pale yellow layers beneath. At the base of older trunks the bark becomes dark brown with shallow furrows and broad ridges which are broken into oblong thick plate-like scales.

Cork initiation. In early spring growth the epidermal cells have little cuticle. The hypodermal layer appears more regular than the epidermal cells and slightly larger (Fig. 22). Within four or five centimeters of the terminal bud, incipient lenticels can be found forming beneath stomata in the hypodermis (Fig. 23). The mature lenticels of early summer differ from those of late summer by the formation of large vacuolated cells at the edges of the lenticels (Fig. 24). Those formed in late summer not only lack these large cells at the side but also form in the conventional, elongate, lens-like shape (Fig. 25). Frequently these develop further into rounded openings with a well-defined phellogen layer marking the inner margin (Fig. 26). The cork formed the first year is confined to lenticular areas during early growth but spreads laterally to encompass the entire stem by late fall. Generally the first year stem generates three or four phellem layers and only one layer of phelloderm.

PRUNUS VIRGINIANA

Twigs. Smooth, slender reddish to grayish brown with numerous, rather conspicuous but pale lenticels, slightly elongated longitudinally the first year and becoming dark red-brown in their second year.

Bark. Smooth but slightly roughened with red-brown dots formed by enlarged lenticels, becoming rough with persistent dark reddish brown scales which can be peeled in thin papery layers exposing green bark below.

Cork initiation. Very young stems show epidermal cells which tend to be square with a thin cuticle. The adjacent cortical cells were observed to be two or three times the size of other cells in the cortex and were without regular arrangement. Only three or four centimeters behind the terminal bud the cuticle increased in thickness and the hypodermal cells were found in more orderly alignment beneath the epidermis. The hypodermis was frequently found divided to form long sectors of phellogen (Fig. 27), commencing ten to fifteen centimeters behind the apex and in subsequent first year growth. These sectors often joined to form longer and more continuous layers of phellem, some of which developed into lenticels and formed scurfy sections of the twig. Not more than two layers of phellem and one layer of phelloderm were observed during the first year of growth. At the same time on second year stems, as many as eight or ten cell layers of phellem were observed with still only one cell layer of phelloderm (Fig. 28).

QUERCUS FALCATA

Twigs. Rusty or orange-colored, pubescent or nearly glabrous, somewhat irregularly round during the first year.

Bark. Pale or dark brown to nearly black, cracking on old trunks into shallow, broad, scaly ridges separated by narrow fissures.

Cork initiation. The epidermal and hypodermal cells of the apical meristem soon form into regular layers around the stem near the terminal bud (Fig. 29). About ten centimeters back on the twig a well-defined hypodermis was found showing divided cells (Fig. 30). This primary phellogen proliferates several cell layers of phellem, usually eight to ten in subsequent first year growth. The outer layers become heavily suberized while the layers next to the phellogen appear empty (Fig. 31).

In second year stems the phellogen lays down eight or ten cell layers under the first year cork. The latter exfoliates, for the most part, leaving remnants here and there around the stem.

RHUS COPALLINA

Twigs. Stout, velvety, greenish red, slightly zigzag in early growth, becoming pale reddish brown and marked by conspicuous dark-colored lenticels.

Bark. Smooth, light brown tinged with red, becoming roughened in horizontal lines and sometimes cracking into papery scales.

Cork Initiation. Meristematic twigs show well-defined epidermis and two or three adjacent cell layers in uniformly parallel arrangement.

On each micro-section (20 to 30 micra thick) cut from this region, as many as five to ten raised stomata were observed (Fig. 32). Eight to ten centimeters behind the apical meristem was found the first cork cambium three or four cell layers beneath the epidermis (Fig. 33). This phellogen was initiated at several points involving a single cell or in sectors involving several cells around the stem during the first two weeks of growth (Fig. 34). This seems to be the only division taking place in the first year of growth. The cells which are cut off to the outside become suberized by the end of the first two weeks and remain in this condition until the growing season begins the following year.

When growth begins the second year, the phellogen forms three or four layers of cork (Fig. 35). This internal expansion causes a partial exfoliation of the outer bark into papery scales. In each succeeding year of stem growth similar layers of cork are added inside that formed previously. Only one layer of phelloderm was observed in two year old stems.

SAMBUCUS CANADENSIS

Twigs. Thick but soft, greenish, becoming light brown with a purplish tinge.

Bark. Smooth, dark brown with small warts, becoming scaly on old stems.

Cork initiation. In twig meristems the well-defined epidermal cells are covered with a thin cuticle. The outer two cell layers of the cortex were in regular rows while the remainder consisted of loosely-packed cells

showing frequent intercellular spaces. Immediately behind the terminal bud the hypodermis divides to form phellogen (Fig. 36). Division continues until at a distance of eight or ten centimeters in back of the terminal bud, ten or more cell layers of phellem form. In this region the epidermis completely disappears. Occasional flared lenticels were seen in the developing cork, sharply cut into the cortex (Fig. 37). Only one layer of phellodern was observed.

ULMUS AMERICANA

Twigs. Slender, green, smooth or sometimes downy, soon becoming light red-brown, often tinged with yellow and marked by scattered inconspicuous lenticels.

Bark. Dark gray, divided by irregular longitudinal fissures into broad flat-topped ridges, rather firm though sometimes in very old trees coming off in flakes. Bark internally stratified by thick conspicuously whitish layers alternating with layers of a dark brown.

Cork initiation. Meristematic twigs show about three layers of uniformly shaped cells around the outside. The epidermis forms but little cuticle up until the time phellogen is first differentiated five or six centimeters behind the terminal bud (Fig. 38). Phellogen increases within ten centimeters of the apical meristem during the first two weeks of growth (Fig. 39). At the base of the twig the phellogen cuts off about a half-dozen layers of cork during the remainder of the growing season, the two outermost of which become heavily suberized and cut off the epidermis completely (Fig. 40). When the spring growth begins the second year, the old phellogen again becomes active and lays down another half-dozen layers of phellem, pushing

the first year cork away. As the resulting pressure increases almost all of the first year cork disappears leaving only remnants here and there around the stem.

DISCUSSION

DEFINITION OF TERMS

Bark. The word "bark" is popularly used to designate all tissues outside the vascular cambium; the word, when used in this study, applies only to the phellogen and the tissues differentiated by it.

Cork. The word "cork" refers specifically to phellem. Mature cork is considered to be several layers of heavily suberized cork which is compressed enough to cause splitting and exfoliation of the epidermis. According to Eames and MacDaniels (5) and confirmed by Brown (1), primary periderm produces cork of two types:

Annulose cork. That cork which is composed of thick-walled, filiform cells, radially flattened is called annulose. The lumen of the cells is usually impregnated with a dark-staining material. Compression causes the flattening of the cells. The majority of woody stems produce this type of cork.

Wing cork. Cork which forms ridges external to the epidermis is called wing cork. The cells are thin-walled, empty, filiform, and elongated radially. This type of cork apparently occurs infrequently, having been found in only two out of sixteen species investigated, namely, *Evonymous alata* and *Liquidambar styraciflua*. Eames and MacDaniels (5) also report *Quercus suber* as being of this type.

Periderm. The periderm is that tissue originating in the cortex of a stem and composed of phellogen, phellem, and phelloderm. During cork formation, the phellogen proliferates phellem or cork centrifugally and phelloderm centripetally. This activity is unilateral rather than of a reciprocal nature, in which phellem is generated to a much greater extent than phelloderm. In this investigation only one layer of phelloderm was observed. Anatomically there is little difference between phelloderm and cortical parenchyma except that the former exhibits radial arrangement corresponding to the phellogen cells.

While phellogen or cork cambium is a secondary lateral meristem, all of the tissue produced by it, which is secondary tissue, may be called primary periderm, to distinguish it from an inner or secondary periderm which may be differentiated later. A cork cambium is similar in most respects to a vascular cambium, except that generally the tissues differentiated from it are less extensive.

ANALYSIS OF DATA

The phellogen or cork cambium and its derivative tissues, phellem or cork and phelloderm, comprise the protective structure of the stem. It appears to arise in consequence of tangential expansion of the stem. The phellogen may be derived from any one of three tissues, namely, the epidermis, the hypodermis or the cortical parenchyma. It originates most commonly in the hypodermis, frequently appearing first beneath the stomata. This may result in the formation of lenticels, from which it spreads laterally to form a cylinder of cork cambium. Repeated tangential

division of the phellogen produces an allignment of cells in radial rows. Those differentiated to the outside and in greater numbers usually lose their protoplasts, become heavily suberized, and mature as cork. In some instances layers of phellem cells remain fully expanded between the phellogen and the outer phellem layers, which have become thinly compressed and suberized. In Rhus copallina, phellogen was formed without apparent formation of phellem. The action of the phellogen in this case seems to be simply that of shutting-off the layers to the outside.

The phelloderm was always observed to be a single layer, and characteristically parenchyma-like, arranged radially, continuous with the phellogen.

The phellogen apparently functions for a short part of the growing season only, generally in the early spring, for the majority of stems examined.

In the initiation of lenticels, phellogen was first found beneath stomata in several instances. In these examples the lenticel developed, instead of typical cork, loosely packed unsuberized cells known as complementary tissue. Interleaving this tissue lateral rows of more compact cells known as closing layers were formed. Continuing pressure developed from the proliferation of additional complementary tissue and closing layers which caused the epidermis to bulge outward forming the characteristic lens shape of immature lenticels. In later stages the epidermis broke and curled back while the complementary tissue and closing cells flared outward.

In Acer negundo, instead of periderm, the only protective tissue which appears to exist over the first winter is the epidermis with its heavy cuticle. Parts of the circumference were observed thus protected even in four year stems.

The results of this investigation indicate that periderm apparently varies in its mode of formation with each species. Thus, no particular uniformity appears to exist among the specimens observed which can be associated phylogenetically. This is in complete accord with the findings of Möller (9). The stems studied differentiate cork in varying amounts during the first year as follows: none in Rhus copallina; one or two layers in Fagus grandifolia, Prunus virginiana and Quercus falcata; two to four layers in Liriodendron tulipifera and Platanus occidentalis; about six layers in Ulmus americana; eight or more layers in Alnus meritima, Diospores virginiana and Sambucus canadensis; and in lenticular areas in Acer negundo and Acer rubrum (Tables I and II). From this it can be seen that no uniformity exists as to the extent of cork formation. The complete investigation brings out additional significant points concerning periderm formation as follows: First, the period of the primary phellogen activity is strikingly brief, probably lasting for no more than three weeks in most cases. Secondly, phelloderm was never observed to be more than one cell-layer thick. Third, the phellogen was formed in the hypodermis in the majority of cases and infrequently in the cortical parenchyma and epidermis.

SUMMARY

The origin of the periderm in the twigs examined in this investigation was, with one exception, always in the hypodermis. In the exception, Rhus copallina, the origin was three layers beneath the epidermis. (The preliminary investigation disclosed one species, Liquidambar styraciflua, showing epidermal origin of the periderm). The mode of formation varied with the species examined and no phylogenetic relationships could be determined. In those stems which formed a complete ring of cork initially, it appeared as though lenticular development was delayed until after the ring cork was laid down. Representatives of this type include Alnus maritima, Fagus grandifolia, Quercus falcata, Rhus copallina, Sambucus canadensis, and Ulmus americana.

Several species developed annulose cork from lenticular cork. Among those in this category were, Acer negundo, Acer rubrum, Diosporos virginiana and Platanus occidentalis. In only two of these, Acer rubrum and Platanus occidentalis, was the origin observed first beneath stomata further developing into lenticels, and eventually spreading to form annulose or ring cork.

With few exceptions, cork formation seems to be an early spring phenomenon of the twig. If cork formation is delayed the first year then it forms in early spring of the second year (e.g., Acer negundo).

Liriodendron tulipifera was the only species observed which formed cork toward the end of the growing season.

The time of mature cork formation varies from early the first year to the sixth year in the stems investigated.

Phelloderm was never found to be more than one layer thick in the stems observed, while phellem was generated in patches or continuous layers varying from one to a dozen or more layers in thickness.

TABLE I

NAME	ORIGIN OF PHELLOGEN	EXTENT OF PHELLEM	EXTENT OF PHELLODERM	TIME OF ORIGIN & TYPE OF CORK	TIME OF MATURE CORK FORMATION
Acer negundo	Hypodermis	In patches - not uniform	One layer	Early 2nd year - lenticular	3 to 6 years
Acer rubrum	Hypodermis - beneath stoma; develops into lenticel	In patches - not uniform	One layer	Early 1st year - lenticular	Irregularly from 2 to 6 years
Alnus maritima	Hypodermis	10 to 12 layers	One layer	Early 1st year - annulose	Early first year
Diospyros virginiana	Hypodermis	8 to 10 layers	One layer	Early 1st year - lenticular	Early first year
Fagus grandifolia	Hypodermis	1 layer around circumference or lenticular	One layer	Early 1st year - annulose	Early second year
Liriodendron tulipifera	Hypodermis	Not uniform - 2 or 3 layers except under lenticels	Not continuous - one layer when observed	Late 1st year - lenticular	End of first and second years

TABLE I (CONTINUED)

NAME	ORIGIN OF PHELLOGEN	EXTENT OF PHELLEM	EXTENT OF PHELLODERM	TIME OF ORIGIN & TYPE OF CORK	TIME OF MATURE CORK FORMATION
Platanus occidentalis	Hypodermis - beneath stoma - develops into lenticel	3 or 4 layers - lenticular	One layer	Early 1st year - lenticulate	Late first and early second year
Prunus virginiana	Hypodermis	1 or 2 layers	One layer	Early 1st year - lenticulate, then annulose	Early second year - annulose
Quercus falcata	Hypodermis	1 or 2 layers	One layer	Early 1st year - annulose	Late first and early second year
Rhus copallina	Cortex, 3 cell layers inside epidermis	None 1st year. Layers outside of phellogen become suberized.	One layer	Very early 1st year - annulose	Very early second year
Sambucus canadensis	Hypodermis	10 or more layers	One layer	Early 1st year - annulose	Early first year
Ulmus americana	Hypodermis	About 6 layers	One layer	Early 1st year - annulose	Early second year

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APPENDIX

PLATE I ACER NEGUNDO

Figure 1. Meristematic stem with columnar cells and thick cuticle. x 430.

Figure 2. Epidermal cells elongated laterally. Subepidermal cells dividing radially at a point 15 centimeters back of apex. x 430.

Figure 3. Phellogen of hypodermal origin in a second year stem. Note breaks in cuticle. x 430.

Figure 4. Lenticel formed in two year old stem. x 430.

Figure 5. Suberized epidermal cells after phellogen has generated a few layers of phellem. x 210.

PLATE I

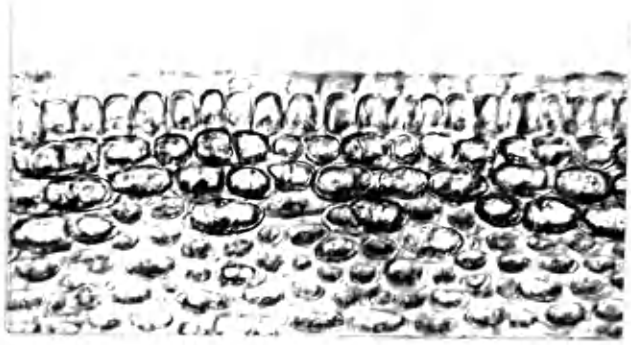


Fig. 1

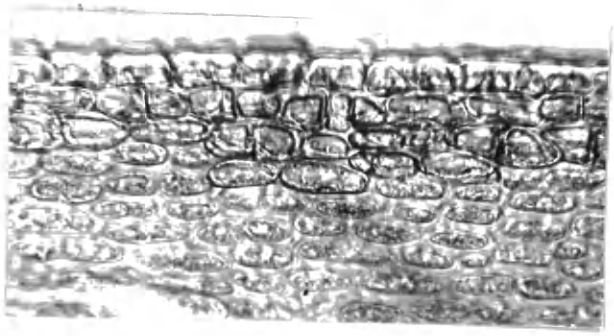
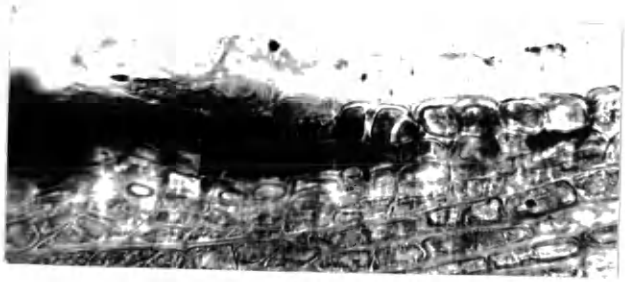


Fig. 2

Fig. 3



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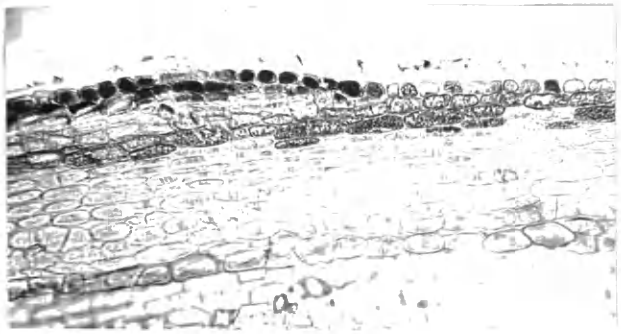


Fig. 5

PLATE II ACER RUBRUM

Figure 6. Meristematic stem. Epidermal surface irregular. Cuticle undeveloped. x 430.

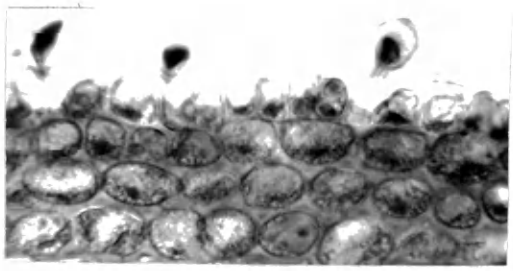
Figure 7. Meristematic stem. Later stage of growth showing epidermal cells radially elongated and with heavy cuticle. x 430.

Figure 8. Divided hypodermis beneath stoma near the apex. x 430.

Figure 9. Large lenticel developed from divided hypodermis beneath stoma. x 430.

Figure 10. Lenticels "dotting" the surface of first year stem. x 210.

PLATE II



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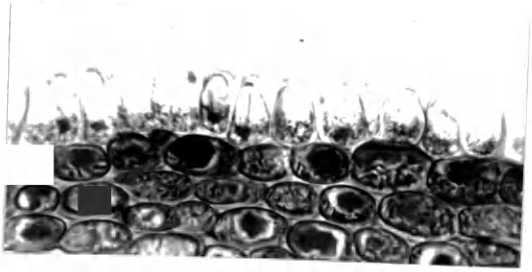

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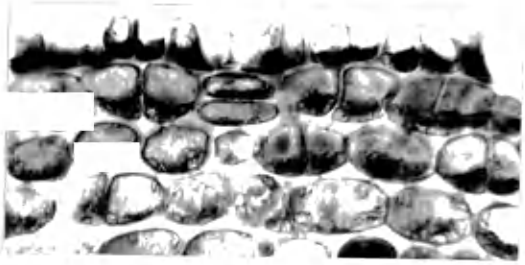


Fig. 8

Fig. 9

Fig. 10

PLATE III ALNUS MARITIMA

Figure 11. Hypodermal cells divided near a stoma in meristematic stem, six centimeters from the apex. x 430.

Figure 12. Phellogen and cork in long layers in first year stem. x 430.

Figure 13. Developing lenticel with numerous layers of phellem heavily suberized. x 430.

Figure 14. Mature lenticel burst from pressure of phellem beneath showing typical flare. x 430.

PLATE III

Fig. 11

Fig. 12

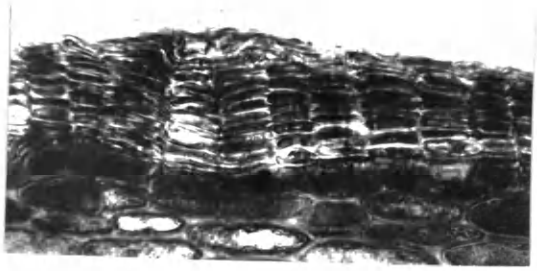


Fig. 13

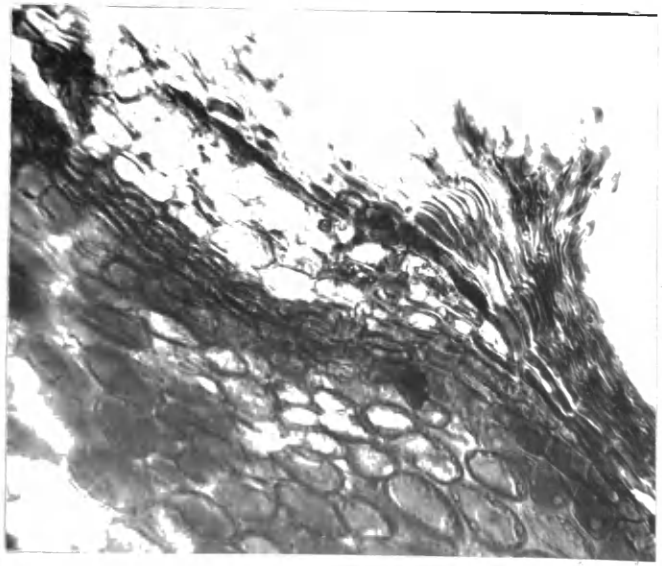


Fig. 14

PLATE IV DIOSPOROS VIRGINIANA

Figure 15. Hypodermis dividing in stem tip which appears incompletely differentiated. x 430.

Figure 16. Several layers of phellem composed of irregularly shaped cells. x 100.

Figure 17. Phellogen sharply delineated forming a closed ring around the stem. x 430.

PLATE IV

Fig. 15

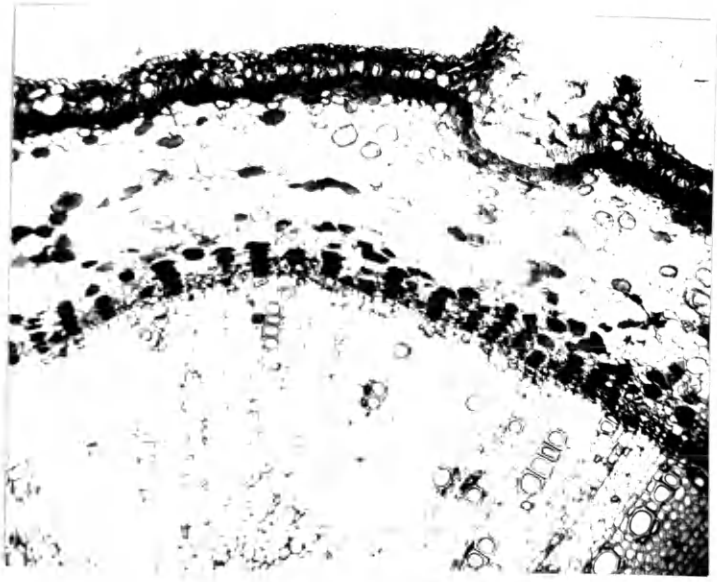


Fig. 16

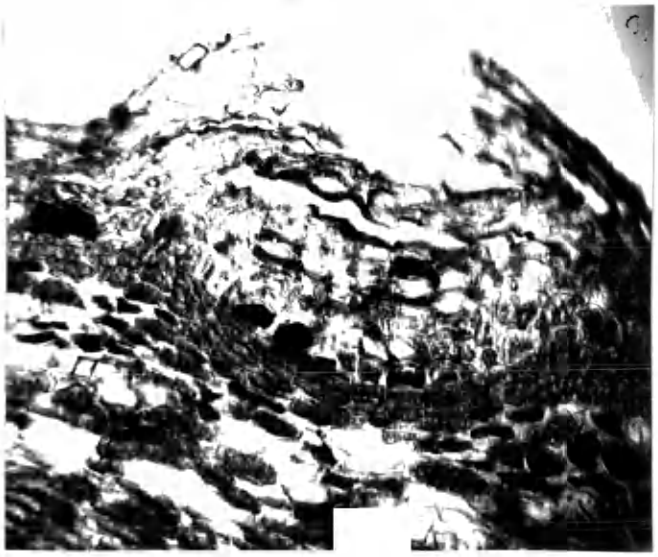


Fig. 17

PLATE V

FAGUS GRANDIFOLIA

Figure 18. Meristematic stem with irregular epidermis. Hypodermis divided to form phellogen. x 430.

Figure 19. Lenticel on second year stem showing several layers of phellem. Epidermis shriveled. x 430.

LIRIODENDRON TULIPIFERA

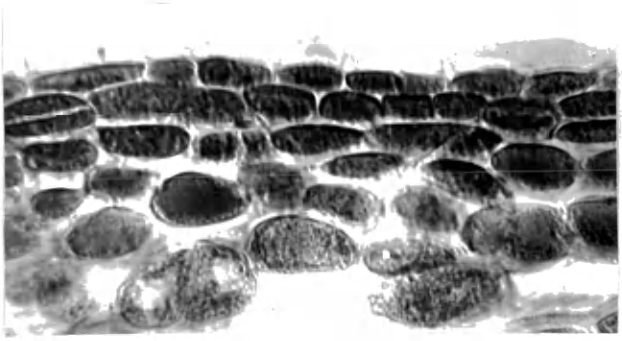
Figure 20. Epidermal cells laterally elongated with heavy cuticle. Hypodermis with divided cells. x 430.

Figure 21. Lenticulate cork formation with adjacent phellogen. x 430.

PLATE V

Fig. 18

Fig. 19



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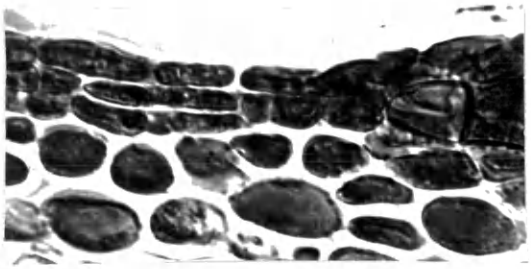


Fig. 21

PLATE VI PLATANUS OCCIDENTALIS

Figure 22. Meristematic stem showing epidermis with thin cuticle. Hypodermis with larger cells and more regular than the epidermal cells. x 430.

Figure 23. Incipient lenticel formed beneath a stoma and within five centimeters of the apex. x 430.

Figure 24. Lenticel formed early showing large vacuolated cells at edges. x 430.

Figure 25. Typical lenticel formed late in summer - without large cells at edges. x 430.

Figure 26. Lenticel formed by phellogen deeply turned into the cortex. x 430.

PLATE VI

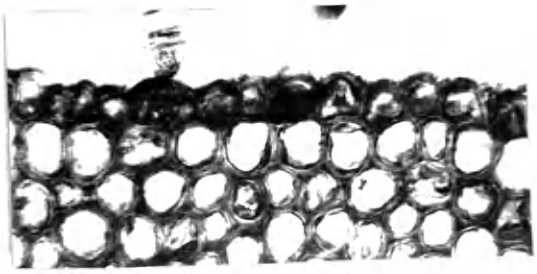
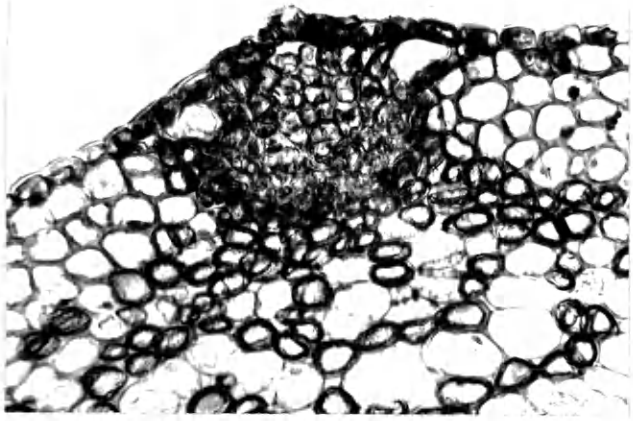


Fig. 22

Fig. 23



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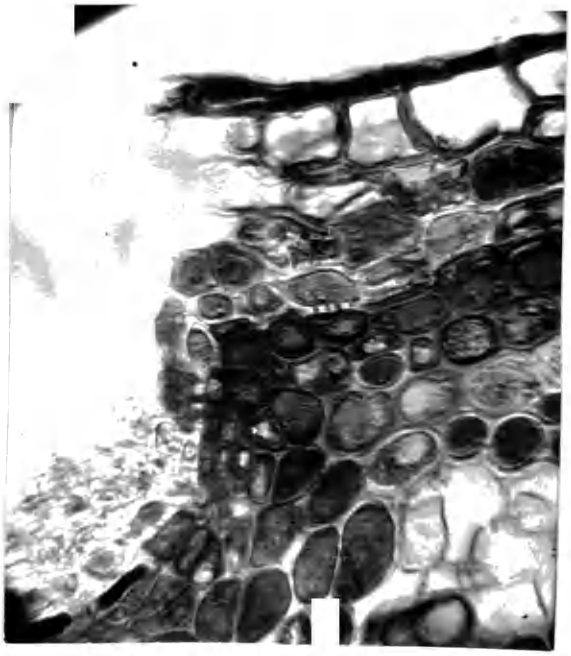

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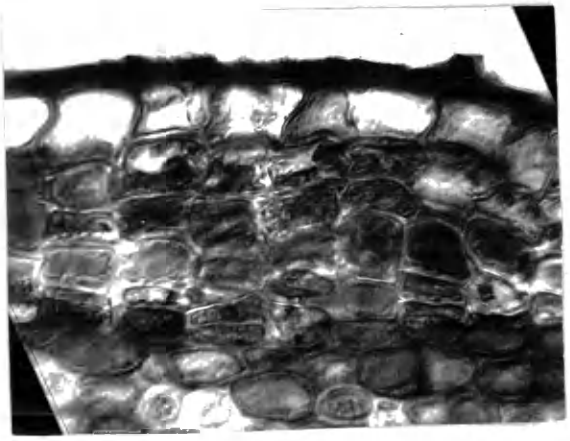

Fig. 25

PLATE VII

PRUNUS VIRGINIANA

Figure 27. Hypodermis divided to form a long sector of phellogen at about ten centimeters behind apex. x 430.

Figure 28. Phellem formed on second year stem at same time phellogen is generated in the twig. x 430.

QUERCUS FALCATA

Figure 29. Meristematic stem showing early differentiated hypodermis. x 430.

Figure 30. Well-defined phellogen ten centimeters in back of apex. x 430.

Figure 31. Several layers of phellem in late first year growth. Note empty cells next to phellogen. x 430.

PLATE VII

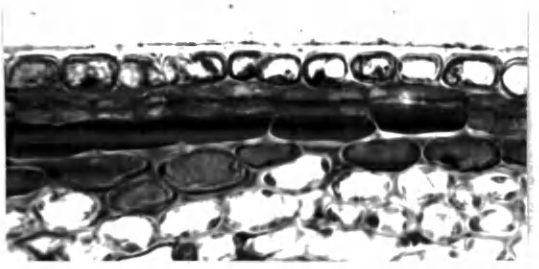

Fig. 27

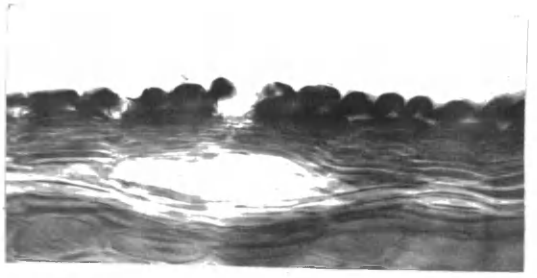

Fig. 28

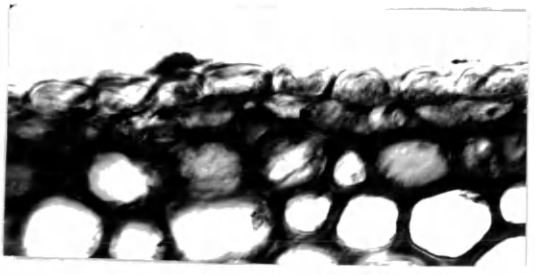

Fig. 29

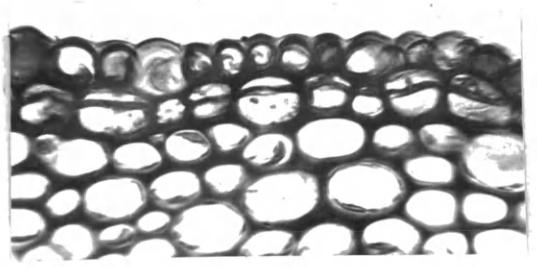

Fig. 30

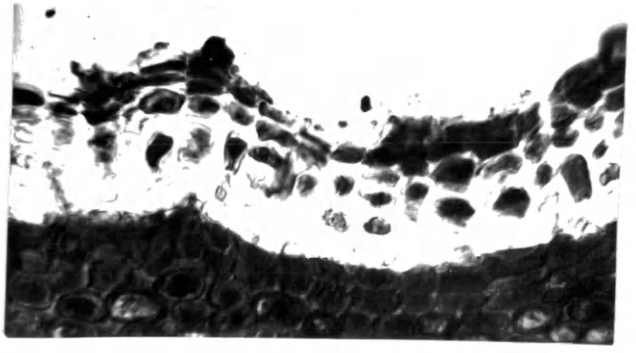

Fig. 31

PLATE VIII RHUS COPALLINA

Figure 32. Raised stoma commonly observed on meristematic twigs. x 430.

Figure 33. Phellogen generated three cell layers beneath the epidermis. x 430.

Figure 34. Continuous sector of phellogen formed in the cortical parenchyma. x 430.

Figure 35. Cork formed during second year showing heavily suberized cells from first year cortex. x 430.

PLATE VIII

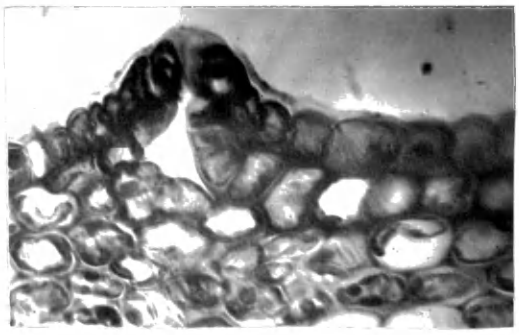

Fig. 32

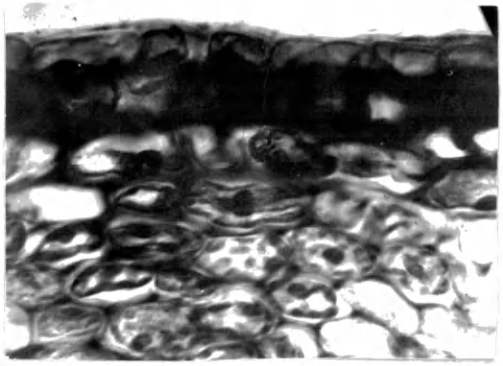

Fig. 33

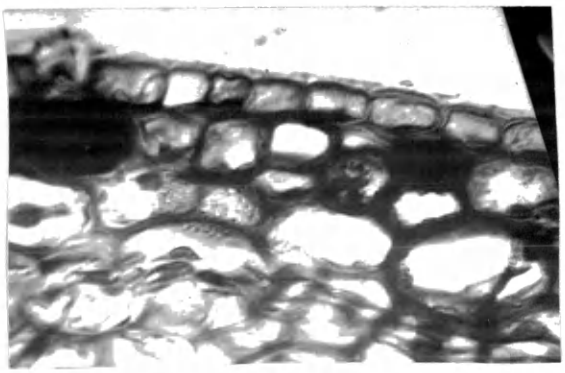

Fig. 34

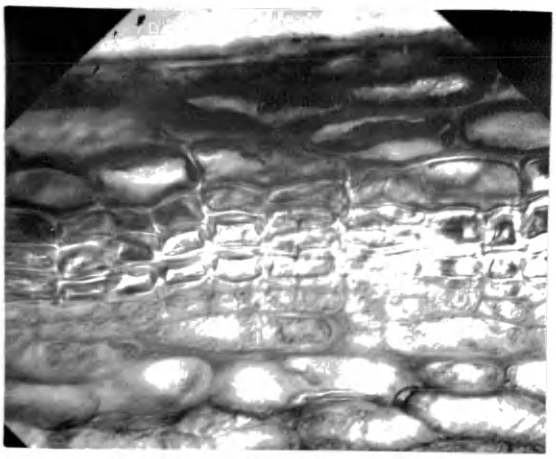

Fig. 35

PLATE IX

SAMBUCUS CANADENSIS

Figure 36. Phellogen from hypodermis in region of the apex. x 430.

Figure 37. Flared lenticel with phellogen deeply cut into the cortex. x 430.

ULMUS AMERICANA

Figure 38. Hypodermis divided. Epidermal cells showing thin cuticle in meristematic twigs about five centimeters behind the apex. x 430.

Figure 39. Phellogen formed in wide sector just behind the point of initiation. x 430.

Figure 40. Cork formed at the base of twig. Two outer layers heavily suberized cutting off the epidermis. x 430.

PLATE IX

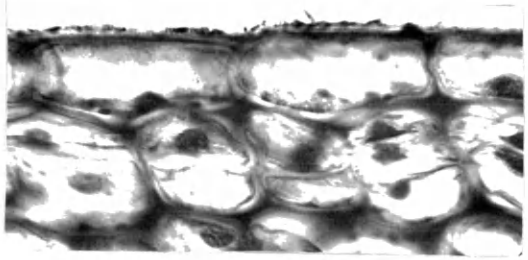

Fig. 36

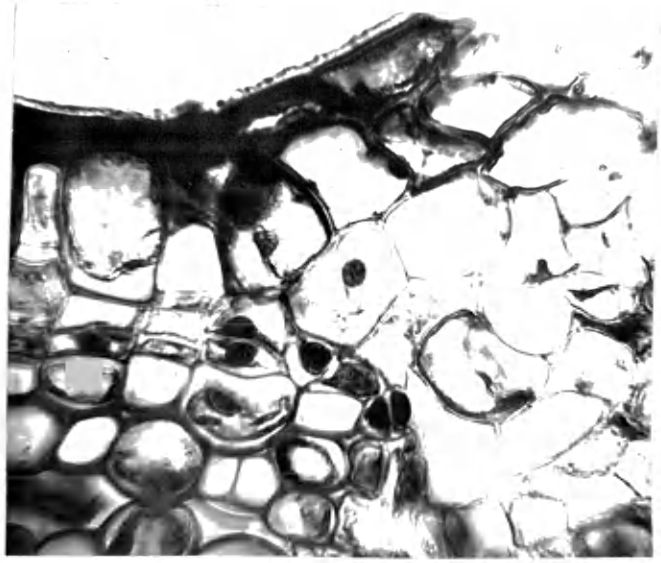

Fig. 37

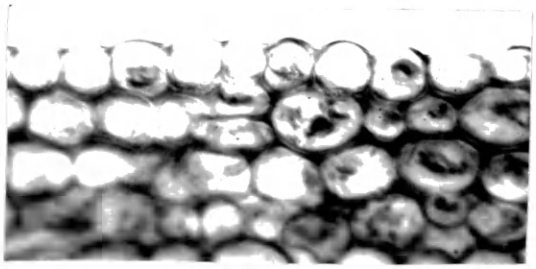

Fig. 38

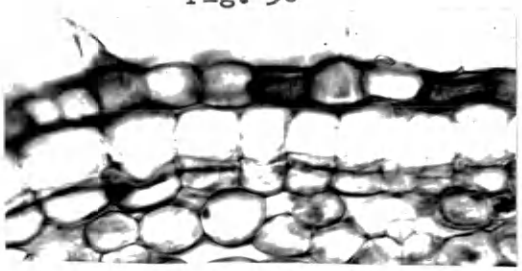

Fig. 39

Fig. 40

VITA

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	1946 (summer)	none	
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	1948-1950	none	

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