

COMPARATIVE ANATOMY OF CERTAIN HYBRID SHRUBS
AND THEIR PARENTS

by Paul V. Beck.

B. S. 1916, Opla. A. P. M.

Submitted to the Department of Botany and the
Graduate School of the University of Kansas in
partial fulfillment of the requirements for the
Degree of Master of Science.

Approved:

W. C. Stevens

Head of the Dep't of Botany.

June 3, 1924.

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INTRODUCTION

The study of transmitted characters in hybrid offspring has become the chief method of determining the laws of heredity. Usually, since the rediscovery of Mendel's law, this study has been one of quantitative plant or animal-breeding when clearly recognizable characters were observed for several generations. Many cytological studies have also been made of hybrids, especially during recent years. The anatomical studies of plant hybrids have not been so common.

Henslow, (31) compared a hybrid *Digitalis* with its parents in a very minute way, considering the knowledge of plant anatomy of the time. He found in the size and shape of the hairs and other structures the hybrid was intermediate between its parents.

Wettstein ('88) compared the leaves of four coniferous hybrids and found them exactly intermediate between their parents in number of stomata, depth of epidermal cells, and number and arrangement of the sclerenchyma cells of the bundles.

Noble ('88) compared *Clematis Jackmanni* alba with its parents and found it had flowers resembling both parents. He explained it that the *C. patens*, a spring-flowering, and *C. Jackmanni*, an autumn type, seem to set up a kind of rivalry to see which is the stronger. Old wood in May, June, and July bears double, semi-double solitary flowers of a bluish French-grey as the *C. patens* and then young shoots in August and September bear single white flower in pairs on a long raceme as the *C. Jackmanni*.

Hildebrand ('89) found in a cross between *Oxalis latifolia* × *O. tetraphylla* that the characteristically distinct hairs of each species might both arise from a single epidermal cell of the offspring.

Branza ('90) compared the tissue masses of certain seed hybrids and of *Cytisus Adami*, a graft hybrid, with that of their parents. A similar study of the latter by MacFarlane differs in many details

The most extensive and intensive study of plant hybrids in relation to their parents was made by MacFarlane ('90, '91). He compared the minute structure of the following hybrids with that of their parents: *Philageria Veitchei*, *Dianthus Grievei*, *Geum intermedium*, *Ribes culverwelli*, *Saxifraga*

Andrewsii, Erica Watsoni, Bryanthus erectus, Masdevallia chel-
soni, Cypridium Lleanum, and Cytisus Adami (a graft hybrid).

His conclusion is summed up in these words, "We may recall the facts advanced as to colour, flowering period, chemical combinations, growth, and vigor, which, though scanty, and fragmentary in their nature, all point to the conclusion that hybrids are intermediate between their parents in general life phenomena." On the divergence of some hybrids or parts of hybrids towards one parent, he explains it on a purely physical basis, of under or over nutrition, or through advantageous or disadvantageous position. Except for this mistaken conclusion, his study constitutes a great contribution to the study of heredity and is so regarded by the Editor of the Gardener's Chronicle ('93).

Henslow ('93) in a study of Rhododendron hybrids found that one parent often impresses some peculiarity which he calls sexual hybridity, but that common characters are more or less intermediate between their parents.

Farmer ('97), in studying a hybrid fern, decided that inheritance is the result of an imaginary struggle between purely hypothetical combatants, and thus accounts for the resemblance of this or that cell to one or the other parent.

The rediscovery of Mendel's law in 1900 explained in a new way the tendency of hybrids to resemble one or the other parent as of dominance and recessiveness. The studies since that time have usually been of the plant-breeding type.

MacDougal ('07) in a study of hybridization of wild plants states that anatomical study of the hybrids and the parents to which it has been referred would be a good method of determining whether or not it is a true hybrid. He cautions that it might not be accurate because of the tendency toward one parent.

DeVries ('10) calls those qualities which in crossing conform to Mendel's law bisexual or varietal characters, and those which give intermediates uni-sexual or specific characters.

"The points of difference between parents can be all uni-sexual or all bi-sexual, or some of them uni-sexual and others bi-sexual. In the first case the parents are to be considered as elementary species, in the second as varieties; in the third, however, the principles affords no decision." (p587). He

further states that in experiments in hybridization we must--

"confine our attention to certain points of difference and leave all the rest out of consideration as of subordinate importance.

If the character is bi-sexual and behaves in a Mendelian fashion we may immediately infer that the two parents are to be considered

as varieties. If it is uni-sexual they are elementary species, of which the one must have been derived from the other---by mutation."

East ('12) chose flower size in *Nicotiana*, an invariable character from the standpoint of environment, and found in the F_1 generation that it is strictly intermediate. Among the flowers in the F_2 generation, he found also flowers identical with each parent.

Molloch ('21) found in a cross between *Hordeum vulgare* × *H. murium*, two species which differed in a large number of morphological characters, that the hybrid died, probably due to the failure to harmonize between the reactive systems of the two species. He states, "There are all degrees of incompatibility of reaction systems in species crosses."

Tedin ('23) found that two forms of *Camelina*, differing from each other in almost every character, had probably two factors that influenced leaf shape. The interpretation was that AABB = pinnatifid leaves, aabb = entire leaves, AAbb = pinnatifid with shorter and broader lobes than aaBB = deeply dentate single leaves.

Anyone who has undertaken a comparison of hybrids must agree with MacFarlane in his statement that, "When a

hybrid is the product of parents that are widely divergent in histological details the comparison will be easy, but when we attempt to compare a hybrid with two parents which are regarded as species, but whose chief specific differences are those of colouring and size, it is almost or quite impossible to detect any blending of parent characters even though these may occur."

The study of hybrids has generally been considered a good means of verification of doubtful hybrids. It has not always been so fruitful for determining the laws of heredity.

Davenport ('07) states that "The common mistake has been to note a few remarkable individuals and exceptional instances, and from these attempt to deduce the 'laws of descent'.----To determine the facts of heredity with any degree of reliability, we must study the race as a whole and not simply the separate individuals that compose it. The laws of descent are to be discovered by a critical study, not of individuals, but of entire populations sufficiently large to be safely representative. Unfortunately, the application of the statistical method to the study of this subject is comparatively new, and as it is extremely laborious, the accumulation of a large mass of material will of necessity be a somewhat slow process." (p478).

The study of the detailed anatomy of whole races of hybrids would be extremely tedious but with the advance of our knowledge of minute structure of plants and the perfecting of our methods of studying them, it will some day no doubt be attempted. It is known that species differ in the details of their anatomy as much or more than in their external macroscopic features. There are certain features which are greatly modified by environment and the age of the plant. Great care must be exercised in comparing these features.

Since shrubs offer good subjects for anatomical study and many hybrids have already been produced among them, I have selected them for this comparative study.

The following shrubs were secured:

Berberis neubertii = *B. vulgaris* × *Mahonia aquifolia*

Syringa chinense = *S. vulgaris* × *S. persica*

Forsythia intermedia = *F. suspensa* × *F. viridissima*

Lonicera bella = *L. tartarica* × *L. morrowii*

Lonicera notha = *L. Ruprechtiana* × *L. tartarica*

Lonicera muendiensis = *L. bella* × *L. Ruprechtiana*

Lonicera muscaviensis = *L. morrowii* × *L. Ruprechtiana*

From the cross and longitudinal sections of the stems of these hybrids and their parents it was apparent that the first, *Berberis neubertii* and its parents, offered the most points of difference. It was therefore selected for the major part of this study.

The origin of *B. neubertii*, which is usually considered an inter-generic hybrid, is described in *L'Illustration Horticole* as follows; " Il a ete trouve, en 1850, dans un jeune plant, issu de graines recueillies sur un *Berberis atropurpurea* et sur un *Berberis (Mahonia) aquifolia*, croissant tous deux l'un pres de l'autre, par M. Aug. Nap. Baumann, horticulteur a Bolwiller (France), et est evidemment le resultat d'un croisement artificiel entre ces deux especes, si diverses par le port; croisement opere par quelque insecte butineur."

The *B. neubertii* plant from which this study was made was secured from Farquhar who secured it from ^{the} Arnold Arboretum.

In general characteristics of leaf and stem it agrees with the description and illustration in *L'Illustration Horticole*, the illustration in *Gardener's Chronicle*, and the description in *Bailey's Encyclopedia of Horticulture*, but differs in two very important details. My specimen is spined, but the descriptions

and illustrations give it as spineless. The leaves are grouped as those in *B. vulgaris* in the axils of the spines, while the descriptions give them as single and somewhat sheathing the stem as described in *Mahonia aquifolia*. The second difference may be the result of the first, which is probably a reversion to one of its parents, *B. vulgaris*. Farquhar stated in a letter that he did not have a spineless plant but that as far as he knew it was a true hybrid. The only explanation for the decided change in the plant since it was first produced in 1850, would be that it has reverted back in that respect to one of its parents, in this case *B. vulgaris*.

Farmer in his study of a hybrid fern found that it had a tendency to revert to one or the other parent in certain particular characteristics and plants obtained from cuttings of such branches grew and remained true. The reverted branch did not in every particular resemble the one parent but this one parent became more strongly pronounced. He considered this a striking illustration of the unstable character of a hybrid.

The determination of the true hybridity of my specimen was therefore my first problem. As will be observed later, it agrees with what we may expect in a true hybrid.

DISCUSSION

General Appearance

Mahonia (sometimes called Berberis) aquifolia is an evergreen, broad-leaved, spineless shrub with odd-pinnate leaves.

It has minute subulate stipules. The base of the leaf is sheathing from one-half to completely surrounding the stem. The glossy leaves of firm texture give it a stiff Xerophytic appearance.

Its habit of growth is by sudden limited, tender terminal shoots

which are later strengthened. Berberis vulgaris is a deciduous,

spined, simple-leaved shrub. The spines are morphologically

leaves and the foliage leaves are borne on short branches in

their axils. The growth is more gradual and indefinite than

that of Mahonia and the branches are more pendulous and graceful.

The texture is less firm and the appearance truly mesophytic.

It has very minute subulate stipules and below them the petiole

is flattened and partly sheathed and indistinctly jointed.

The hybrid, B. neubertii, is classed as a semi-evergreen

in the habitat of Boston. My specimen lost its leaves with

the first snow but a few leaves still clung to the branches.

The spines are similar to those of B. vulgaris and the foliage

leaves are borne on short stems in their axils. The growth

is indefinite, resembling that of B. vulgaris, but it has a

tendency toward the stiff appearance of Mahonia. It has very minute stipules and jointed petiole but the petiole is much larger than that of *B. vulgaris*. It may be said to have a general appearance intermediate between that of its parents.

The Leaf

Since Mahonia aquifolia has a compound leaf and Berberis vulgaris a simple leaf, a comparison is difficult because of the many differences. The hybrid has simple leaves and in this is dominated by *B. vulgaris* but in many details it is clearly influenced by the leaf of Mahonia.

In shape, the Mahonia leaflet (Fig. 3) is oblong-ovate, sessile, or nearly so, and the sides of the base are unequal. The leaf of *B. vulgaris* (Fig. 1) is oblong-spatulate with a petiole 8-10mm long and indistinctly jointed near the base. *B. neubertii* has a leaf (Fig. 2) of a similar shape to that of *B. vulgaris* but the petiole is intermediate in both breadth and length between the petiolule of Mahonia and the petiole of *B. vulgaris*. The stipules are very similar to those of *B. vulgaris*. The sheathing base of the petiole below the stipules and joint is much broader than that of *B. vulgaris*, a tendency

toward the base of the leaf of Mahonia.

The margin of the leaflet of Mahonia is spinulose-dentate with lobes from 5-10mm apart. There is a prominent veinlet for each lobe. *B. vulgaris* has a setulose-dentate leaf with the lobes from 1-1.2mm apart, and a small veinlet for each lobe. *B. neubertii* has a spinulose-dentate leaf and thus follows Mahonia, but exceeds it in the size of the lobes and distance between them in some cases, and sometimes nearly approaches the leaf of *B. vulgaris* in size of lobes and distance apart. On the same branch, the leaves of *B. neubertii* are quite variable in the size of the lobes and their distance apart. They have a prominent veinlet for each lobe. The spines of the leaf are very similar in length and texture to those of Mahonia being much more rigid than those of *B. vulgaris*. The spines in all cases are continuations of the group of sclerenchyma cells which form the margin of the leaves. The sclerenchyma cells are fewer in number in *B. vulgaris* and therefore the spines of the leaf are less rigid.

In Figures 1,2,&3, the general type of venation of the leaves may be observed. Mahonia (Fig.3) has 5-6 primary lateral veins and between each of these 3-6 veinlets from the midrib. The type of venation agrees with what we might expect from the shape of the leaf. *B. vulgaris* (Fig.1) has 3-5 primary lateral veins and between each of these as many as 16 small veinlets from the midrib. In venation, *B. neubertii* (Fig.2) agrees very generally with *B. vulgaris* but has fewer veinlets from the midrib and in this shows a tendency toward Mahonia.

The color of the leaf of Mahonia is a yellowish green and lustrous when young but dark green and lustrous when mature. The leaf of *B. vulgaris* is a pale or grayish green beneath but a dark green above. It is dull in appearance. The leaf of *B. neubertii* agrees in color with that of *B. vulgaris*.

Upper epidermal cells as shown in Figures 4,5,&6 show the lateral walls of *B. vulgaris* (Fig.4) to be symmetrical while those of Mahonia (Fig.6) are very sinuous or undulated. The hybrid (Fig.5) has cells in shape similar to those of *B. vulgaris*

but the size of the cells is greater than in either parent.

The stomata are found on the lower epidermis of the leaf only and are surrounded by two or more epidermal cells not distinguished by their form. I found by count that the number of stomata averaged 260 per sq.mm in Mahonia, 216 in *B. neubertii*, and 176 in *B. vulgaris*. The mean between Mahonia and *B. vulgaris* is 218 which is closely approached by *B. neubertii*. This agrees with MacFarlane's observations of *Philageria Veitchii* and other hybrids. The cross-sections of the stomata as shown in Figures 10, 11, & 12 show many differences but they are not always constant. It will be noted that the stoma of *B. vulgaris* (Fig. 10, H) agrees with that of *B. neubertii* (Fig. 11, H) in general shape of the guard cells. The stomata of Mahonia are more difficult to find in cross-section. The particular one in Figure 12, H, is a typical form. It will be observed that the guard cells are not sunken as might be supposed by the surface view (Fig. 7-9) but somewhat external to other epidermal cells whose walls are seen through the guard cells.

The lower epidermal cells of the Mahonia leaf and those of the petiole, have, in their outer wall, a network of thickening, stippled in Figure 9 and shows in the epidermal cells of Figure 12, H, and Figure 13, F. This is very conspicuous in mature leaves but was not found in young leaves. *B. vulgaris* has no such thickening, as shown in Figures 7, 10, & 15, F. The hybrid has a very indistinct network of thickening as shown in Figure 8, F, in mature leaves only. This character, which behaves as an intermediate, was one of the most convincing proofs of the hybridity of my specimen.

In the cross-section of the leaves as shown on Plate II there are in Mahonia (Fig. 13) two distinct rows of palisade cells and a third row which is intermediate between palisade cells and spongy parenchyma. *B. neubertii* (Fig. 14) has two rows of distinct palisade cells and the third (Fig. 14, D) somewhat intermediate and thus clearly follows Mahonia. However, the length of palisade cells in the hybrid exceeds that of *B. vulgaris*. The greater thickness of the leaf of the hybrid than either parent is thus partly accounted for by the larger number of rows of

palisade cells from one parent and the greater length from the other. There are also more rows of spongy parenchyma cells in the hybrid than in either parent. Mahonia has an average of 5-6 rows of spongy parenchyma, *B. vulgaris* has 4-5 rows, but the hybrid has 7-9 rows. In this *B. neubertii* goes beyond either parent as it does also in the size of the cells as shown in Figures 13, 14, & 15, E. Since these plants were growing under similar environment and this appears as a constant characteristic, it may be considered as inherited.

The cross-section of the midrib in all three shows, near the apex, a single continuous bundle with sclerenchyma cells extending to both upper and lower epidermises. Numerous cross-sections of the midrib show that the bundle of the midrib of the Mahonia leaf divides much farther up the leaf than in *B. vulgaris*. In Figures 1, 2, & 3, in each case at A the bundle is continuous with sclerenchyma extending to both the upper and lower epidermises. At B, the bundle has divided into three and at C, into 5, and at D, (Fig. 3, only) into 9 bundles. The positions of A, B, & C in *B. vulgaris* and *B. neubertii* are nearly

the same and therefore *B. vulgaris* dominates in the character. Where the bundles are divided into three groups, medullary rays separate them and the sclerenchyma is entirely surrounded by parenchyma cells. The number of thin-walled parenchyma cells in the petiole of *B. vulgaris* is 3-5 rows, in the petiolule of Mahonia 4-6 rows, and in the hybrid 5-7 rows. The hybrid thus exceeds both parents in this character which partly accounts for the larger petiole. In the petiole of Mahonia, the sclerenchyma forms a complete ring around the vascular area. This is not usually true in the stems of Mahonia as will be observed later. Near the base of the leaf the bundles again form a semicircle because of the sheathing base of the leaf. In *B. vulgaris*, the vascular area never forms a complete ring but somewhat more than a semi-circle in the petiole and in this is followed by *B. neubertii*.

In both Mahonia and *B. vulgaris*, the midrib is prominent below the blade of the leaf as shown in Figures 13&15. The hybrid has more rows of sclerenchyma cells than either parent and a larger midrib but the relative thickness of the blade of

the leaf almost equals that of the midrib. The small veins scarcely exceed the ^{rest of the} blade in thickness in *B. neubertii*

because the rest of the blade is just about as thick, while in both parents they are prominent on the under side of the leaf.

Epidermal Hairs

Papillose epidermal hairs occur very generally on the lower epidermis of the *Mehonia aquifolia* leaf and always on the young stem. They average 8μ in height and 12.5μ in diameter.

They are not found on *B. vulgaris* nor *B. neubertii* which would show this to be a recessive character, but no conclusion may be drawn from this one example.

For comparison, in *Lonicera Morrowii*, many epidermal hairs are found on leaves and young stems. On the stems they are very irregular in length from .08mm to .48mm with as many as 360 to the sq.mm. In *L. tartarica* usually no epidermal hairs are found although they are sometimes found on young leaves. The hybrid, *L. bella*, has epidermal hairs varying in length from .04-.32mm and averaging 120 to the sq.mm. It appears in this case that the hybrid has the epidermal hairs of *L. morrowii* reduced by half in number and size.

Lonicera Ruprechtiana has few epidermal hairs but broader at the base and more pointed than those of *L. morrowii*. They vary in length from .08mm-.32mm and have about 76 to the sq.mm. The hybrid, in this case *L. Muscaviensis*, has epidermal hairs intermediate in size, shape, and number between its parents. There are an average of 160 to the sq.mm and they vary in length from .04-.32mm.

Lonicera notha, which is a hybrid between *L. tatarica* and *L. Ruprechtiana*, has again an intermediate condition. It has hairs from .02-.2mm in length and about 56 to the sq.mm.

Lonicera muendiensis, a cross between *L. bella* and *L. Ruprechtiana*, has hairs varying in length from .03-.24mm and width about ⁹⁶_^ to the sq.mm. The shape of the hairs also shows the influence of both parents.

These examples would all point to an intermediate condition in the inheritance of epidermal hairs in *Lonicera*.

These observations along with those of Hildebrand on the hybrid of *Oxalis latifolia* x *O. tetraphylla* where both kinds of epidermal hairs were inherited on a single cell of the hybrid,

and similar observations by MacFarlane on *Ribes Culverwellii*, *Saxifraga Andrewsii*, and *Carduus Carolorum* which have distinct types of hairs inherited from both parents, would certainly show that no rule obtains in the inheritance of epidermal hairs. These latter are classed by MacFarlane as examples of Bi-sexual Heredity.

The Stem

Epidermis

The stomata on the young stem of *Mohonia aquifolia* are more numerous than on older stems. A pair of guard cells in this region is larger than the other epidermal cells. I found 56 to a sq.mm of area in the first internode. As the stem lengthens, the stomata do not grow but the epidermal cells enlarge particularly in length until there are but 23 or less to a sq.mm of area. The stomata^{affanatus in} are about .03mm in diameter. In *B. vulgaris*, the number of stomata averages 23 per sq.mm of epidermal area in the 5th internode where the stem has ceased elongation. The number of stomata in the parents is thus not very different. In the hybrid, the number of stomata is greatly reduced. In several counts on

younger and older areas, I found the number to average but 9 per sq.mm of epidermal area. No explanation is offered for this apparent discrepancy.

The size of epidermal cells in Mahonia, after the stem has lengthened, is .08mm long x .02mm wide. *B. vulgaris* averages .04x.02mm and *B. neubertii* .06x.02mm showing an intermediate length in the epidermal cells of the hybrid.

Numerous perforations are found in the lateral ^{epidermal} cell-walls of *B. vulgaris* as shown in Figure 24,A. They are also found in Mahonia and the hybrid.(Fig.26,A) A comparison in number is difficult to make. They were more conspicuous in young Mahonia cells than in older cells. The hybrid, according to my observation, showed a reduced number of these perforations below that of either parent.

The Cortex

The cortex of Mahonia (Fig.16&19,B) consists entirely of parenchyma cells. There is no distinct endodermis separating the cortex from the pericycle but Solereder has considered the primary bast-fiber ring as part of the pericycle and I see no

reason why it should not be so considered. There is no typical collenchyma. The parenchyma cells of the cortex are large, average .03mm (variation .02-.04mm) ^{in diameter and} average .06mm (variation .02-.12mm) in length. The cell-walls are irregularly thickened with numerous perforations. The number of rows of cells is regular toward the outside because the young stem is round but is very irregular toward the inside because of the discontinuous bast-fiber ring. The average depth of cortex of several specimens was 7.2 cells.

The cortex in *Berberis vulgaris* is composed entirely of thin-walled cells usually of large size. The average diameter is .03mm (.02-.04mm) and the length .13mm (.08-.24mm.). The cells contain numerous disc-shaped chloroplasts. The walls are not perforated and not thickened. The number of rows is irregular in conformity with the angled stem and the irregular bast-fiber ring. At the angles of the stem there may be only 2 cells radially but there are 6-8 cells where the bast-fiber rings indent. The average depth for several sections was

4.4 cells.

The cortex of *B. neubertii* (Fig.17&20,B) has perforated and irregularly thickened cell-walls, thus following *Mahonia*. The cells average .10mm (variation .06-.14mm) long and .03mm (.02-.06mm) wide. The mean between the length of cortex cells in *Mahonia* and *B. vulgaris* is .095mm which shows *B. neubertii* to be practically intermediate in length. The average radial depth of cortex in *B. neubertii* for several counts is 3.3 cells which is less than that in either parent. The general arrangement of the cells of the cortex is like that found in *B. vulgaris* in conformity with the irregular bast-fiber ring on the inside and the angled stem on the outside. The cortex of the hybrid is thus an irregular zone similar to *B. vulgaris*, perforated and irregularly thickened walls similar to *Mahonia*, and length of cells intermediate between the two, and fewer cells radially than either.

Primary Bast of the Pericycle

The primary bast forms the outer part of the pericycle in

all three forms. In Mahonia, it is usually a discontinuous ring of groups of bast fibers as shown in Figures 22 & 25,C. The number of fibers in a group may vary from a few as shown in Figure 19,C, to many as shown in Figure 22,C. In one stem I observed, it was continuous for nearly half the circumference of the stem. Cork forms beneath the bast groups as well as around them at times, thus cutting them off, and later they break away.

The primary bast of *Berberis vulgaris* forms a continuous ring around the stem. It varies greatly in number of cells radially having as few as 3 cells in the depressions and as many as 12 which cause the angles of the stem. (Fig.27,C.)

The bast is persistent for a longer time than in Mahonia, partly because it forms a continuous ring and partly because of the undulations which provide for the pressure of growth from within by straightening out as the stem increases in size. Cork forms beneath it, thus resulting in its ultimate breaking away.

B. neubertii very clearly follows *B. vulgaris* in the arrangement of its primary bast (Fig.20,23,&26,C). It is arranged

in an undulating continuous ring, thus providing for expansion as the stem grows and causing the angles in the young hybrid stem similar to that of *B. vulgaris*.

In width of bast radially, the hybrid exceeds *B. vulgaris*, having an average of 7.9 cells for several sections counted, while *B. vulgaris* has only 6.3 cells.

The size of the primary bast fibers of *Mahonia* is smaller in both length and diameter than those of *B. vulgaris*.

The length in *Mahonia* averages .8mm while in *B. vulgaris* it averages 1.1mm. The hybrid bast averages 1.0mm which very closely approaches the mean, (.95mm), between the two parents.

For comparative length of bast see Figures 31, E, F, & G, which represents an average length in each case of *Mahonia*, *B.*

neubertii and *B. vulgaris*. In diameter, the individual

bast fibers, measured at the widest area, were for *Mahonia*

22 μ (variation 19-27 μ), for *B. vulgaris* 25 μ (variation 12-

35 μ), and for *B. neubertii* 24 μ (variation 19-27 μ). The mean

between *Mahonia* and *B. vulgaris* is 23.5 μ which is closely

approached by the average diameter of the hybrid bast. In both length and diameter the primary bast of *B. neubertii* is intermediate between that of its parents.

Macerations were made of sections of primary bast fibers by putting small sections into chromic acid and also into nitric acid and potassium chlorate heated in a test-tube, and thrown into water at the proper time to stop action. Individual bast fibers of *Mahonia* are shown in Figure 31. Circular pits are common, as shown in surface view by rings and in the side walls as areas not darkened. Figure 31, A&C, shows lines running longitudinally with the fibers which appear as irregular thickenings and are not dissolved by nitric acid. The deposits within the cell, shaded black, are soluble in nitric acid.

The primary bast of *Berberis vulgaris*, as shown in Figure 33, has circular pits and also pits very much elongated running diagonally across the bast fibers. These

particular thin areas were very conspicuous in *B. vulgaris* but were not found in the bast of *Mahonia*. The deposits referred to in *Mahonia* bast were not found in the bast of *B. vulgaris*.

In the bast of the hybrid (Fig.32), circular pits are found as in both parents. Deposits (Fig.32,C), which are soluble in nitric acid but in greater abundance than in the bast of *Mahonia*, and also the diagonal elongated pits (Fig.32,B), similar to those found in *B. vulgaris* are both found in the bast of *B. neubertii*.

The primary bast of the hybrid is dominated by *B. vulgaris* in being a continuous undulated area surrounding the stem, the undulations allowing for expansion in growth. It exceeds *B. vulgaris* in amount and prominence, especially in young stems as shown in the greater number of cells radially. The individual bast fibers are intermediate in length and diameter between the parents. Deposits, soluble in nitric acid, are found in the hybrid similar to, but in

excess of, those in Mahonia. Elongated diagonal pits, common to *B. Vulgaris*, are found in the bast of the hybrid. These facts offer additional proof of the true hybridity of my specimen.

Cork

Cork arises in the outer part of the parenchyma of the pericycle just beneath the primary bast. In Mahonia it appears later than in *B. vulgaris*. In a rapidly growing stem of Mahonia, I found it in the 7th internode, while in *B. vulgaris*, I found it in the 2nd internode. The hybrid cork arises in the 2nd internode and thus follows *B. vulgaris*.

Since Mahonia has a discontinuous bast fiber ring, cork cells arise both between and beneath the groups of bast as shown in Figure 22,D, thus cutting off the bast completely and it soon begins to break apart. The epidermis and cortex hold several bast groups together but between these groups they break apart in large longitudinal

strips, a fact recognizable at the surface. In *B. vulgaris* the bast-fiber ring is continuous around the stem and therefore the cork forms beneath it as a continuous regular growth which later cuts off the bast. The bast breaks at the narrower places but still persists for some time as narrow longitudinal strips on the outer part of the cork, the crevices between them showing on the outer bark. *B. neubertii* shows a very close resemblance to *B. vulgaris* in the occurrence and growth of cork and its ultimate effect upon the stem.

Parenchyma of the Pericycle

The parenchyma of the pericycle in *Mahonia* (Fig. 16&19, D) has from 4-6 cells radially outside the primary pbleom. The cell-wall is unevenly thickened and perforated and the cells retain their shape, though flattened somewhat, for many years (Fig. 22&25, E). I did not find any sections in which these cells were crushed.

The area of parenchyma of the pericycle in *B. vulgaris* (Fig. 18&21, D) conforms to the undulated bast fiber ring,

having many large cells at the angles and few smaller cells at the indentations. The cell-walls are somewhat thickened although not as much as in Mahonia. As growth continues and the bast fiber ring, later replaced by cork, straightens out the undulations, the cells of the corner areas are compressed and flattened and the indentations widen by growth of the cells and elongation radially with many inter-cellular spaces forming, thus making the parenchyma of the pericycle an area continuous in width around the phloem. The cells are not crushed up to the 8th year.

The hybrid (Fig.17&20,D) is very similar to *B. vulgaris* in parenchyma of the pericycle in that the angles of the stem are wide in area and the depressions are narrow. The cell-walls are irregularly thickened and perforated (Fig.36 of Pl.II) as in Mahonia. The cell number varies radially from 4 in the depressions to 8 in the angles of the stem. Mahonia has 5-6 cells radially, *B. vulgaris* has an average of 9, and *B. neubertii*, an average of 6. It more nearly approaches Mahonia in number of cells but is similar to

B. vulgaris in the irregularity of the area in conformity with the angled stem. In thickness of cell-walls, *Mahonia* exceeds that of *B. vulgaris* and also that of *B. neubertii*.

Primary Phloem

The primary phloem of all three consists of sieve tubes and also of septate prosenchyma cells tapering at both ends. These tapering ends overlap and the side walls are pitted or have thin areas. No distinct differences were observed in the primary phloem of the three except that the amount of primary phloem in proportion to primary Xylem is greater in *Mahonia* than in *B. vulgaris* or the hybrid. The latter are very similar.

Secondary Phloem

The secondary phloem consists of sieve tubes and numerous septate prosenchyma cells with ends tapering to a point or simply rounded. In *Mahonia* (Fig.34 of Pl.III) these prosenchyma elements are unevenly thickened and numerous intercellular spaces are formed (Fig.35 of Pl.II) in the older phloem

by the breaking apart of the cell-walls. These show in the walls on edge as lenticular intercellular spaces. Similar intercellular spaces occur in *B. vulgaris* but are less frequent and the walls are less thickened. *B. neubertii* (Fig.37 of Pl.II) is very similar to *B. vulgaris* in the number of intercellular spaces appearing in the septate prosenchyma of the phloem but the walls are thickened more nearly like those of *Mahonia*. In all three, the primary phloem is not crushed for a number of years. *B. vulgaris* and *B. neubertii* have numerous secondary bast fibers which may help prevent the crushing of the other phloem elements.

Secondary Bast

No secondary hard bast is made by *Mahonia*. The cell-walls of the septate prosenchyma cells are perceptible thickened (Fig.35, Pl.II) which may serve a similar function of strengthening as is served by secondary bast. In *Berberis vulgaris*, secondary hard bast fibers resembling rod cells (Fig.27,0), occur singly in the outer part of the phloem but in the inner phloem they occur in tangential rows. These

bast fibers average .2mm in length. Secondary hard bast may be considered a unisexual character as it occurs in only one parent. In *B. neubertii*, similar hard bast fibers occur, only in much greater abundance than in *B. vulgaris*. Figure 26,N, shows these bast fibers just beginning to thicken their walls. They have been completely thickened by the end of the second growing season in both *B. vulgaris* and *B. neubertii*. Figure 26,O, shows a cross-section of these mature bast fibers. The hybrid is this dominated by *B. vulgaris* in the character of secondary bast but exceeds it in amount.

Primary Xylem

The primary Xylem of all three subjects is very similar. It is surrounded toward the pith by wood parenchyma with strengthened walls, septate prosenchyma, and prosenchyma with pointed ends and thickened walls, similar to primary bast-fibers. In *B. neubertii*, there is more of this bundle sheath area than in either parent, as shown in Figure 23,P, as

compared with Figures 22&27. These cells are usually stored with food and the cell-walls are thickened and pitted. In *B. vulgaris*, the amount of thickening of cell-walls is less than in *Mahonia*. The hybrid follows *Mahonia* except that it has a larger amount of sclerenchymatous medullary sheath abutting on the Xylem..

Secondary Xylem

Cross, longitudinal, tangential, and macerated sections were made of the Xylem areas of the three subjects. The Xylem is made up in all three of tracheal tubes, tracheids, wood fibers, wood parenchyma, and septate prosenchyma. All of these cells have thickened walls and pits. The tracheids have bordered pits, the wood fibers have simple circular pits, the tracheal tubes have either elongated pits as shown in Figure 28,B, or circular pits as shown in Figure 29,B. The circular pits have a narrow slit opening as shown in Figures 29&30,B. Many of the smaller tracheal tubes have spiral thickenings of the wall in addition to bordered pits which are common to all three subjects but especially to *Mahonia*.

A comparison of the Xylem elements is difficult because in general they are very similar.

Mahonia has a very few large tracheal tubes as shown in Figure 25. *B. vulgaris* not only has more of these tracheal tubes (Fig. 24&27, I) but they are larger. The average diameter of many tubes measured for Mahonia was 40u., for *B. vulgaris* 57u., and for the hybrid 48u. The hybrid thus is intermediate in the size of tracheal tubes but is like *B. vulgaris* in number as shown in Figures 23&26, I.

Wood fibers from macerated tissues of all three subjects show a general similarity in pits and shape. In length, from many measurements, I found the average for Mahonia to be .38mm for *B. vulgaris* .34mm and for the hybrid, .36mm which is the mean between that of the parents.

The tracheids are found in groups in longitudinal areas either bordering a group of wood fibers or medullary rays. Any comparison is difficult because of the similarities. In length from macerated sections, I found the average tracheids

for Mahonia to be .23⁸mm for *B. vulgaris* .270mm and for the hybrid .247mm. This shows the average length of the hybrid tracheid to be slightly less than the mean between that of the parents (.254mm) but it has approximately an intermediate length.

The wood-parenchyma is very little developed in Mahonia but more common in *B. vulgaris*. It usually borders the medullary rays. *B. neubertii* apparently exceeds *B. vulgaris* in this, but a comparison is difficult to make.

The wood prosenchyma with delicate cross-walls across the lumen is common to all three but more common in *B. vulgaris* than Mahonia. The hybrid apparently follows *B. vulgaris* in this character.

Medullary Rays

Broad primary medullary rays separate the individual vascular bundles from each other in all three subjects. The cell-walls are perforated as shown in Figures 28, 29, & 30, F. As stated by Solereder, the primary medullary rays are not closed by inter-fascicular wood. The length of medullary rays is apparently greater in *B. vulgaris* than in Mahonia and the vertical distance between rays is greater in Mahonia

than in *B. vulgaris*. The hybrid apparently follows *B. vulgaris* in both characters.

The Pith

The pith of *Mahonia* is homogeneous and walls are equally thickened throughout. It is never crushed so far as I was able to observe. *B. vulgaris*, as stated by Solereder, has a heterogeneous pith with two areas. The outer area is thick-walled and remains alive for some time and is used for food storage, while the inner area is not thickened and soon dies. (Fig. 24&27, K&L). The hybrid has a heterogeneous pith (Fig. 23&26, K&L) but the area which remains alive and is thickened is wider than in *B. vulgaris*. The central dead area of the pith is smaller in size than in *B. vulgaris*. Although approaching *B. vulgaris*, the pith of the hybrid may be said to have part of the character of both parents. This may be considered an example of bisexual heredity in which part of the pith of *Mahonia* and part of that of *B. vulgaris* are both inherited by the hybrid.

The Flowers

My specimen of *Berberis neubertii* did not bloom in 1924 and therefore I could not compare the flowers.

CONCLUSION

The *Berberis Neubertii* plant from which this study was made is undoubtedly a true hybrid. It agrees with what we may expect in hybrids from previous studies. It has no new characters not present in either parent.

B. neubertii is usually considered a bi-generic hybrid. In some characters, it behaves as an inter-specific hybrid, in others as an inter-varietal hybrid, and in others as neither. It therefore belongs to that group "which affords no decision." (DeVries)

Those characters common to one parent only, called unisexual by MacFarlane and DeVries, may behave as intermediates. The network of thickening found on the lower

epidermis of the Mahonia leaf but not found on *Berberis vulgaris* is reduced by half or less in the hybrid. This character furnishes a very good proof of the true hybridity of my specimen.

The evergreen leaf of Mahonia and the deciduous leaf of *B. vulgaris* are inherited as semi-evergreen. The stiff, xerophytic appearance of Mahonia and the graceful, mesophytic appearance of *B. vulgaris* are inherited as a semi-xerophytic appearance in the hybrid.

Papillose epidermal hairs found on Mahonia stems and lower leaf epidermis but not on *B. vulgaris*, do not appear in the hybrid. Epidermal hairs in *Lonicera* in the hybrids studied behave as intermediates in both size and number.

The amount of secondary bast in *Berberis neubertii* exceeds that found in only the one parent, *B. vulgaris*.

Characters observed in *B. vulgaris* but not in Mahonia in which the hybrid closely approaches *B. vulgaris* are: spines which are morphologically leaves with the leaves

borne on short stems in their axils; jointed petiole; diagonal pits in the primary bast; and the size, shape, and thickness of walls of the secondary bast.

Characters observed in *Mahonia* but not in *B. vulgaris* in which *Mahonia* is closely approached by the hybrid are: second and third row of palisade cells of the leaf; the perforations and thickened walls of the cortex parenchyma; and certain soluble deposits and longitudinal thickenings in the primary bast-fibers.

Cases of bisexual heredity are not common in this hybrid as they were not in those studied by MacFarlane. The heterogeneous pith of *B. vulgaris* and the homogeneous pith of *Mahonia* is an example. The hybrid has apparently taken some of the thickened cells of *Mahonia* and the central thin-walled area of *B. vulgaris*. Another example is in the primary bast. Diagonal long pits are inherited from *B. vulgaris* and longitudinal thickenings and soluble deposits from *Mahonia* bast, both being found in the hybrid bast.

Characters common to both parents, called bi-sexual by MacFarlane and De Vries, may closely resemble one parent. Those in which Mahonia dominates in the F_1 generation are: texture of the leaf, margin of the leaf, number of rows of palisade cells of the leaf, and number of pericycle parenchyma cells radially.

Those characters in which *B. vulgaris* dominates in the F_1 generation are: habit of indefinite growth; size of stipules; color, shape, and general venation of the leaf; shape of upper epidermal cells of the leaf; shape of guard cells; number of bundles in the midrib; general character of the cortex, primary bast, cork, and parenchyma of the pericycle; and time of appearance of cork.

Many characters common to both parents, but differing in amount or size, are intermediate in the hybrid; as: number of stomata of the leaf; length of stem epidermal cells, length of cortex cells, wood-fibers, and tracheids; length and diameter of primary bast; diameter of tracheal tubes; and amount of thickening of cell-walls of parenchyma of the pericycle and septate phloem prosenchyma.

There are some characters common to both parent in which the hybrid exceeds both parents in amount, as: size of the leaf epidermal cells, length of palisade cells of the leaf, number of sclerenchyma cells of the midrib transversally, thickening of the sides of the blade as compared with the midrib, number of primary bast cells radially, amount of wood parenchyma cells, and amount of sclerenchymatous medullary sheath abutting on the xylem in the stem.

A few characters common to both parents in which the hybrid has less than either parent, are number of stomata of the stem and number of cells of the cortex radially.

While anatomical study of hybrids increases the number of characters observable, it also increases the complexity and difficulty of the study in its interpretation of the laws of heredity. It is generally recognized that microscopic details as well as macroscopic characters are heritable and it seems well established that they should be considered

in any study of the transmission of characters in hybrids.

ACKNOWLEDGEMENT

Acknowledgement is hereby given to Professor W. C. Stevens, Head of the Department of Botany of the University of Kansas, who suggested this topic, and whose constant encouragement and kindly criticisms have made this study possible.

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PLATE I

Fig. 1. Leaf of *Berberis vulgaris* showing general type of venation, drawn from leaf cleared with chloral hydrate. xl.

Fig. 2. Leaf of *Berberis neubertii*. xl. (Same as Fig.1)

Fig. 3. Leaflet of *Mahonia aquifolia*.x.5. (Same as Fig.1)

Fig. 4. Upper epidermis of leaf of *B. vulgaris* showing nuclei and upper end of palisade cells. x 312.

Fig. 5. Upper epidermal cells of *B. neubertii*, showing nuclei and upper end of palisade cells. x 312.

Fig. 6. Upper epidermis of *Mahonia aquifolia* leaf showing nuclei and upper end of palisade cells. x312.

Fig. 7. Lower epidermis of *B. vulgaris* leaf showing stomata and nuclei. x312.

Fig. 8. Lower epidermis of leaf of *B. neubertii* showing stomata and nuclei, and also network of thickening. (F).x312.

Fig. 9. Lower epidermis of *Mahonia* leaf showing stomata, nuclei, and thickening in the form of a network. (F).x312.

Fig. 10. Two stomata of *B. vulgaris* in a cross section, showing guard cells, bordering epidermal cells, and air space. x312.

Fig. 11. Two stomata of *B. neubertii*. x312.(Same as Fig.10)

Fig. 12. Two stomata of *Mahonia*. x312. (Same as Fig.10)

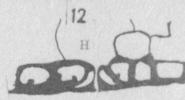
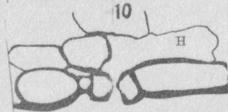
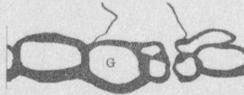
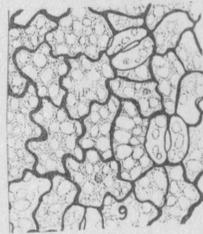
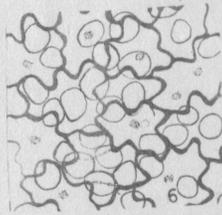
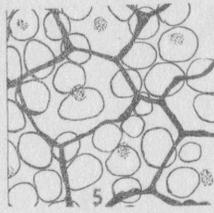
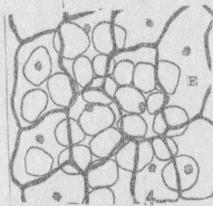
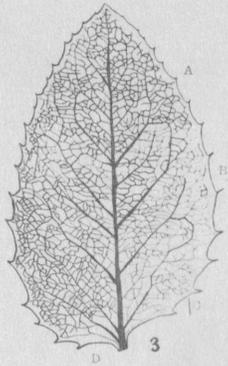
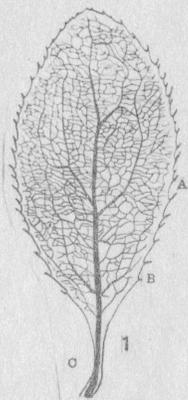


PLATE II

Fig. 13. Cross section of leaf of *Mahonia aquifolia* near center of leaf. x208.

Fig. 14. Cross section of leaf of *Berberis neubertii* near center of leaf. x208.

Fig. 15. Cross section of leaf of *Berberis vulgaris* near center of leaf. x208.

Index for above figures:

- A - Upper epidermis.
- B - Upper row of palisade cells.
- C - Second row of palisade cells.
- D - Third row of mesophyll showing gradual transition to spongy parenchyma.
- E - Spongy parenchyma.
- F - Lower epidermis.
- G - Phloem of midrib bundle.
- H - Xylem of midrib.
- I - Cortex.
- J - Air space.
- K - Sclerenchyma cells forming bundle sheath.

Fig. 34. Phloem prosenchyma of *Mahonia* stem showing cell-walls just beginning to thicken.

Fig. 35. Same as Fig. 34, after cell-walls have thickened and air spaces have formed between them.

Fig. 36. Cork (A), phellogen (B), and parenchyma of the pericycle (C) of *Berberis neubertii*, showing perforations in the cell-walls of the pericycle.

Fig. 37. Septate phloem prosenchyma of *Berberis neubertii* stem. Similar cells are found in the phloem of *B. vulgaris*.

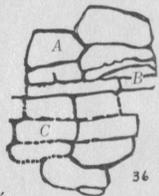
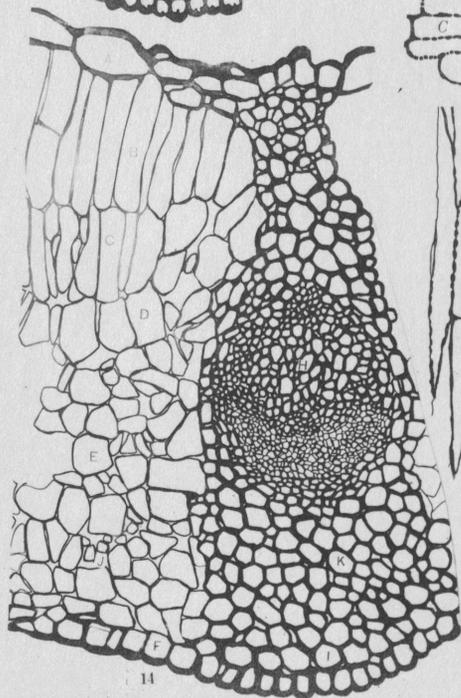
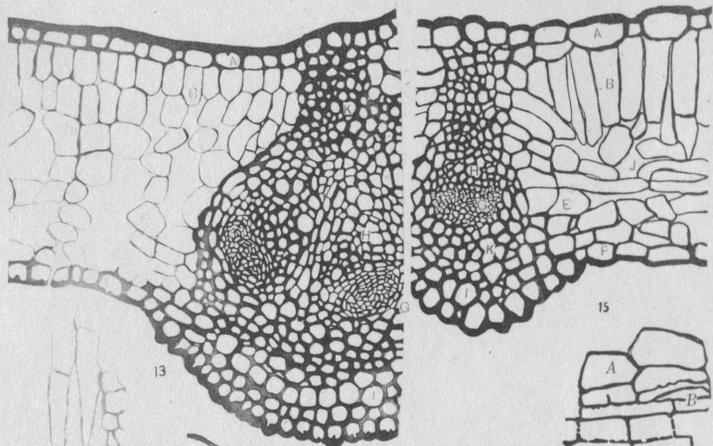


PLATE III

Fig. 16. Cross-section of 2nd internode of rapidly growing stem of *Mahonia aquifolia*. x115.

Fig. 17. Cross-section of 2nd internode of rapidly growing stem of *Berberis neubertii*. x115.

Fig. 18. Cross-section of 2nd internode of rapidly growing stem of *Berberis vulgaris*. x115.

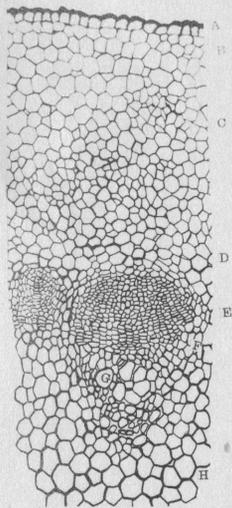
Fig. 19. Cross-section of 5th internode of rapidly growing stem of *Mahonia*. x150.

Fig. 20. Cross-section of 3d internode of rapidly growing stem of *B. neubertii*. x150.

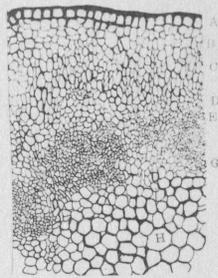
Fig. 21. Cross-section of 3d internode of rapidly growing stem of *B. vulgaris*. x150.

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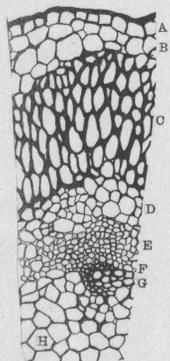
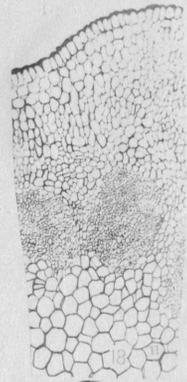
- A - Epidermis.
- B - Parenchyma of the cortex.
- C - Bast-fibers or sclerenchyma of pericycle.
- D - Parenchyma of the pericycle.
- E - Primary and early secondary phloem.
- F - Medullary rays.
- G - Primary and early secondary xylem.
- H - Pith.



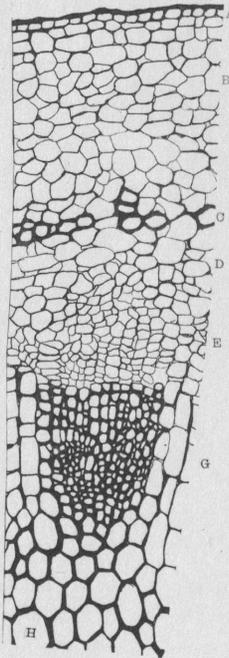
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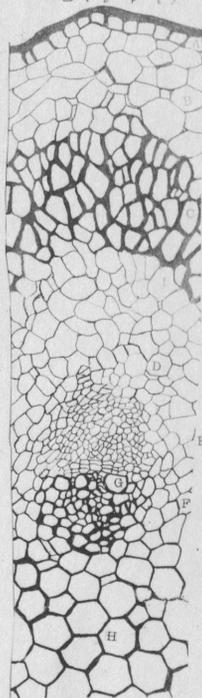
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PLATE IV

Fig. 22. Cross-section of one year old stem of *Mahonia aquifolia*. x75.

Fig. 23. Cross-section of one year old stem of *Berberis neubertii*. x75.

Fig. 24. Cross-section of one year old stem of *Berberis vulgaris*. x75.

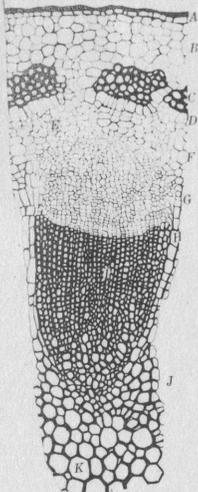
Fig. 25. Cross-section of two year old stem of *Mahonia aquifolia*. x75.

Fig. 26. Cross-section of two year old stem of *B. neubertii*. x75.

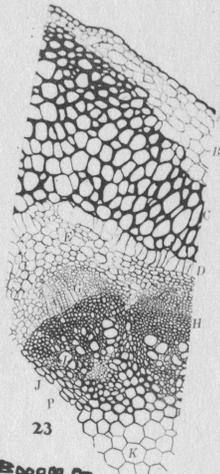
Fig. 27. Cross-section of two year old stem of *B. vulgaris*. x75.

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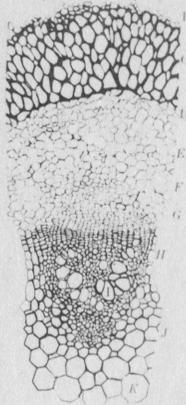
- A - Epidermis.
- B - Parenchyma of the cortex.
- C - Bast-fibers of sclerenchyma of the pericycle.
- D - Cork formed by the phellogen of the cork-cambium.
- E - Parenchyma of the pericycle.
- F - Primary phloem.
- G - Secondary phloem.
- H - Medullary ray.
- I - Secondary xylem.
- J - Primary xylem.
- K - Central pith.
- L - Outer pith, which in *B. vulgaris* and *B. neubertii* is the only area with thickened cell-walls.
- M - Phellogen, or cork-cambium.
- N - Secondary bast, just beginning to thicken its walls.
- O - Secondary bast. Fig. 26 - Cross-section.
Fig. 27 - Longitudinal section.



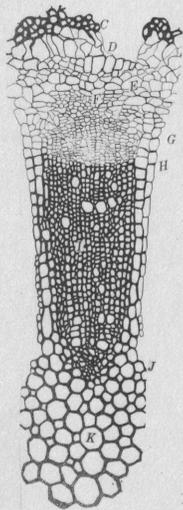
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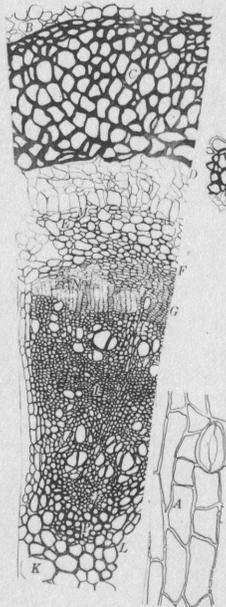
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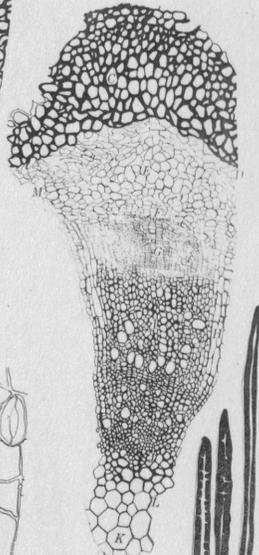
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PLATE V

Fig. 28. Tangential section from wood area of *Mahonia aquifolia* stem. x208.

Fig. 29. Tangential section from the wood area of *Berberis neubertii* stem. x208.

Fig. 30. Tangential section from the wood area of *B. vulgaris*. x208.

Index for above figures:

- A - Primary xylem tracheal tube showing spiral thickening of cell-wall.
- B - Secondary xylem water-tube showing pits.
- C - Water-tubes of secondary xylem showing pits and spiral thickenings.
- D - Tracheid^s showing bordered pits.
- E - Wood fibers showing simple pits.
- F - Medullary rays in cross-section showing perforations.
- G - Tracheal tube showing spiral thickening in one part and simple pits in the other. (unusual)

Fig. 31. Individual primary bast-fibers of *Mahonia aquifolia* showing longitudinal thickenings and soluble deposits. x208.

Fig. 32. Individual primary bast-fibers of *Berberis neubertii*, showing longitudinal thickenings, soluble deposits, and elongated diagonal pits, in addition to round pits. x208.

Fig. 33. Individual primary bast-fibers of *Berberis vulgaris*, showing elongated diagonal pits and round pits. x208.

