

COMPARATIVE ANATOMY WITHIN  
THE GENUS HYDRANGEA

by

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## INTRODUCTION

Rehder ('27) describes the members of the Saxifragaceae as herbs, shrubs, or small trees. The leaves, he states, are alternate or opposite and usually without stipules. The flowers, which are five merous, regular, and either hypogynous or perigynous, are either axillary or in terminal corymbs and occasionally in panicles. The fruit is either a several seeded capsule or berry. The family is composed of about 75 genera with 700 species widely distributed in both hemispheres.

The genus *Hydrangea* represents 65 species of deciduous upright shrubs, excepting *H. petiolaris* which climbs by aerial roots. The leaves are opposite as a rule but quite often are whorled in *H. paniculata*; *H. quercifolia* is the only member of the genus having lobed leaves which are also the largest found in the genus.

The species of *Hydrangea* are natives of North and South America and east Asia south to Java. The following species are native to North America; *arborescens*, New York to Iowa and south to Florida and Louisiana; *cinerea*, North Carolina and Tennessee

to Georgia and Alabama; *quercifolia*, Georgia and Florida to Mississippi; and *radiata* in North and South Carolina. From North China we have *Bretschneideri*; West China, *xanthoneura setchuenensis*; and *paniculata* and *peltiolaris* from Japan and China.

These ornamental shrubs are grown chiefly for their showy flowers.

## LITERATURE

The work that has been published on the genus *Hydrangea* shows that very little work has been done so far; however, numerous references are made relative to the value of certain species of *Hydrangea* in landscaping and gardening. Of the various species mentioned, *H. quercifolia* or the "Oak-leaved *Hydrangea*" as it is commonly called, perhaps receives most attention in popular literature. This species is not only prominent for its large panicles of flowers, Sargent says, (1890) but also for its beautiful habit of growth; in the south, which is the native habitat for this species, *quercifolia* often attains a height of fifteen feet. Almost as attractive as the flowers or the plant growth are the large lobed leaves, which assume a beautiful red color in the fall.

In *Silva of North America* reference is also made as to the great value of *H. petiolaris* as a climbing shrub. The flowers are not as attractive as some of those of other species of the group, but the plant is excellent to cover old walls, stones, etc.

Rehder, ('97) has published a detailed account of the external features of the members of this genus, and which has been very helpful in describing the leaves of the various species. In his work he also gives the distribution and the original habitat of the various species.

Solereder, ((08) has collected the published literature on the Saxifragaceae, and in it refers quite often to the genus Hydrangea. Since Solereder used Holle's work, I will give a brief resume of the work published by Holle in ('97). *Beiträge zur Anatomie der Saxifragaceen und deren systematischen Berwerthung; Botanischer Centralblatt.*

1. Simple, single-celled hairs encrusted with calcium carbonate.
2. Accessory cells of the stomata variable
3. Raphide bundles standing mostly vertically in the midst of the mesophyll.
4. Sclerenchyma ring absent.
5. The cortical parenchyma cells next the cork ring have quite large cavities.
6. The cork ring is produced by the innermost layer of cortical parenchyma.
7. The outermost layers of the cortex are relatively narrow and collenchymatous.

8. The tracheal tubes have scalariform perforations.
9. The prosenchyma (in the xylem) has bordered pits.
10. The vascular bundles (in the leaves) usually connect with both epidermises with poorly developed strengthening tissue.

Engler and Prantl in Die Naturlichen Pflanzenfamilien. III Teil, 2 Abteilung distinguish the American and the Asiatic forms by means of the ovary and the seeds. The Asiatic forms, they say, have half superior ovaries and round or broadly-elliptic, unstriated seeds, while the American forms have inferior ovaries with elliptic, longitudinally striated seeds.

## METHODS

The material which I used in my study was collected in the Arnold Arboretum by Professor Stevens in August 1928. The species were wrapped separately in cheese cloth and preserved in a 4% formalin solution.

In the spring before I began my study in September 1929, some of the material I have used was taken from the formalin and sealed in shells containing 70% alcohol. From this material I selected all the petioles, leaf blades, and the greater part of the stems used in this study, excepting the material used for tests which was cut directly from the formalin, and placed it in equal parts of 80% alcohol and glycerin. A similar set of material I put through Jeffry's vulcanizing process, ( Bot. Gaz. May 1928), but this I found unsatisfactory for my material, as the vulcanizing seemed to disintegrate the bark so that an entire section was never gotten.

For sectioning I enclosed all of my material in hard paraffin. I used both a Spencer

sliding microtome and the Thompson-Jeffry sliding microtome manufactured by the Bausch and Lomb Optical Co. I seemed to get better results with the latter microtome, especially <sup>when</sup> cutting the older and harder sections. The stem sections were cut at ten to twelve microns; the petioles, midribs and margins were cut at eight to ten microns. In all cases the petiole sections were taken midway between the base of the leaf blade and point of attachment; the midrib sections were taken midway between the leaf tip and base of the blade.

To cut the sections I used either a Valet or Gillette safety razor blade. The Spencer microtome was equipped with a special holder for using the safety razor blades. This holder proved quite a convenience in removing and sharpening the blades, which is essential for thin sections. The blades I used on the Thompson-Jeffrey microtome were fastened to the lower side of an ordinary microtome knife with hard paraffin, so that the bevel of the blade extended just beyond the edge of the knife.

The leaves which I used for drawing venations were bleached with ordinary bleaching

powder. After bleaching and washing in water, they were cleared with a saturated solution of chloral hydrate.

The sections were cleared and mounted in sandarac according to the following schedule. However, in many cases the schedule had to be altered according to the species, as some required longer bleaching than the others.

1. Cut sections and place in 70% alcohol.
2. Wash in water to remove alcohol.
3. Place sections on slide and add bleaching solution. (Note, the bleaching powder solution is unstable, so should be made up fresh each day.) The sections at this stage should be watched under the microscope to determine how long they should be bleached. If left too long, the cortex is very likely to be broken down.
4. Wash off bleaching solution with water.
5. 20% hydrochloric acid 3-4 minutes.
6. Wash in water 4-5 minutes.
7. Clear with a saturated solution of chloral hydrate.

8. Wash in water to remove chloral hydrate.
9. 40% alcohol 3-4 minutes.
10. 70% alcohol 3-4 minutes.
11. 95% alcohol 3-4 minutes.
12. Mount in sandarac.

To make macerations for study of individual cells, I used Schlutze's method. I found it better to macerate a quarter section of a stem rather than mere longitudinal sections.

The vénation, leaf-margin, and epidermis drawings were made by means of a right angle, arc-light, micropojection apparatus.

The photomicrographs used in this thesis are positive prints made from plates which were obtained by projecting the image on Cramer Dry Plates by means of a microscope. The time of the exposure varied, as two different lights were used, from 6 seconds when using a clock-fed 5 ampere carbon-arc lamp, to 20 seconds when using a 150 watt Mazda bulb. More contrast and better plates were obtained in all cases when the carbon-arc light was used.

The ink drawings were mounted on card board 22 by 28 inches and photographed by using

a large dry plate camera with the diaphram set at 32 for the venation drawings and at 64 for the epidermis and cross section of leaves. The time of the exposure was 6 seconds when the diaphram was set at 32 and 9 seconds when the diaphram was set at 64.

For the prints, I used copying paper and made an exposure of 45 seconds for the plates which were exposed 6 seconds and an exposure of one minute when the plates had been exposed 9 seconds. The light used in printing was a 50 watt frosted Mazda bulb held about fifteen inches from the paper.

## STEMS

*H. arborescens*, varieties *urticifolia* and  
*grandiflora*.

### Primary Tissues.

#### Epidermis.

The epidermises of this species and two varieties are very similar, (Figs. 16 and 18). As seen in surface view, the cells are rectangular in each case; the cell cavities of the variety *urticifolia* are slightly larger than those of the species *arborescens* and variety *grandiflora*. The vertical diameter of an epidermal cell, which in most cases is the greater, measures .06 mm.; while the tangential diameter is about .035 mm. and the radial diameter about .018 mm.

Trichomes of the simple clothing-hair type, which characteristically point upwards, are found on the younger portions of the stems, but the stem soon becomes glabrate. The trichomes of the species and its two varieties are similar and about .16 mm. in length. As is characteristic of the genus, the trichomes are heavily encrusted with calcium carbonate.

Tannin bodies are found in the epidermis of the species and two varieties; and an especially large amount of tannin occurs in the epidermal cells of variety *urticifolia*.

A thin cuticle measuring .003 mm. in thickness is found on the epidermis of the younger stems. No cutinization is present.

#### Primary Cortex.

The primary cortex has about the same thickness in the species and two varieties; in stems having a diameter of 5 mm. the primary cortices measure about .2 mm. in thickness in each case. The greater part of the cortex is taken up by the 6-7 cell layers of collenchyma.

The cortices of this group are almost identical; and are different from those of the other species studied, one outstanding difference being the shape of the cells of the collenchyma. In the species studied heretofore, the cells of the collenchyma in cross section were ellipsoidal in shape and have the tangential walls thickened; the collenchyma cells of this group are rectangular

in cross section and have radial and tangential walls of about the same thickness. As seen in longitudinal sections, the cells of the collenchyma are rectangular in shape, have vertical diameters of .07 mm. and radial diameters of .025 mm. Since the radial walls are about as thick as the tangential walls, the collenchyma is not crushed as early as we find it in the other species.

The cortical parenchyma consisting of 3-4 layers of thin-walled cells contains a small amount of starch and a few crystal sacs filled with raphide crystals of calcium oxalate. The crystal sacs are prominent because of their relatively great size, becoming .055 mm. wide and about .08 mm. in vertical length.

#### Primary Xylem.

The primary xylem of species *arborescens* and varieties *urticifolia* and *grandiflora* consists of 20-22 protoxylem points with the metaxylem exterior and filling in between and thus completing the vascular cylinder.

The protoxylem points, each consisting of 6-7 radial rows of tracheal tubes, are subtended

by a lignified medullary sheath 2-3 cell layers wide. Between these radial rows of primorodial tracheal tubes is quite a large amount of unlignified, thin-walled xylem parenchyma in which stored starch is found.

The metaxylem completing the vascular cylinder is very limited in radial extent, there being one to two layers of tracheal tubes and a very few scattered tracheids. Between the tracheal tubes is a small amount of xylem parenchyma containing a little stored starch.

In cross section the annular tubes measure .025 mm., and the slightly larger metaxylem tubes measure .035 mm. in cross section. The length of an annular element is about .12 mm., while an element of a metaxylem tracheal tube is approximately .16 mm. long.

#### Primary Phloem.

This will be discussed with the secondary phloem.

#### Pith.

The unlignified pith in this species and

its varieties is a quite outstanding feature since lignification of the pith is a common character of the genus.

As seen in longitudinal sections, the majority of the pith cells are hexagonal. The radial diameter measuring .19 mm. is by far the greater, the vertical diameter being about .05 mm.

The pith is relatively large in the species and two varieties, measuring about 5 mm. in cross section in a stem having a diameter of 7 mm.

Crystal sacs containing raphide crystals of calcium oxalate are commonly found in the pith of the younger stems. No reserve foods are found in the pith other than the starch commonly found in the medullary sheath.

#### Secondary Tissues.

##### Periderm.

As in the majority of the species, the cork cambium is formed in the outermost part of the cortical parenchyma. The periderm measures about .17 mm. in species *arborescens* and variety *urticifolia* while that formed in variety *grandiflora*

measures .23 mm. ; in all three cases the stem sections measured about 5 mm. in cross section. The cork cells, which have undulated tangential walls, have radial diameters of .02 mm., tangential diameters of .03 mm., and vertical diameters of .04 mm.

The collenchymatous phelloderm varies in thickness from 3-5 cell layers. It is interesting to note that in variety *urticifolia*, the phelloderm formed is broader in cross section than the cork, the phelloderm measuring about .09 mm. and the cork about .07 mm.

An abundance of starch and protein is stored in the phelloderm.

#### Phloem.

In cross section, the phloem, both primary and secondary, measures approximately .12 mm. radially. Quite an outstanding feature of this group is the unusual amount of starch stored in the parenchyma of the outer phloem region and almost as prominent as the stored starch is the protein found in the phloem tissues.

The few sieve tubes are rather large,

measuring .03 mm. in cross section; and while sieve tube elements have vertical diameters of .07 mm. The companion cells are made evident by the quantity of protein they contain. In cross section they are .02 mm. by .01 mm., and vertically they extend approximately the length of a sieve tube element.

#### Secondary Xylem.

Perhaps the most outstanding feature of the secondary xylem in this group is the great number of tracheids which are in definite radial rows. In these radial rows of tracheids is an occasional tracheal tube and on either side of the rows are the xylem rays. Scattered wood fibers are sometimes found along the sides of the tracheids. It is interesting to note that when wood fibers are found, the tracheids adjoining them are smaller than usual, suggesting that perhaps the tracheid and wood fiber have come from the same cambial initial.

Secondary tracheal tubes measure approximately .02 mm. in cross section, whereas

tubes of the metaxylem measures as much as .035 mm. across. However, the vertical diameter of a secondary tracheal tube element measures as much as .35 mm., which is more than twice the vertical diameter of a primary tracheal element.

In cross section an average-sized tracheid measures .02 mm. tangentially and .013 mm. radially and its length is about .6 mm. Wood fibers measure about .01 mm. in cross section, with cavities half this broad. The length of a wood fiber is approximately .9 mm.

An abundance of xylem parenchyma, the cells of which measure .02 mm. in cross section and have vertical diameters of .07 mm., contains a large amount of starch.

Both uniseriate and multiseriate rays occur in this group. The multiseriate rays, 3-4 cells wide, are found adjoining the protoxylem points and extend to the outer edge of the phloem. The uniseriate rays as stated above, are found on either side of the radial rows of tracheids; these, too, extend to the outer edge of the phloem.

An average sized cell of the ray, (those

nearer the lower and upper extremities have greater vertical diameters) measures .019 mm. in cross section and .06 mm. vertically.

As in the xylem parenchyma, much starch is found stored in the rays.

*Hydrangea Bretschneideri* and varieties *lancifolia*  
and *glabrescens*.

Primary Tissues.

Epidermis.

The epidermal cells of the species and two varieties are very much alike (Figs. 20- 22). As seen in surface view the cells are so very irregular that it is difficult to distinguish the tangential from the longitudinal diameters. The longer diameter of an average-sized cell is .04 mm. and the shorter diameter is .02 mm.

The presence of tannin in the epidermal cells is a constant feature in the species and the two varieties.

The trichomes found on the young stems are very interesting; there being trichomes of the simple cylindrical clothing-hair type and also longer ligulate ones in great abundance. We would expect to find fewer trichomes on variety *glabrescens*; however, from the material used in my study I could not note an appreciable difference in size or numbers.

As in the species *paniculata*, the trichomes

of the simple-clothing-hair type are heavily encrusted with calcium carbonate; however, the ligulate trichomes show very little of such encrustation, although we do find an occasional projection of the cuticle from the trichome wall.

The simple clothing-hair type of trichomes measure approximately .35 mm. in length, approximating those of paniculata; the ligulate trichomes are much longer, extending as much as 2 mm.

#### Primary Cortex.

Rehder describes *H. Bretschneideri* as having "chestnut-brown bark peeling off in thin flakes". In the youngest material which I studied, I found this distinctive brown color; however, I find the dark brown color due to the dead epidermis and collenchyma tissues. The cortex of a one-year old stem measuring 2 mm. in cross section has a thickness of .1 mm.; of this cortex the stretched, dead collenchyma occupies about .06 mm. The cortical parenchyma, which contains a few crystal sacs, measures about .04 mm. in thickness.

Because of the early formation of

internal cork, the cortical tissues soon die, and become crushed, (Figs. 115-117), making it impossible to give the dimensions of individual cells.

#### Primary Xylem.

The primary xylem is about the same in the species and the two varieties, there being from 16-20 protoxylem points at the second internode of the current year's growth.

The tracheal tubes of the protoxylem in the species and two varieties are in definite radial rows; there being usually six tubes in each row. Between the radial rows of tracheal tubes is a large amount of unlignified wood parenchyma containing much starch.

Around each protoxylem point is a partially lignified bundle sheath, slightly thicker than the sheath found in varieties of paniculata. In this thick-walled bundle sheath is found large quantities of oil; an especially large amount being found in *H. Bretschneideri* sp.

In cross section the tracheal tubes of the protoxylem are approximately .02 mm., the tangential and the radial diameters being approximately the

same. The vertical diameter of the tracheal elements are approximately .3 mm.

#### Metaxylem.

Very little metaxylem is formed exterior to the protoxylem; however, the protoxylem points are connected by the metaxylem. A few thick-walled fibers are found adjoining the tracheal elements of the metaxylem. The tracheal elements of the metaxylem are very similar to those of the secondary xylem and measure .03 mm. in cross section and have vertical diameters of .09 mm.

#### Pith.

The pith of *Bretschneideri* species and varieties *lancifolia* and *glabrescens* is lignified, but not to such a great extent as in *paniculata* and its varieties.

Variety *glabrescens* has a pith measuring approximately 3 mm. in cross section, but the stem of this variety is 5 mm. in thickness, while the stems of the species and variety *lancifolia* measure 2 mm. in thickness and have piths measuring 1.2 mm. and 1 mm. respectively.

We remember that the pith of *paniculata* and *peticolaris* had numerous crystal sacs containing

raphide crystals of calcium oxalate. There are very few crystal sacs in the pith of *Bretschneideri* and none at all in the two varieties.

The pith cells in *Bretschneideri* and its varieties vary in size, the largest measuring approximately .14 mm. radially, 166 mm. tangentially, and of approximately .06 mm. vertically.

A quite outstanding feature of the species and two varieties is, the large amount of oil stored in the pith, especially in *glabrescens*.

#### Secondary Tissues.

##### Periderm.

One of the most outstanding features of this group is the early formation of a phellogen and the large amount of cork produced. In the species and the two varieties the phellogen is formed by the innermost row of cortical parenchyma. In the table below are give the number of rows of cells in the cork, the thickness of the periderm, stem, etc.

|                        | Thickness<br>of stem | Rows of<br>cork cells | Thickness of<br>phellogen | Thickness of<br>periderm |
|------------------------|----------------------|-----------------------|---------------------------|--------------------------|
| H. Bretsch-<br>neideri | 2 mm.                | 11-12                 | .08 mm.                   | .32 mm.                  |
| var. lanci-<br>folia   | 2 mm.                | 12-13                 | .06 mm.                   | .24 mm.                  |
| var. glab-<br>rescens  | 5 mm.                | 14-15                 | .1 mm.                    | .4 mm.                   |

The cell walls of the parenchymatous phellogen are slightly thickened. Schizogenous intercellular spaces are very common in the phellogen; especially large spaces are found in the variety glabrescens.

A large amount of starch is stored in the phellogen of the species and two varieties, varieties, lancifolia having the least amount of starch but a little more protein than the other two. Very little oil is found in the phellogen of the two varieties but quite a large amount is stored in the phellogen of Bretschneideri.

#### Phloem.

The phloem tissue of this group is approximately the same in the species and the two varieties.

Relatively little phloem is formed in any species of *Hydrangea*, but there are no indications of the phloem being crushed in a two-year's old stem.

The phloem in the species and the two varieties measures from .05 to .07 mm. in thickness. Sieve tubes measure approximately .0275 mm. in cross section, and the vertical diameters of the elements average .06 mm. The companion cells, which are slightly smaller than the sieve tubes in cross section, measure .02 by .01 mm., but may have vertical diameters of .06 to .08 mm.

In the phloem of *Bretschneideri* a great amount of oil is stored, but very little oil is found in the phloem of varieties *lancifolia* and *glabrescens*. The amount of protein found in the phloem is about the same in the species and two varieties.

#### Secondary Xylem.

The secondary xylem of variety *glabrescens* shows several marked differences from that of *Bretschneideri* and variety *lancifolia*.

To compare the amount of secondary xylem formed in one growing season, I have measured the thickness of the secondary xylem produced the first year in the species and the two varieties.

The medullary rays found in the group are either uniseriate or biserial; however, those found in *Bretschneideri* species are mostly biserial. The rays vary from 6-12 cells in depth and extend from .3 mm. to .48 mm. vertically, individual cells of the rays are approximately .03-.04 mm. vertically, .03 mm. radially, and .017 - .02 mm. tangentially.

Starch is stored in all the rays of this group; an exceptionally large amount being found in the primary rays of variety *glabrescens*. Oil is found in rays of *Bretschneideri* only.

*Hydrangea cinerea* and variety *sterilis*.

In a study of these two stems I find very little difference in their cellular structure; however, there is a quantitative difference, especially in the amount of collenchyma and secondary xylem formed the first growing season. Because of this great similarity I shall discuss the two stems together, pointing out the differences where found.

Primary Tissues.

Epidermis.

As seen in surface view the epidermal cells are relatively small and very irregular, (Figs 26 and 27). It is impossible to distinguish the tangential from the vertical diameters by their length, as in some cells the vertical diameter is the longer while in others the tangential diameter is the greater. The longer diameter of an average-sized cell is .04 mm. and the shorter about .03 mm. The radial diameters are more constant, being about .02 mm.

Very few scattered trichomes are found on the epidermis of the species and its variety. These found are of the simple clothing-hair type

and measure approximately .24 mm. in length.

A very few scattered cells of the epidermis contain a small amount of tannin.

A cuticle measuring .005 mm. in thickness is found on the epidermis of the species and its variety. No cutinization is present.

#### Primary Cortex.

The primary cortex of the variety *sterilis* is quite interesting because of its collenchyma immediately below the epidermis, with walls at the corners quite unusually thick, some as much as .01 mm. Intercellular spaces in the collenchyma are very small, and only a few are found in the variety *sterilis*.

The cortical parenchyma of this species and variety varies little from that of the other species; large crystal sacs measuring .06 mm. in cross section and having a vertical diameter of .08 mm. to .1 mm. are quite common.

In a cross section of a stem measuring 2.7 mm. in thickness the primary cortex of variety *sterilis* measures .18 mm.; of this, the

four cell layers of collenchyma occupy about .13 mm. The cortex of *cineraria* measures approximately .14 mm. in thickness, and of this the collenchyma occupies .07 mm. In the latter case, the stem section measures 2.1 mm. in thickness.

#### Primary Xylem.

The protoxylem which indents the pith at twenty points, varies little from that already discussed for the other species; the tracheal tubes are in definite radial rows of 6-7 tubes and between the rows occurs unlignified wood parenchyma containing more protein than starch and a very small quantity of oil.

In cross section the protoxylem tubes measure approximately .027 mm., while the vertical diameter of a tracheal element measures about .12 mm.

A lignified medullary sheath, the cells of which have vertical diameters of .07 mm. and cross diameters of .025 mm., subtends the protoxylem points.

#### Metaxylem.

The protoxylem points, which are quite far apart, are connected by the metaxylem between them. Very little metaxylem is differentiated

exterior to the points. The tracheal tubes, which compose the bulk of metaxylem, measure .03 mm. in cross section and the elements have vertical diameters of .13 mm. The xylem parenchyma of the primary xylem contains quite a large amount of starch.

Pith.

The pith of *cinerea* and its variety *sterilis* is unusual in not being lignified, excepting the medullary sheath, and the cells are extraordinarily large, measuring as much as .15 mm. in cross section and .12-.14 mm. vertically.

Crystal sacs in the pith of this species and variety are quite rare and very little starch and no oil are stored in the pith.

Periderm.

<sup>b</sup>  
The cork cambium is formed in the outermost part of the cortical parenchyma. Very little cork is formed the first growing season; there being only four layers of cork cells in *cinerea* and two layers in variety *sterilis*. The phelloderm is very thin, there being just a few thin-walled parenchyma cells formed below the cork cambium.

The cork cells have tangential diameters

of approximately .04 mm. and radial diameters of approximately .024 mm. In cross section, the cells of the phelloderm measure approximately .04 mm. and both tangentially and radially .02 mm.

Very often starch is stored in the phelloderm, but stored food is entirely lacking in the phelloderm of this species and its variety.

#### Phloem.

There is much more phloem in this species than in any other studied in this research. The phloem is a one-year-old stem measuring 1.2 mm. in cross section measures .12 mm. in radial thickness.

The primary rays are continued by pericyclic cells which arch over the phloem; in the ray cells between the phloem groups a great amount of starch is stored.

An especially large amount of phloem parenchyma containing much starch is also found in this species and its variety, this making up the greater part of the phloem tissues.

In cross section, the sieve tubes measure approximately .03 mm. in diameter and the unusually diminutive companion cells about .15 mm.; the vertical diameters of the sieve tubes and companion cells are approximately .08 mm.

### Secondary Xylem.

The secondary xylem in *cinerea* and the variety *sterilis* is practically the same in structure; however, in *cinerea* measuring approximately .48 mm. and in variety *sterilis* about .3 mm. in radial thickness; but the stem of *cinerea* is slightly the larger, being 2.7 mm. in thickness and the stem of the variety 2.1 mm.

Another marked difference between wood of the species and the variety is the much greater amount of starch stored in the rays of variety *sterilis*.

The secondary xylem as a whole is characterized by numerous tracheids and fewer tracheal tubes. Together, the tracheal tubes and the tracheids make definite radial rows.

Xylem parenchyma is found abundantly in the variety *sterilis*, its individual cells measuring approximately .02 mm. in cross section and .08 mm. longitudinally.

Tracheal tube elements measure .03 mm. in cross section and have vertical diameters of approximately .06 mm. Fiber tracheids measure about .02 mm. in cross diameter and .96 mm. longitudinally, the cavity being about .0075 mm.

Both uniseriate and multiseriate rays are found in this species and variety. The multiseriate rays usually three cells wide, are found between the protoxylem points. The rays may be as much as 16 mm. in vertical depth, or they extended the full length of the section, but I was not able to tell the exact vertical depth. Individual ray cells have vertical diameters of approximately .06 mm. while the radial diameters may be from .04 mm. to .05 mm. and the tangential diameters from .02 to .03 mm.

As was stated above, much starch is stored in the rays of variety sterilis.

*H. paniculata*

Primary Tissues,

Epidermis.

The stem epidermis of this species is covered with single celled trichomes of the simple clothing-hair type averaging .32 mm. in length. The walls of the trichomes are quite rough due to encrustation with calcium carbonate. Within a short time the trichomes wither due to the early formation of cork.

The epidermal cells, hexagonal in surface view, are quite small, the radial diameter being only .02 mm.; tangentially, the cells measure .03 mm. and .04 mm. longitudinally. A few cells in the younger stems contain tannin bodies.

Primary Cortex.

The primary cortex of *H. paniculata* is quite limited due to the presence of a starch sheath. Immediately below the epidermis are 3-4 cell layers of collenchyma; the outermost row of which contains starch grains, no doubt associated with chloroplastids.

An average sized cell of the collenchyma measures .04 mm. radially and tangentially and .07 mm. longitudinally.

Between the collenchyma and starch sheath are from 2-3 cell layers of large parenchymatous cells, the largest of which measures .06 mm. across. Numerous raphide crystals of calcium oxalate are found in the cortical parenchyma.

The starch sheath consists of parenchymatous cells which are slightly elongated tangentially. An averaged sized cell of the starch sheath measures .05 mm. tangentially and .03 mm. radially. Within the starch sheath are numerous, large starch grains, the largest of which measures approximately .01 mm. in diameter.

#### Pericycle.

The pericycle measures approximately .12mm. in cross section. Immediately below the starch sheath are three layers of parenchymatous cells which have their walls slightly thickened. Tangentially, these cells measure approximately .03 mm., radially, .02 mm. Beneath these three layers of cells which

have their walls slightly thickened are 2-3 layers of larger thin-walled cells which contain numerous crystals of calcium oxalate.

#### Primary Cortex.

At the second internode of the current year's growth in elongation, the protoxylem indents the pith at twenty-three points. Radially, the primary xylem measures .16 mm. The tracheal elements are arranged in radial rows, each row having 4-5 water tubes. In cross section, the protoxylem tubes measure approximately .03 mm. and longitudinally the elements measure about .01 mm.

A small amount of starch is found in the bundle sheath subtending the protoxylem points.

#### Primary Phloem.

For a discussion of the primary phloem see the discussion of the phloem below in secondary tissues.

#### Pith.

The pith of this species varies little from the pith of the other species studied. However, quite a large amount of oil as evidenced by the

Sudan III test is found in the pith of this species.

#### Secondary Tissues.

##### Periderm.

It is interesting to note that the phellogen originates in the thick-walled, parenchymatous cells immediately below the starch sheath. Individual cork cells measure approximately .02 mm. radially, .04 mm. tangentially, and .03 mm. vertically. The radial walls of the cork cells are wavy due to the tangential pull.

In a one-year-old stem the phelloderm measures approximately .16 mm., the stem having a diameter of approximately 3.4 mm. The cells of the phelloderm are also elongated tangentially, their tangential diameter being .05 mm., while their radial diameters are approximately .02 mm.

Considering the primary and secondary phloem together it may be said that in the genus as a whole very little phloem is formed; the primary and secondary phloem vary little, and in the oldest stems, the primary phloem shows no signs of being crushed.

In a stem measuring 3 mm. in cross section the phloem measures .16 mm. radially. The

sieve tube elements measure approximately .02 mm. in cross section and about .08 mm. longitudinally. The phloem parenchyma and companion cells are about the same size as the sieve tubes.

The phloem of this species seems to be a good storage organ as an abundance of starch, oil and protein are found there.

#### Secondary Xylem.

The tracheal tubes are scattered throughout the secondary xylem. At the end of the first year's growth, a cylinder of secondary xylem measuring .32 mm. in cross section has been laid down.

The radial and tangential diameters of sieve tubes measure approximately .03 mm., and the vertical extent of an element is about .3 mm. As in the other species of this genus, the side walls are definitely marked with scalariform pits.

*H. paniculata* has an exceedingly great number of wood fibers. Near the close of the summer's growth a very large number are arranged in quite definite radial rows. In cross section the fibers measure approximately .01 mm.; the

cavity is about one half this diameter.

Longitudinally, an average sized fiber extends for a distance of 1 mm.

In longitudinal sections, the tracheids are seen to be arranged in quite definite radial rows. These radially arranged rows might easily be mistaken for pith rays; however, the radial rows extend just to the outer edge of the xylem, and the vertical diameter is much greater than the radial. In cross section, the tracheids measure approximately .02 mm.; the vertical length is approximately .08 mm.

The medullary rays are quite similar to those of variety *praecox*. They are uniseriate and extend three or four cells vertically. The individual cells measure approximately .04 mm. radially, .04 mm. longitudinally, and .02 mm. tangentially. The walls have numerous simple pits.

Much starch is found stored in the secondary rays.

*H. paniculata grandiflora.*

Primary Tissues.

Epidermis.

Scattered trichomes of the simple-clothing-hair type are found on the epidermis of this variety. These trichomes measuring .48 mm. in length are longer than those found on the hybrid form, whose trichomes average .32 mm. in length. The trichomes of this variety have thicker walls (.01 mm.) than those of *paniculata praecox*. In *paniculata* we remember that the cavity of the trichomes extended to the apex while in this variety the cavity is almost occluded by the thicker walls. The trichomes are heavily encrusted with calcium carbonate.

As seen in surface view the epidermal cells are very irregular, making it difficult to compare the longitudinal and the tangential diameters. The longer diameter of the typical cell is approximately .06 mm. and the shorter about .03 mm.; radially the cells measure about .035 mm.

A considerable amount of tannin is found

in the epidermal cells of this variety, but not so much as is found in the epidermal cells of *H. paniculata praecox*.

#### Primary Cortex.

The primary cortex which measures radially about .25 mm. in a stem having a diameter of 5 mm. is limited towards the interior by a definite starch sheath, as in the case of *paniculata* and variety *praecox*.

Immediately below the epidermis are four to five rows of collenchyma, the cell walls of which are sharply thickened at the angles. The outermost cell layer of collenchyma contains numerous starch grains, which are no doubt associated with chloroplastids. Between the collenchyma and starch sheath are two to three cell layers of cortical parenchyma in which are found numerous crystal sacs.

The starch sheath is very evident when the sections are stained with a solution of potassium iodide containing iodine. Its cells measure approximately .07 mm. in tangential diameter, while the radial diameter is only .03 mm.

The pericycyle, measuring approximately .08 mm. radially, is composed of four to five layers of parenchyma cells with slightly thickened walls. This zone is characterized by numerous, large

intercellular spaces. The cells average .02 mm. radially and .04 mm. tangentially.

#### Primary Xylem.

The protoxylem points are very close together, there being 26 points at the second internode of the current year's growth. Between the definite radial rows of ten to twelve protoxylem elements is a large amount of unlignified wood parenchyma containing much oil and very little starch.

Radially the primary xylem cylinder measures approximately .24 mm. Individual tracheal tubes of this primary xylem measure .03 mm. in cross section and 1.2 mm. longitudinally.

A partially lignified medullary sheath subtends the protoxylem points.

The major part of the metaxylem is found between the protoxylem points. Thick walled tracheids are common in the metaxylem, but fibers are lacking in the primary xylem. The tracheal tubes, which measure .04 mm. in cross section, are slightly larger than the elements of the protoxylem, which measured .03 mm. in cross section.

#### Pith.

The pith of this variety is interesting in that only the central portion is lignified, and

in this region simple pits are most numerous.

More oil is found in the pith of this variety than in the pith of paniculata of variety praecox; however, this variety contains much less starch than paniculata or variety praecox.

#### Secondary Tissues.

##### Periderm.

As in variety praecox, the phellogen is produced by the collenchyma. In a stem having a diameter of 3.6 mm. the periderm measures approximately .24 mm. in thickness, and this is composed of three to four layers of phelloderm about .14 mm. thick radially. Individual cells of the cork have radial diameters approximating .025 mm., while the tangential diameters average .05 mm. Cork cells of this variety have vertical diameters of approximately .07 mm.

The phelloderm is characterized by numerous large intercellular spaces. The tangential diameter of an average sized cell of the phelloderm is nearly twice its radial diameter, in the one case .05 mm. and .025 mm. in the other.

Very little reserve food is found in the tissues of the periderm.

Phloem.

Anatomically, the phloem of this variety varies little from the phloem of *praecox*; however, we note a greater amount of oil in this variety. The size of the phloem cells of this variety is approximately the same as given for the other two varieties.

Secondary Xylem

The greatest difference in the secondary xylem of this variety and variety *praecox* and *paniculata* is in the number of tracheids, as appears in the following table:

|                                  | Tracheal Tubes per sq. mm. |
|----------------------------------|----------------------------|
| H. <i>paniculata praecox</i>     | 311                        |
| H. <i>paniculata</i>             | 347                        |
| H. <i>paniculata grandiflora</i> | 417                        |

Since there is such a great number of tracheal tubes per sq. mm., there are fewer tracheids. The number of fiber tracheids, however, per sq. mm. is about the same for the species and its two varieties. There are no noticeable differences in the sizes of cells found in secondary xylem of this group.

The rays are practically the same for the varieties, measuring .06 mm. while the rays of *paniculata* average .04 mm.

*H. paniculata praecox.*

Primary Tissues.

Epidermis.

The epidermis of this species is remarkable in that all the cells contain tannin. In surface view the epidermal cells are little more than five times as long as broad, measuring .11 mm. in length and .02 mm. in breadth, (Fig. 29). It is also interesting to note that the end walls are oblique; in fact the angle is so sharp as to make the cells fiberlike. The epidermis is soon superceded by cork due to the early activity of a subepidermal phellogen. There are no trichomes present on the stem of this species.

Primary Cortex.

The primary cortex consists of two cells layers of collenchyma and six of parenchyma. Interspersed through the parenchyma of the cortex are large parenchymatous cells measuring .06 mm. in cross section and containing an abundance of raphide crystals of calcium oxalate. A large amount of starch is stored in the cortical parenchyma of this species. In a stem measuring 3.5 mm. in cross section the primary cortex measures .16 mm.

### Primary Xylem and Phloem.

The primary phloem, which contains an abundance of protein, consists of four or five layers of cells. The sieve tube elements average .02 mm. in cross section and .06 mm. in longitudinal section and the companion cells vary little in size from the sieve tube elements. The numerous rays are connected over the phloem by pericyclic cells appearing like continuations of the rays.

The twelve protoxylem points of the primary xylem cylinder, each consisting of 7 to 8 rows of radially arranged elements, indent the pith. Between these radially arranged rows of primary xylem elements are the xylem parenchyma and the lignified rays which are gorged with starch. Surrounding the protoxylem points are heavily lignified cells of the medullary sheath. These cells of this species are parenchymatous and differ little from the rest of the pith cells other than in having slightly thicker walls. In cross diameter the protoxylem elements measure .03 mm. and longitudinally .2 mm.

The primary xylem throughout the genus is characterized by the great number of tracheal

tubes and large amount of wood parenchyma; it is interesting to note that no tracheids or fibers of any kind are found until after secondary thickening has taken place.

#### Pith

The cells of the lignified pith vary little in size although those in the central portion are slightly larger than those nearer the xylem. It is interesting to note that no starch is stored in the pith of this species; however, a small amount of oil as evidenced by the Sudan III test is found in the pith nearest the xylem. All the pith cells have simple pits. In cross section the cells are approximately .16 mm., in longitudinal sections, .06 mm. In most cases the pith cells are slightly longer radially than tangentially.

#### Secondary Tissues.

##### Periderm.

The periderm consists of eleven layers of cells, seven of which are cork cells, Holle ('93) states that the phellogen originates in the innermost part of the primary cortex; however, in this species I find that the phelloderm is formed in the collenchyma immediatley below the

epidermis. The phellogen consists of 3 to 4 rows of cells adjoining the primary cortex. Tangentially the cork cells are .04 mm.; radially .02 mm., and longitudinally .16 mm.

Phloem;

The secondary phloem varies little from the primary phloem, and there is about three times as much secondary as primary in the one-year-old stem.

Xylem.

In the few months growth, (April to August) quite a large amount of secondary xylem was laid down, the addition being .48 mm. in thickness. The tracheal tubes average .04 mm. in cross section and the longest elements of the tubes are approximately .08 mm. in length. The walls of the tracheal tubes have scalariform pitting while the end walls have scalariform perforations. These two characteristics occur throughout the genus. Fiber-tracheids .03 mm. in diameter and .36 mm. long and with an irregular cavity about .015mm. are very common.

In the secondary xylem I find a great amount of xylem parenchyma resembling tracheids except for the lack of bordered pits. The cells of this tissue are approximately .03 mm. in cross section and .12 mm. longitudinally.

The rays are uniseriate and vary in longitudinal extent from three to twenty-eight cells. Longitudinally the cells average approximately .06 mm. and radially .03 mm. A great amount of starch is stored in the rays.

*Hydrangea petiolaris.*

Primary Tissues.

Epidermis.

The stem epidermis is decidedly roughened due to peglike projections of the cuticle, (Fig 33). The cells are not as large as those of *H. paniculata*, having an average vertical diameter of only .04 mm. and tangential diameter of .02 mm. The epidermal cells of the two species are also quite different in shape;; Those of paniculata being somewhat fiberlike, while those of petiolaris are more rectangular.

Very little if any tannin is found in the epidermal cells of *H. petiolaris*, while a great abundance occurs in *H. paniculata*.

No trichomes are found on the stem of this species.

Primary Cortex.

In this species, at the second internode of the current year's growth in elongation, a cork cambium has been formed by the innermost part of the collenchyma. Below the phelloderm there are four rows of parenchymatous cells which belong to

the primary cortex and among these are large crystal sacs, the largest of which measure approximately .08 mm. in diameter. Due to the early formation of cork, the collenchyma is soon crushed, making it impossible to give individual cell dimensions.

The primary cortex is heavily loaded with starch.

#### Primary Xylem and Phloem.

Seen in cross section the primary phloem extends radially approximately .04 mm., and the sieve tube elements about .015 mm. radially, .03 mm. tangentially, and longitudinally .12 mm. The companion cells are slightly smaller than the sieve tube elements.

An abundance of starch and an ordinary amount of protein are found in the phloem.

The protoxylem is distributed in fourteen points which indent the pith. Within each point there are from ten to thirteen rows of radially arranged protoxylem tubes. In cross section these measure approximately .025 mm. radially and tangentially and their elements are about .18 mm. long.

Separating the innermost protoxylem elements from the lignified medullary sheath are from two to four layers of parenchyma cells well stored with starch.

#### Pith.

The pith is a continuous cylinder which extends radially between the protoxylem points, and here a small amount of starch is stored. Among the pith cells are many crystal sacs containing numerous raphidæ crystals. The pith cells which are hexagonal in cross section have simple pits. In cross section the larger pith cells measure approximately .04 mm. and the smaller approximately .02 mm. in diameter; the vertical diameter, which is the greater, measures approximately .06 mm.

#### Secondary Tissues.

##### Periderm.

The phellogen of *H. petiolaris* is formed in the innermost layer of cortical collenchyma. In the one-year-old (Fig. 138) stem, seven cell layers of cork and four cell layers of phelloderm have been laid down. This phelloderm contains an abundance of starch.

The periderm in a stem having a radius

of 3 mm. measures approximately .24 mm. An average sized cork cell measures .04 mm. tangentially, and .02 mm. radially and approximately .012 mm. vertically.

#### Phloem.

As in *H. paniculata* *praecox*, very little secondary phloem is formed in proportion to the amount of secondary xylem. The secondary phloem varies little from the primary phloem; however, there seems to be more starch stored in the phloem tissues after secondary thickening has taken place.

#### Secondary Xylem.

Secondary thickening takes place relatively very rapidly in *H. petiolaris*. Although very little secondary phloem has been formed in the one-year-old stem, the secondary xylem measures approximately .72 mm. radially.

The secondary rays are strikingly different from the rays of *H. paniculata*. *H. paniculata* has uniseriate rays, the largest of which are twenty eight cells in longitudinal depth,

while *H. petiolaris* has multiseriate rays which average four cells tangentially, (.07 mm.) and the longest are 104 cells in depth, (1.92 mm.). The individual ray cells measure approximately .02 mm. vertically and tangentially, and .04 mm. radially.

The already thick walls (.01mm) of the rays become irregularly thickened by the deposition of cellulose in the form of projections, appearing peglike in cross section.

The tracheal tubes are arranged in quite definite radial rows on either side of which is a radial row of wood fibers and tracheids; adjoining these rows are the multiseriate rays and between the tracheal elements, radially, is the xylem parenchyma.

In cross section the xylem parenchyma and tracheids are practically the same size, about .02 mm. radially and tangentially and the cavity is approximately .01 mm. across. Longitudinally the fibers measure 1.44 mm., and the xylem parenchyma cells approximately .08 mm. The radial and tangential diameters of the tracheal tubes are about .03 mm., and their vertical diameter is approximately .13 mm.

*H. quercifolia.*

Primary Tissues.

Epidermis.

Numerous clusters of trichomes, as many as seven ligulate trichomes to a cluster, arising from a multicellular base cover the young stem of *H. quercifolia*. Some of the longer trichomes measure 2 mm. in length, but the average length is about 1 mm., (Fig. 25).

The epidermal cells, which are quite regular as seen from the surface, have vertical diameters of .04 mm. and tangential diameters of .02 mm.; radially, the cells measure .015 mm.

Tannin is found very commonly in the epidermal cells of *H. quercifolia*.

A cuticle measuring .005 mm. in thickness is found covering the stem epidermis of this species.

Primary Cortex.

The primary cortex of a stem having a diameter of 4.8 mm. is about .16 mm. thick; the 5-6 cell layers of collenchyma measure about .12 mm. in thickness.

The cells of the collenchyma contain much tannin, especially those nearer the epidermis. It seems that in all cases tannin is associated either with cells containing chloroplastids or cells containing stored starch.

In the parenchyma of the cortex are scattered radial rows of parenchyma cells filled with starch. These arise in the regions of the collenchyma containing starch and adjoin the outer limits of the rays.

#### Primary Xylem.

The protoxylem is arranged in twenty-two points which slightly indent the pith. The metaxylem, which is laid down between the protoxylem points, completes the vascular cylinder and is composed of scalariform pitted tracheal elements, tracheids, and xylem parenchyma. The tracheal elements measure .03 mm. in cross section and have vertical diameters of .13 mm. The tracheids resemble the cells of the xylem parenchyma, have cross diameters of .02 mm. and vertical diameters of .09 mm. The lignified xylem parenchyma has numerous simple pits.

Subtending the protoxylem points is a thick, heavily lignified, prosenchymatous bundle sheath which shows slight lignification. It contains much starch and a small amount of tannin. The protoxylem is composed of definite radial rows of 4-6 elements each and thin-walled parenchyma cells are found between the annular vessels.

Quite a large amount of starch and an ordinary amount of protein are found in the parenchyma of the metaxylem.

#### Pith.

The pith of *H. quercifolia* is characterized by the following statements:

1. It is different from that of the other species I have studied in having no lignification.
2. Many of the cells throughout the pith contain tannin.
3. Extremely large cells are found, some of the largest measuring .18 mm. in cross section.

#### Secondary Tissues.

##### *Periderm.*

The cork cambium is formed in the

outermost part of the cortical parenchyma and by midsummer of the second year only two rows of cork cells have been formed; likewise, a very narrow layer of phellogen consisting of thin-walled cells is formed.

In a stem measuring 4.8 mm. in cross section, the periderm is approximately .08 mm. thick. The individual cells of the phellogen have tangential diameters of .03 mm. and radial diameters of .015 mm. The cork cells, which are quite regular in shape, have tangential diameters of .045 mm. and radial diameters of .02 mm.

We remember that the species *Bretschneideri* and its varieties were characterized by the early formation and great amount of cork formed in a one-year-old stem; we might characterize *quercifolia* by the small amount and late formation of its cork.

#### Phloem.

A very striking feature in the anatomy of this stem is the very few scattered bast fibers in the outer part of the phloem, which in fact, is not characteristic of the genus. In cross section

the fibers measure approximately .015 mm. and their cavities are of unusual size, measuring .008 mm. across. Because of their scarcity I did not see any of the bast fibers in longitudinal sections to determine their length.

The phloem is an older stem having a diameter of 7 mm. measures approximately .12 mm. in thickness. Phloem parenchyma predominates in this species and is much used for the storage of starch.

The radial and tangential diameters of a sieve tube elements is about .08 mm. The companion cells are usually a little smaller in cross section but their vertical diameters vary with the length of the sieve tube elements.

#### Secondary Xylem.

Quite outstanding features of the secondary xylem are: first, the relative scarcity of tracheal tubes and abundance of tracheids and fiber tracheids; second, the relatively large medullar rays.

In the species *Bretschneideri* we

remember there were 300 tracheal tubes per sq. mm. as an average number; in *quercifolia* the number is approximately 200.

Quite outstanding are the large multi-seriate rays. Tangential sections measuring 8 mm. in length contained only a fraction of any ray.

Tangential sections show the larger rays to be from 4-5 cells wide; however, as in most of the species of *Hydrangea*, there are both uniseriate and multiseriate rays.

The sizes of the cells found in the secondary xylem are practically the same as for other species here reported. The tracheal tubes of the scalariform type measure .03 mm. in cross section and .1 mm. vertically. The tracheids measure approximately .0205 mm. in cross section and about 1.1 mm. in length. The fiber tracheids are slightly smaller (.0175), in cross section but measure as much as 1.5 mm. in length.

Wood parenchyma is very common, with cells measuring .02 mm. in cross section and approximately .08 mm. vertically.

*H. radiata.*

Primary Tissues.

Epidermis.

As seen in surface view the epidermal cells are usually six sided. They are unusually small, averaging .035. vertically and tangentially and .027 mm. radially. Rannin is found in the majority of the epidermal cells of this species.

The stem of this species has very few trichomes of the simple clothing-hair type, measuring .07 mm. in length. They arise from a multicellular base consisting of 7 to 8 cells. As in other species of this genus, the trichomes are heavily encrusted with calcium carbonate.

Primary Cortex.

The primary cortex of a stem having a diameter 6 mm. consists of 5 cell layers of collenchyma and 3 to 4 cell layers of parenchyma, together measuring .12 mm. It is the tangential walls of the collenchyma that are thickened; consequently, when secondary thickening takes place, the rows of collenchyma are soon crushed.

Very few crystal sacs are found in the cortical parenchyma. An average sized collenchyma cell has the following dimensions; radial, .04 mm., vertical tangential, .025 mm., vertical, .045 mm. An average sized cell of the cortical parenchyma measures .02 mm. radially, .025 mm. tangentially, and .024 mm. vertically.

#### Primary Xylem.

The eighteen points of the protoxylem slightly indent the pith; the metaxylem which is soon formed between the protoxylem points completes the primary xylem cylinder. Unlignified wood parenchyma between the radial rows of the primary tracheal tubes contains quite a large amount of stored starch.

In cross section the primary tracheal elements, which are slightly larger and more numerous than the secondary trachela btubes, are .035 mm. wide; the vertical diameter of a primary tube element is approximately .14 mm.

#### Pith.

The pith of this species shows no lignification; neither does it contain any stored

food. Very few crystal sacs are found in the pith of this species.

As in *H. quercifolia*, extremely large pith cells are found here, some of the larger measuring .18 mm. in cross section.

#### Secondary Tissues.

##### Periderm.

The cork cambium is formed in the outermost part of the cortical parenchyma. A layer of four rows of cork is formed early the first growing season. Individual cork cells have tangential diameters of approximately .03 mm. and radial diameters of .02 mm. An unusual feature of this species is the collenchymatous natures of the phelloderm.

As in the other species of this genus, quite a large amount of starch is stored in the phelloderm.

##### Phloem.

Very little phloem is formed as a rule in this genus; however, the phloem formed the first growing season until August measures .13 mm.

radially. Sieve tubes are sparse, but a relatively large amount of phloem parenchyma is formed, the outer region of which is filled with starch. In cross section, the sieve tubes measure approximately .015 mm.; the companion cells, in cross section, measure .0075 mm. radially and .015 mm. r tangentially, the same as the sieve tubes. The vertical diameters of sieve tube elements and companion cells are about .08 mm.

#### Secondary Xylem.

The secondary xylem of *H. radiata* is sharply marked from the primary xylem by having scattered tracheal tubes and numerous thick-walled tracheids.

In a cross section of a stem having a diameter of 6 mm., the secondary xylem produced the first growing season measures approximately .35 mm. in thickness. Relatively few tracheal tubes and fiber tracheids and a correspondingly greater number of tracheids are found in this species.

The tracheal tubes, which are scalariform pitted, average .03 mm. in cross section and their elements have vertical diameters of approximately

.52 mm. The numerous tracheids measure .02 mm. in cross section; their cavity is about half the cross diameter or .01 mm. The length of the tracheids averages .08 mm. and the length of the fiber tracheids about 1.12 mm.

Both uniseriate and biseriate rays are found in this species; vertically, the rays extend 1.44 mm. The cells at the upper and lower extremities of the rays have much larger vertical diameters than do the cells in between.

An average-sized ray cell measures .03 mm. radially, .04 mm. vertically, and .02 mm. tangentially.

The rays are sharply marked when the sections are stained with KII because of the great amount of starch stored in them.

An abundance of xylem parenchyma with numerous simple pits is found in this species, and as a rule, is very similar to the ray parenchyma.

*H. xanthoneura setchuenensis.*

Primary Tissues.

Epidermis.

As seen in surface view the epidermal cells are very irregular and also quite small (Fig 34) the longest diameter of an average-sized epidermal cell being approximately .03 mm. and the shortest about .02 mm., since the epidermal cells are so irregular in surface view, no distinction in size can be made between the longitudinal and tangential diameters. The radial diameter of an epidermal cell is approximately .02 mm.

Very few trichomes are found on the youngest portion of the stem; however, those found are quite large, measuring .4 mm. in length and .08 mm. in breadth at the base. The customary encrustation with calcium carbonate is present on the trichomes of this species.

A very thin cuticle, measuring .005 mm. in thickness, is found in the stem where the epidermis is yet intact; cutinization is absent.

### Primary Cortex.

The primary cortex in a cross section of a stem having a diameter of 2.4 mm. measures .24 mm. The five layers of collenchyma having thickened tangential walls, measure .08 mm. across. In the cortical parenchyma are scattered cells containing numerous tannin bodies.

Because here the .01 mm. thickness of the tangential walls of the collenchyma exceeds the .0003 mm. thickness of the radial walls, the primary cortical parenchyma is soon crushed between the resistant collenchyma and the early and abundant cork formation.

### Primary Xylem.

Eighteen protoxylem points slightly indent the pith. Between each point metaxylem is soon formed completing the vascular cylinder. In each point of the protoxylem are from 10 to 12 rows of tracheal elements, between which are only the primary unlignified rays; this is quite an outstanding feature of this variety, as a great amount of xylem parenchyma is found between the radial rows of primary xylem in the other species; there is, however, a small amount of xylem parenchyma around the protoxylem points. A lignified

medullary sheath of one to two cells outlines the pith. In cross section, the primary tracheal tubes measure approximately .03 mm.; tracheal tube elements have vertical diameters of .14 mm. The end walls, excepting near the periphery of the cells, are dissolved out leaving a definite tube.

A few scattered tracheids are found in the metaxylem.

#### Pith.

The pith of this species shows no lignification, a fact which is quite outstanding, as the pith of the majority of the species is characteristically lignified. The pith cells are from 6 to 8-sided and have greater cross diameters than vertical diameters; an average-sized cell measures .11 mm. in cross section and has a vertical diameter of .08 mm. A small amount of oil and no starch is found stored in the pith.

The cells of the medullary sheath are quite different: being lignified, having slightly thicker walls, measuring .02 mm. in cross section and .08 mm. in vertical diameter.

### Primary Phloem.

Since there is no distinction between the elements of the primary and secondary phloem, the primary phloem is discussed with the secondary phloem below.

### Secondary Tissues.

#### Periderm.

A very active cork cambium originates in the outermost part of the cortical parenchyma; the periderm formed the first growing season in a stem having a diameter of 3.5 mm. measuring .26 mm. in radial thickness.

An average-sized cell of the 9 to 10 cell layers of cork has a tangential diameter of .03 mm., a radial diameter of .015 mm. and a vertical diameter of .035 mm. The phelloderm consisting of 8 to 10 rows of tangentially elongated cells is very interesting, because of its collenchymatous nature, and the presence of large crystal sacs and scattered inter-cellular spaces. Quite a large amount of protein

and a small amount of starch are stored in the phelloderm of this species.

#### Phloem.

The phloem, both primary and secondary in a stem 3.5 mm. in diameter measures .1 mm. across radially. The sieve tubes are very sparse, but are exceedingly prominent, measuring .035 mm. in cross section, with elements .1 mm. long.

As seen in cross section the companion cells are rectangular in shape, with the longer cross diameter parallel with the sides of the sieve tube. In longitudinal sections, the vertical diameters of the companion cells are seen to be about the same as those of the sieve tube elements. A great amount of phloem parenchyma containing much protein and a small amount of starch composes the bulk of the phloem tissues.

#### Secondary Xylem.

The secondary xylem is sharply marked from the primary xylem by its fewer tracheal tubes and correspondingly greater frequency of tracheids and fibers, these being absent, or at least very few, in the primary xylem. The tracheal tubes

are so scattered as to make it difficult to determine the extent of one year's growth.

A large amount of xylem parenchyma in quite definite radial rows is found in the secondary xylem and closely associated with the xylem parenchyma are the uniseriate and biserrate rays which contain a great amount of stored starch. Their short vertical extent of 7 to 8 cells is an important anatomical feature for classification.

In cross section the scalariform tracheal tubes measure approximately .03 mm., and the vertical diameter of a tube element is about .08 mm.

The numerous tracheids average .02 mm. in cross section while the cavity is about half the cross diameter and the length of a tracheid is about .11 mm. Wood fibers measuring .013 mm. in cross section and .96 mm. in length are in close association with the tracheal tubes; the small cavity, .007 mm. in cross section, extends the entire length of the wood fiber.

## SUMMARY OF THE STEMS.

In the preceding pages I have discussed the anatomy of the various species and varieties, but have not given much attention to a comparison of the various anatomical features. Some of the features are common to the genus as a whole, while other features are peculiar to a species or a species and its variety. Those features which are common to the genus as a whole are summarized below, passing from the epidermis inward.

### A. Bark.

1. A cuticle averaging .001 mm. in thickness is found on the young stems.
2. The majority of the young stems are covered with trichomes of the simple clothing-hair type which are encrusted with calcium carbonate.
3. A collenchymatous hypoderm 4-5 cell layers thick is found immediately below the epidermis. Tannin and starch are commonly found in the collenchyma.

4. The primary cortex is relatively broad and the outermost part is stretched and broken quite early.
5. A cork cambium is formed in the outermost part of cortical parenchyma early the first year.
6. The primary and secondary phloem which are very much alike are formed in relatively small amounts.

B. Wood.

1. A procambium cylinder with an average of eighteen protoxylem points at the second internode of the current year's growth.
2. Metaxylem is formed between the protoxylem points to complete the vascular cylinder.
3. Both uniseriate and multiseriate rays are found in the majority of the species.
4. Tracheids and fiber tracheids are common on all the species.
5. Scalariform tracheal tubes are common throughout the genus.
6. Xylem parenchyma is common and contains much starch.

C. Pith.

1. About half the species studied have lignified pith.
2. The pith cells adjoining the protoxylem points are prosenchymatous, with thickened walls, and are always lignified.
3. Very little stored food is found in the pith.

These features, as stated above are common to the majority of the species; however, they are variable and will be discussed more in detail. Other features too are given which are found only in a species or a species and its variety or varieties.

The epidermis as seen from the surface has either of two general types of cells, elongated and somewhat rectangular or very irregular with very little difference in the tangential and vertical diameters. The following species have epidermises of the first type mentioned; *petiolaris*, (Fig. 33), *Bretschneideri* and varieties *landifolia* and *glabrescens* (Figs. 20, 21, and 22), *xanthoneura setchuenensis*, (Fig. 34); *quercifolia* should perhaps be included in this group, as the cells are elongated but have

pointed ends, (Fig. 30). The following species have epidermal cells of the second named type; paniculata and varieties praecox and grandiflora, (Figs. 23, 24, and 29), cinera and variety sterilis, (Fig. 26 and 27), radiata, (Fig. 31), arborescens and varieties urticifolia and grandiflora, (Figs. 16 and 18).

Trichomes of the simple clothing-hair type, varying from .2 mm. to 1.3 mm. in length, are found on the stems of the following species: cinerea and variety sterilis, xanthoneura setchuenensis, paniculata and varieties grandiflora and praecox, and arborescens and its varieties urticifolia and grandiflora.

Two kinds of trichomes are found on the stems of Bretschneideri and its varieties lancifolia and glabrescens; these are of the simple clothing-hair type (Fig. 19), some being ligulate. The stem of quercifolia is covered by clusters of ligulate trichomes arising from multicellular bases, (Fig. 25). The variety praecox and petiolaris have no trichomes on their stems.

The cortex usually consists of 3-4 rows of collenchyma and 5-6 rows of thin-walled parenchyma. It varies from .1 mm. in *Bretschneideri* and .18 mm. in *cinerea*. The cells of the collenchyma usually have walls greatly thickened up to .01 mm. in *xanthoneura setchuenensis*. Since the tangential walls are so much thicker than the radial walls, the collenchyma is soon crushed by the early formation of cork. However, in *arborescens* and varieties *urticifolia* and *grandiflora*, the radial walls are about as thick as the tangential walls; consequently, the collenchyma is not crushed as early in the stems of this group. The crushed collenchyma and epidermis of *Bretschneideri* give to the stem a deep brown color.

In the cortical parenchyma are found numerous crystal sacs filled with crystals of calcium oxalate. The crystal sacs have an average width of .035 mm. and length of .05 mm. Exceptionally large sacs are found in the cortex of *arborescens*, where they are .055 mm. wide and .08 mm. long.

A starch sheath is found only in *paniculata* and its varieties; the pericycle is

parenchymatous and contains abundant starch.

The phloem is produced in very small amounts in all the species and varieties and the secondary phloem shows very little difference from the primary phloem. The sieve tube elements average .02 mm. in cross section and .06 mm. in longitudinal section.

Cork is formed in varying amounts, but exceptionally large amounts are formed in *Bretschneideri* and its varieties *quercifolia* has the least amount of cork it having only 2 cell layers the first growing season. The cork cells average .025 mm. radially, .05 mm. tangentially, and .06 mm. vertically. In the species *paniculata* and varieties the phellogen is formed by the collenchyma. In all the other forms studied the cork cambium originates in the outermost part of the cortical parenchyma.

The phelloderm varies, being either parenchymatous or collenchymatous. The following species have a collenchymatous phelloderm; *Xanthoneura setchuenensis*, *arborescens* and varieties *urticifolia* and *grandiflora*, *petiolaris*, *cinerea* and variety *sterilis*, *quercifolia*, and *paniculata* and its varieties *praecox* and *grandiflora*.

Intercellular spaces are common in the phelloderm of *Bretschneideri* and its varieties and in *paniculata grandiflora*. Large crystal sacs are also commonly found in the phelloderm of the forms studied. Starch is found in the phelloderm of all the species, but oil is found only in the phelloderm of *Bretschneideri* and its varieties.

Very little can be added to the discussion of the phloem but the following may be noted:

1. There is very little phloem formed in the genus.
2. The secondary and primary phloem are almost identical.
3. The sieve tube elements average about .0275 mm. in cross section and have vertical diameters varying from .05 mm. to .08 mm.
4. Large amounts of starch and protein occur in the phloem.

No prominent variations are found in a study of the xylem. Most outstanding are the rays

which vary considerably within the group, being either uniseriate, biseriate or multiseriate or a combination of any two or all three. The species *paniculata* and varieties *praecox* and *grandiflora* have uniseriate rays; *Bretschneideri* and varieties *lancifolia* and *glabrescens* have both uniseriate and biseriate rays, while the following have uniseriate and multiseriate rays; *quercifolia*, *cinerea* and variety *sterilis*, *petiolaris*, and *arborescens* and its varieties *urticifolia* and *grandiflora*. The rays also vary greatly in depth; the longest rays of *petiolaris* measure 1.92 mm. in depth, but sections of *quercifolia* and *cinerea* 16 mm. long did not show both extremities of the rays. An averaged-sized ray cell has a vertical diameter of .06 mm., but the cells near the extremities of the rays are much longer, measuring as much as .09 mm. in *arborescens*.

The tracheal tube elements are scalariform pitted and have scalariform perforations in the end walls; they average .03 mm. in cross section and about .09 mm. vertically. At the second

internode of the current year's growth there are from 18-22 protoxylem points indenting the pith. The protoxylem elements are radially arranged and average .021 mm. in cross section. The metaxylem forming between the protoxylem points completes the vascular cylinder.

Both tracheids and fiber tracheids are found in the genus. The tracheids are very much like the xylem parenchyma in form in size, See Figs. 1- 14. The fiber tracheids average .7 mm. in length. Wood fibers are found in each species studied but are never very numerous. They average .9mm. in length. Starch is found in the parenchyma of the primary xylem and abundantly in the rays.

The following species have lignified pith, while the pith of the other members shows no lignification; *Bretschneideri* and varieties *lancifolia* and *glabrescens*, *paniculata* and varieties *praecox* and *grandiflora*, and *petiolaris*.

The pith cells are 6-8 sided as seen in cross section and average .1 mm. radially, .06 mm. tangentially and .073 mm. vertically.

The pith cells of *quercifolia* are extremely large, measuring as much as .18 mm. in cross section. The pith cells adjoining the primary xylem are prosenchymatous and have thicker walls than those in the central portion.

Very little starch is stored in the pith, but oil is found in the pith of the following species; *paniculata* and varieties *grandiflora* and *praecox*, *peticolaris*, abundantly in *Bretschneideri* and varieties *lancifolia* and *glabrescens*, and *Zanthoneura setchuenensis*.

Numerous large crystal sacs containing crystals of calcium oxalate are found in the pith of the following species; *quercifolia*, *paniculata* and varieties *grandiflora* and *urticifolia*, *arborescens* and varieties *urticifolia* and *grandiflora*, while fewer and smaller sacs occur in the pith of *peticolaris*.

ANATOMICAL KEY OF STEMS.

A. Pith lignified:

B. Starch sheath present:

H. *paniculata* and varieties *praecox*  
and *grandiflora*.

BB. Starch sheath absent.

C. Small amount of cork formed the first  
year and phelloderm containing much  
starch. H. *petiolaris*.

CC. Large amount of cork formed the first  
year and phelloderm containing  
relatively little starch. H.  
*Bretschneideri* and varieties  
*glabrorescens* and *grandiflora*.

AA. Pith not lignified:

B. Pith cells containing tannin. H. *quercifolia*.

BB. Pith cells without tannin.

C. Crystal sacs found in the phelloderm.  
H. *Xanthoneura setchuenensis*.

CC. No crystal sacs found in the phelloderm.

D. Numerous tracheids in definite  
radial rows.

H. *arborescens* and varieties  
*grandiflora* and *urticifolia*.

DD. Fewer and scattered tracheids.

E. Stems somewhat herbaceous.

Xylem 1/8th of diameter of stem. *H. cinerea* and variety *sterilis*.

EE. Stems definitely woody, xylem 1/16 th of diameter of stem.  
*H. radiata*.

## LEAVES

*H. arborescens* and varieties *grandiflora* and *urticifolia*.

### General Features.

The leaves of this group are very similar, but vary in minor features. The leaves of variety *urticifolia* are more sharply acuminate and the tips of the leaves of *arborescens* are less sharp and sometimes are rounded. The leaves of *arborescens*, are the largest; are from 6-20 cm. long while the leaves of variety *urticifolia* are from 4-10 cm. long. The leaves of *arborescens* and variety *urticifolia* are somewhat crenate.

The bases are round to cordate. The leaves are glabrous above but slightly pubescent on the under surface along the veins; they are of uniform texture and average about .21 mm. in thickness.

### Epidermis.

The lateral walls of the upper epidermal cells of *arborescens* are slightly undulated, (Fig. 51), a feature lacking in the varieties (Figs. 53, 55); The cells as seen from the surface are irregular in shape,

averaging .055 mm. in diameter. The cells of the lower epidermis are similar; however, those of variety *grandiflora* are slightly larger than those of *arborescens* and *urticifolia*, (Figs. 52, 54, 56). The trichomes found along the veins on the lower surface have quite thick walls which are roughened by encrustation with calcium carbonate, (Fig. 54). A cuticle measuring about .001 mm. in thickness is found on the upper epidermis, but cutinization is absent.

#### Mesophyll.

One layer of palisade cells measuring .04 mm. in length and .17 mm. in cross section, occupies about a third of the mesophyll volume. The cells of the spongy mesophyll are irregular with many large intercellular spaces between them. Large crystal sacs are commonly found in the mesophyll.

#### Midrib.

The midribs are obovate as seen in cross section and project slightly above the leaf.

blade; this projection is composed largely of collenchyma, which is also found on the lower side of the midrib. The vascular tissue is in the form of an arc which is surrounded by thin-walled parenchyma cells, (Figs. 97, 98, and 99).

#### Margins.

The margin of arborescens is the only one studied which is incurved. Collenchyma is also lacking in the margin of this species. The normal leaf structure of variety urticifolia continues to within .17 mm. of the margin where collenchyma is found; collenchyma extending .3 mm. in from the margin, is found in the variety grandiflora and here the outer walls of the epidermal cells are slightly thicker near the margin than farther in.

#### Petioles.

The petioles are relatively quite large as seen in cross section, measuring 2 to 2.5 cm. from the upper to the lower surface and from 2-3 cm. in breadth. Three vascular bundles

enter the petiole but soon divide and redivide so that midway of the petiole there are 11.12 small bundles arranged in a semicircle, (Figs. 127, 128, and 129). Near the leaf blade the bundles fuse to form a vascular arc which continues into the midrib. Three to four cell layers of thickwalled collenchyma are found below the epidermis. The vascular tissues are surrounded by thin-walled parenchyma cells which contain tannin, and among these are crystal sacs filled with crystals of calcium oxalate.

#### Venation.

The midrib passes upward into the leaf apex; from the midrib are given off veins which pass outward and upward along the margin. The veinlet meshes are relatively large, with a frequency of 2 to 3 meshes per sq. mm. Free vein endings occur only in the larger meshes where from 2 to 3 are usually found, (Figs. 36, 37, and 38).

*H. Bretschneideri* and varieties *lancifolia* and *glabrescens*.

In discussing the leaves, I shall describe the leaves of *Bretschneideri* and then point out how the varieties differ from the species.

General Features.

The leaves of *H. Bretschneideri* are 7-12 cm. long, elliptic-ovate to oblong-ovate and have serrate margins. The apices are acute to acuminate and the bases cuneate. The leaves are glabrous above, but pubescent beneath. The leaf blade has a thickness of about .28 mm. and the petioles, which are not winged, are from 1-3 cm. long.

The leaves of variety *glabrescens* are smaller, being from 4-10 cm. long, more elliptic, more coarsely serrate and sparingly pubescent beneath.

As the name of the variety suggests, the leaves of *lancifolia* are lanceolate and have a slightly serrate margin, and are covered on the lower surface with short, fine trichomes which are more numerous and finer than those found on variety *glabrescens* or the species *Bretschneideri*. The leaves of *lancifolia* are from 10-20 cm. long.

### Epidermis.

As seen from the surface, the leaf epidermises of this group are very much alike, the cells being irregular in outline and variable in size, but those of the lower epidermises are distinctly smaller than those of the upper. The cells of the upper epidermis vary from .05-.06 mm. in diameter, while those of the lower epidermis average .04 mm. The radial diameters average .03 mm. (Figs. 57, 62).

The trichomes found on the lower surface of the leaves vary greatly, both in size and in numbers. Those found on the leaves of *Bretschneideri* measure 1.5 mm. in length and are also quite numerous. The trichomes are rather sparse on leaves of variety *glabrescens* but are about the same size as those of *Bretschneideri*. Trichomes occur most abundantly on the leaves of variety *lancifolia*, but they are much smaller and finer than those found on the other members of the group, averaging only 1 mm. in length. In all cases, the trichomes are encrusted with calcium carbonate.

A thin cuticle is found mainly on the upper leaf surfaces, with traces on the lower and there is very little difference in the thickness

of the outer and inner walls of the epidermal cells.

The number of stomata ranges from 207 to 276 per sq. mm. in the group.

#### Mesophyll.

The number of palisade cells and of stomata per sq. mm. of leaf surface in this group have the following averages:

|                   | Palisade cells per sq.mm. | Stomata per sq. mm. |
|-------------------|---------------------------|---------------------|
| H. Bretschneideri | 6,210                     | 207                 |
| var. lancifolia   | 6,250                     | 276                 |
| var. glabrescens  | 5,949                     | 246                 |

The palisade cells in this group, which are .1-.12 mm. long and about .02 mm. wide, occupy about one half the volume of the mesophyll. The cells of the spongy parenchyma are very irregular in outline, leaving numerous large intercellular spaces.

Crystal sacs lying parallel to the leaf surface and averaging .16 mm. in length are very common in the spongy mesophyll, and the bundles of raphide crystals in these sacs are prominent features of bleached leaves.

#### Leaf margins.

As seen in cross section the leaf margins are very blunt. The margin of *Bretschneideri* sp. (Fig. 85), differs from the other two, (Figs. 86 and 87), by having two rows of palisade cells, while back from the margin there is only one row.

Next the margin is a small amount of collenchyma, and the outer and inner walls of the epidermal cells are thicker than those found back from the margin. The cuticle, is thicker at the margin than elsewhere and is somewhat serrate; it measures .003 mm. in thickness.

#### Midribs.

The midribs of the species and its varieties show a marked similarity when seen in cross section (Figs. 100 and 102), excepting that the midribs of *Bretschneideri* and variety *glabrescens*, measuring 1.5 mm. in thickness are distinctly larger than the midrib of variety *lancifolia* which measures about 1 mm. in thickness.

In each case there is a slight projection of the midrib above the leaf blade composed of 4-5 cell layers of collenchyma extending entirely around the midrib. In the ground tissue around

vascular arc is found a notable amount of tannin.

The vascular tissues compose a concentric bundle, the phloem entirely surrounding the xylem.

#### Petiole.

Other than the petiole of variety *lancifolia* being slightly smaller than those of *Bretschneideri*, and variety *glabrescens*, there is little difference in the petioles of this group. In cross section they are ovate with winglike projections at either side of the upper face. ( Figs. 130-132).

Beneath the epidermis are 4-5 layers of collenchyma cells with prominent walls measuring .03 mm. in thickness.

The ground parenchyma of rather loose structure contains numerous crystal sacs and quite a large amount of tannin. At the bases of the petioles are three bundles, one below the middle and a bundle above either side of this one. As the bundles pass through the petiole they gradually fuse to form a concentric bundle, the phloem of which surrounds the xylem.

Venation.

The leaves of this group have prominent midribs from base to apex. From the midrib lateral veins are alternately given off which pass outward and upward along the margins. In bleached leaves, at a distance 2 mm. from the apex we find the midrib and two lateral veins along the margin. As is characteristic of all the leaves, the meshes are relatively quite large, there being an average of 4.5 meshes and of 4 free vein endings per sq. mm. (Figs. 37 - 39).

*H. cinerea* and variety *sterilis*.

General Features.

The leaves of *H. cinerea* are elliptic or broad-ovate to ovate-oblong and are 6-15 cm. long; the leaves of the variety are more broadly ovate but not elliptic. The leaves of both the species and variety have acuminate apices and rounded to subcordate bases; both are glabrous above but grayish tomentose beneath, the tomentum being much more dense on the leaves of *cinerea* than on the variety *sterilis*. The leaf margins of both the species and its variety are serrate, although variety *sterilis* has a more deeply serrate margin. The leaves of *cinerea* are thicker than those of the variety, the former running about .28 mm. in thickness and the latter about .2 mm.

Epidermis.

As seen from the surface, the radial walls of the lower epidermal cells are slightly undulated while those of the upper epidermis are straight, (Figs. 63, 65, and 67). The cells of the lower epidermis are slightly smaller than those

of the upper epidermis, their tangential diameters averaging .045 mm.; while the diameters of the upper epidermal cells average .055 mm. in the same direction.

A few trichomes of the simple clothing-hair type are found on the upper epidermis of *cinerea*, (Fig. 64), but the upper epidermis of variety *sterilis* is glabrous. The lower epidermis in both cases is covered with a grayish tomentum with trichomes of the simple clothing-hair type averaging 1.2 mm. in length.

The outer walls of the epidermal cells of both the species and variety measure about .0025 mm. in thickness while the inner is slightly less, measuring about .002 mm. in thickness. A thin cuticle is found on the upper epidermis, and on the lower epidermis near the margin.

#### Mesophyll.

The palisade tissue consists of one layer of cells measuring .02 mm. in breadth and .063 mm. in length. The spongy tissues are composed of irregular, loosely arranged collenchyma cells and numerous crystal sacs lying parallel with the leaf

surface. The palisade cells occur with a frequency of 5,589 per sq. mm. in the leaves of *cinerea* and 6,782 per sq. mm. in the leaves of variety *sterilis*.

#### Margin.

The leaf blades of this species and its variety have very blunt margins, (Figs. 88 and 89). The margin of variety *sterilis* consists largely of collenchyma, differing in this respect from the margin of *cinerea* which has only a small amount of collenchyma at its extreme edge.

#### Midribs.

The midribs in cross section measure 1.7 mm. from the upper to the lower surface, are broad-ovate and extend slightly beyond the surface of the leaf blade, (Figs. 103 and 104). As in the midribs of the other species, a large amount of collenchyma is found immediately below the epidermis, and in the collenchyma tannin and starch occur abundantly. Surrounding the vascular tissue is a large amount of parenchyma ground tissue in which

numerous crystal sacs are found. The vascular tissues is in the form of two large arcs, the lower being the larger of the two. In both, the phloem entirely surrounds the xylem.

#### Petiole.

Cross sections of the petioles of variety *sterilis* are quite rounded, (Fig 134) and measure on the average 2.3 mm. from the upper to the lower surface, while the average petiole of *cinerea* is crescent shaped, (Fig. 153), as seen in cross section and measures 2 mm. in thickness.

Although the petioles vary in shape, the vascular tissue is very similar in both. At the base of the petiole are three large bundles, two being above and to either side of the thirs. Half-way its length, the petiole has eight small bundles arranged in a semicircle and subtending a larger bundle. At the upper extremity of the petiole the bundles gradually fuse, so continueing into the midrib until in the median portion of the midrib there is a closed vascular arc as stated above.

Venation.

Near the base of the midrib large lateral veins are given off and pass outward and upward toward the margin. Branches from the lateral veins join branches from neighboring lateral veins to form large meshes. Within a mm. of the apex there is an average of 2.5 closed meshes and as many free vein endings per sq. mm. The veinlets, surrounded by distinct border parenchyma, are embedded in the spongy mesophyll.

*H. paniculata* *praecox* and *paniculata*, *grandiflora*.

Since the leaves of these varieties are quite similar, I am discussing them together. Rehder, '27, separates the varieties entirely by the flowers. Variety *praecox* blooms about six weeks earlier than the species *paniculata* and the flowers of variety *grandiflora* are nearly all sterile and in large panicles, sometimes 30 cm. long.

General Features.

The leaves of this group, which are mostly elliptic, although a few may be ovate, have acuminate apices and cuneate bases; they are 5-20 cm. long, (the material which I have shows the leaves of variety *praecox* to be much the larger) and have serrate margins. The petioles vary from 3-5 cm. in length. The leaves of variety *praecox* are glabrous on both surfaces; the upper leaf surface of variety *grandiflora* is sparingly pubescent, while the lower surface has a few trichomes along the veins. The leaves are about .27 mm. thick.

Epidermis.

As seen from the surface, the lateral

walls of both the upper and lower epidermal cells of variety *praecox* (Figs. 72 and 73) are decidedly undulated, while only those of the upper epidermis of *grandiflora* are undulated (Fig. 70). The epidermal cells of variety *praecox* average .11 mm. in tangential diameter while those of *grandiflora* average .06 mm. A thin cuticle is prominent on the upper leaf surface but is absent in places on the lower. Stomata occur with a frequency of 60-75 per sq. mm. on the lower leaf surface only.

The trichomes found on the leaves of *grandiflora* are of the simple clothing-hair type and are heavily encrusted with calcium carbonate. They average 1.2 mm. in length.

#### Midrib.

As seen in cross section, the midribs of variety *praecox* are broad ovate, (Fig. 106), the greater cross diameter being at the lower portion of the midrib. The midrib of *grandiflora*, (Fig 108) extends farther above the leaf blade than does that of *praecox*. The portion of the midrib extending

above the leaf blade is composed mostly of 4-5 cell layers of thick-walled collenchyma. The concentric vascular bundles in both varieties are surrounded by parenchymatous ground tissue. Two small bundles, the phloem of which entirely surrounds the xylem, are found above and to either side of the main vascular bundle in the variety *praecox*. See Fig. 106.

#### Petioles.

The petioles are obovate as seen in cross section with the upper margin slightly projecting at either side to form wings, and other than the petiole of *praecox*, (Fig. 137) being larger than that of *grandiflora*, (Fig. 136) there is little difference between the two.

The vascular structure of the petiole near the middle of its length is very similar to that found in the midribs. There is a large vascular arc subtending a smaller one. In the upper region of the petiole the two arcs fuse to form a closed vascular system. At the base of the petiole there are three large bundles, one near the

lower surface, and one above and to either side of the lower.

Large amounts of tannin and starch are stored in the phloem parenchyma and in the collenchyma immediately below the epidermis.

#### Mesophyll.

About one third the volume of the mesophyll is occupied by the layer of palisade cells, (Figs. 91 and 92), occurring with a frequency of 2,500- 2,800 per sq. mm. of leaf surface. Here the cells are .65 mm. long and .02 mm. wide. The spongy parenchyma, in which the veins are embedded, is composed of loosely arranged irregular cells.

#### Margin.

The leaf margins, (Figs. 91 and 92), of variety *praecox* and *grandiflora* are very blunt as seen in cross section, and they are very much alike in other respects, with perhaps rather more strengthening tissue in *grandiflora* in the form of collenchyma. The outer walls of the epidermal cells

are somewhat thicker than the inner walls. The layer of palisade cells extends to .04 mm. of the margin where the strengthening tissue replaces them. In shape and size the epidermal cells of the margin are very much like those of the rest of the blade.

Venation.

The venation of the varieties of paniculata is quite simple; 3-4 lateral veins alternately branch off from the midrib. Near the apex there is the midrib and a vein extending along either margin. The meshes are somewhat unusually more numerous in this group, there being 6-7 per sq. mm. and in some of the meshes there are one to two free vein endings while on others there are none.

*H. petiolaris*

General Features.

The leaves of this species vary much in shape; from broad-ovate to oval; apices acute to acuminate and bases cordate to rounded. The leaf blade is from 8-10 cm. long and has a petiole 2-8 cm. in length. The margin is serrate; and the leaf has a thickness .32 mm. Very few trichomes are found on the younger leaf while the older is glabrate and in many cases glabrous.

Epidermis.

As seen in surface view the upper and lower leaf epidermises are quite similar; (Figs. 74 and 75), however, the walls of the upper epidermal cells are somewhat undulated whereas those of the lower are more straight. In a cross section of a leaf, we see that the cells of the upper epidermis are more rectangular and have a slightly greater depth than the cells of the lower epidermis. The outer cell walls of both the upper and lower epidermises measure about

.008 mm. in thickness; the inner cell walls are much thinner, being about one fourth (.002 mm.) as thick as the outer cell wall. A cuticle about .0015 mm. in thickness is found covering the surface of the leaf.

A few trichomes measuring .09 mm. in length are found along the veins on the lower leaf surface.

#### Mesophyll.

The mesophyll consists of 1-2 cell layers of palisade cells and quite a large amount of spongy parenchyma, consisting of irregular-shaped cells. It is interesting to note that near the margin there are two rows of palisade cells while farther in from the margin one row of palisade cells is found.

The palisade cells are quite elongated, measuring .02 mm. in cross section and .06 mm. in length. 3,500 palisade cells are found per sq. mm. of leaf surface.

It is noticeable that as a general rule throughout the genus there are approximately 30 stomata per 1,000 palisade cells. In *H. petiolaris* there is an average of 69 stomata per sq. mm. of

leaf surface.

Margin.

In a cross section of a leaf we see that the margin is sharply pointed, (Fig. 94). The outer walls of the epidermal cells of the margin are somewhat thicker than those back from the margin where less epidermal strength might suffice. Ordinarily some collenchyma is found along the margins, but not in this species.

Midrib.

The leaf midrib of this species is quite outstanding, as superficially it seems to be no more than a gradual thickening of the leaf blade with a vein in the central portion, (Fig. 107). From the lower to the upper epidermis the midrib measures .51 mm., whereas the leaf blade has a thickness of .32 mm. The cells of both the upper and lower epidermis are much smaller than those farther away from the midrib, being about .02 mm. tangentially and .0205 mm. radially. The cuticle found on the epidermises of the midrib appears finely serrate in cross section.

A collenchymatous hypoderm of 3-4 cell layers is found above the lower epidermis and a similar hypoderm one cell thick occurs below the upper epidermis. The cells of this hypoderm are much larger than the epidermal cells immediately above them, being about .04 mm. tangentially and .03 mm. radially.

The vascular bundle is surrounded by parenchyma cells, and among those above the bundle are large crystal sacs measuring .08 mm. in cross section.

The xylem in the midrib consists of 18 rows of radially arranged elements. In each row are 3-4 tubes which measure .02 mm. in cross section. A large amount of starch is found in the parenchyma around the ends and between the rows of protoxylem elements.

The phloem is composed largely of phloem parenchyma in which are scattered sieve tubes. Protein and starch are found in large quantities in the phloem tissues.

Just to the exterior of the phloem are

a few scattered fibers, which in cross section measure .02 mm. by .01 mm. These have relatively large cavities; that is, the cavities are more than half the diameter of the fibers.

Petiole.

Cross sections of the petiole taken midway between the blade and the point of attachment with the stem measure 3 mm. in depth. In this region there are two separate collateral bundles; the lower is a large crescent shaped bundle and the upper smaller half-moon shaped bundle lies in the concavity of the larger bundle, (Fig. 138). It is interesting to note that the sheath subtending the protoxylem points in the stem also extends into the petiole. At the base of the petiole there are three vascular bundles, a lower one and one above and to either side. In their course through the petiole, the three bundles fuse to form the lower vascular arc; branches are given off which fuse to form the smaller vascular arc subtended by the larger.

From eight to nine rows of collenchyma are found just below the epidermis of the petiole and adjoining this is a great amount of ground tissue in which are found numerous crystal sacs filled with crystals of calcium oxalate.

Venation.

The venation of the leaves seems very simple. There is one large lateral vein on either side of the midrib which extends within 2 mm. of the apex where branches form a connection with the midrib.

As an average there are 2.27 veinlet meshes and 2 free vein endings per sq.mm.

The veinlets are embedded in the spongy mesophyll, and are surrounded by a distinct parenchyma sheath.

### *H. quercifolia*

#### General Features.

The leaves of *H. quercifolia* are the most outstanding of any found in this genus. They are from 6 to 20 cm. long and the petioles vary from 1.5 to 8 cm. in length. The leaves vary from .1 to .12 mm. in thickness. As the name suggests, the leaves are lobed, each leaf having from three to seven sinuate lobes. In general outline the leaves are ovate to suborbicular and are usually truncate at the base.

#### Epidermis.

The epidermal cells of both the lower and upper epidermises have undulated walls (Figs. 80 and 81), as seen from the surface. The cells vary in size, but an average-sized cell has a tangential diameter of approximately .06 mm. and a radial diameter of about .02 mm. The inner and outer cell walls of both the lower and upper epidermises are extremely thin, being only about .001 mm. in thickness.

#### Mesophyll.

The mesophyll is composed of a single layer of palisade cells and 3-4 cell layers of irregularly shaped spongy parenchyma cells.

The palisade cells are .04 mm. long and .017 mm. wide and occur with a frequency of 6,210 per sq. mm. of leaf surface. In the mesophyll are numerous crystals of calcium oxalate.

Midrib.

Cross sections of the midrib taken midway between apex and petiole are 1.2 mm. from the upper to the lower surface. The sections are quite rounded, with a pointed projection of the upper surface consisting mostly of collenchyma, (Fig. 110).

As is customarily found in this genus, the epidermal cells of the midrib are much smaller than elsewhere over the leaf. Above the lower epidermis are from 3 to 4 cell layers of very thick walled collenchyma, some of the thicker walls measuring as much as .02 mm. across.

Around the semilunar vascular bundle is found the ground parenchyma which is in larger amount towards the lower side. Throughout the ground tissue are cells containing tannin.

The xylem elements are arranged in

twenty four radial rows and the phloem extends around the sides of the bundle to a line even with the lower leaf surface. In the phloem parenchyma cells are large amounts of tannin and starch.

#### Margin.

In a leaf cross section, the margin appears very blunt, (Fig. 93). No collenchyma or extra thickness of the epidermal cells is found to strengthen the margin. The cells of the margin are very much alike and of the nature of spongy parenchyma. In the leaves of most of the species there are two layers of palisade cells near the margin, but in this species there is only one layer near the edge of the leaf.

#### Petiole.

Sections of the petiole taken midway between the leaf blade and the point of attachment to the stem measure 2 mm. from the upper to the lower surface and 3 mm. laterally, (Fig. 139). In this region of the petiole there are

17 separate bundles; 15 of the bundles are arranged in a semicircle and the other two bundles are subtended by the semicircle and have the phloem towards the upper surface of the petiole. At the base of the petiole there are only three large bundles. This is quite outstanding, as ordinarily the bundles fuse as they pass upward through the petiole, but in this case the bundles divide. Near the base of the leaf blade there are six bundles in the petiole; evidently the bundles separate and fuse again in their course through the petiole.

Below the epidermis is a collenchymatous hypoderm of 6-7 cell layers which extends entirely around the vascular tissue. In this collenchyma are found a large amount of tannin and a small amount of starch.

Tufted trichomes like those found on the stem are also found on the petiole of this species.

#### Venation.

Since the leaves of this species are distinctly lobed, the venation is somewhat more

complex than in other species of the genus.

From the midrib, one major vein passes into each lobe, while from these main veins of the lobes, still other veins extend to the serrate margin. In the tip of each lobe there is the one major vein while along the margins are lateral veins from which are branches connecting them with the major vein.

The veins are very prominent when seen from the under surface of the leaf; in cross sections of the leaf the veins extend definitely below the leaf surface, while the veinlets are embedded in the spongy mesophyll.

There are 2.3 meshes per sq. mm. of leaf surface and an average of 1.9 free vein endings in the same area.

*H. radiata*

General Features.

The leaves of this species are quite large as a rule, varying from 6-12 cm. in length of the leaf blade and from 1.5-6 cm., in length of petioles according to the position of the leaf. The double serrate margin is undulated and the tip of the blade is acuminate projected. The leaves are dark green and glabrous above but decidedly pubescent beneath.

Epidermis.

As seen from the surface, the cells of both epidermises are irregular in shape with distinctly undulating walls, (Figs. 78 and 79), vary in size, the average tangential diameter is .07 mm. and radial diameter is .02 mm.

There is very little difference in the thickness of the outer and inner cell walls, although the outer is perhaps a little thicker here and there over the leaf.

A cuticle about .001 mm. in thickness is found on the upper epidermis, while only traces of a cuticle can be observed on the lower epidermis.

### Mesophyll.

The palisade cells occur in one layer and average 4,968 to each sq. mm. of leaf surface. As seen from the surface, the palisade cells have tangential diameters of .013 mm.; the radial diameter is about .04 mm. The cells of the spongy parenchyma are irregular in shape, forming numerous large intercellular spaces.

### Margin.

Cross sections of the leaf show the margin to be very blunt. The normal structure of the leaf continues to within .2 mm. from the margin where the walls of some of the cells are thickened. The outer walls of the epidermal cells of the margin are also thickened, (Fig. 92).

### Midrib.

The midrib is obovate in cross section, gradually tapering from the lower surface to the leaf blade. (Fig. 111). Above the leaf blade is the rounded tip of the midrib composed mainly of collenchyma, some walls of which are as much as .03 mm. thick. The lower portion of the midrib is also largely thick-walled collenchyma.

Surrounding the vascular arc is quite a large amount of ground tissue in which tannin occurs abundantly and a few of the cells contain stored starch.

The vascular bundle is concentric, the phloem entirely surrounding the xylem. Above the main vascular bundle are four small bundles, the phloem of which also surrounds the xylem.

#### Petiole.

The petioles of this species are relatively large, sections taken midway between the base and the blade measuring 2mm. from the upper to the lower surface and having a width of 2.5mm, (Fig. 140). The vascular anatomy of the petiole is very interesting. At the base of the petiole there are three widely separated bundles which divide and redivide so that midway of the petiole there are 9 small bundles, 7 of which are arranged in a semicircle subtending the other two; then approaching the base of the leaf blade, the seven bundles fuse to form a vascular arc, while the other two bundles have fused to form a single large bundle with the phloem towards the upper surface.

Immediately below the epidermis are 5-6 layers of collenchyma the cells of which have extremely thick walls, measuring .02 mm. in cross section. Tannin is found on these cells, especially in the outermost layer next to the epidermis; this storage of tannin would seem to indicate that tannin is perhaps more or less a direct product of photosynthesis.

Venation.

Leaves of this species have a rather simple venation, there being 7-8 major lateral veins from the midrib, and from these, smaller veins are given off which unite with others from the adjoining lateral veins to the meshes. The smallest meshes are relatively large, there being an average of only 1.5 per sq. mm. Free ~~vein~~let endings are as few as 0-2 per sq. mm.

H. *Xanthoneura setchuenensis*.

General Features.

The leaves of this variety are quite large as a general rule, varying from 10 to 20 cm. in length and 3 to 6 cm. in width and averaging .22 mm. in thickness. They are elliptic to elliptic-oblong, abruptly acuminate, cuneate at the base and have serrate margins. The petioles vary from 1-3 cm. in length. Trichomes are found on both upper and lower leaf surface.

Epidermis.

As seen from the surface the cells of the upper epidermis are hexagonal and those of the lower epidermis more irregular, (Figs. 76 and 77). An average-sized cell of the epidermis measures .03 mm. tangentially and .031 mm. radially. The trichomes of the simple clothing hair type average 1 mm. in length. Approximately 203 stomata are found per sq. mm. on the lower leaf surface.

Mesophyll.

About one third of the volume of the

mesophyll is occupied by the palisade layer, (Fig. 96), the cells of which are .06 mm. long and .03 mm. wide; these occur with a frequency of 5,030 per sq. mm.

The cells of the spongy mesophyll are quite compactly arranged, but are irregular in shape, leaving many intercellular spaces.

#### Margin.

The margin of the leaf is very blunt as seen in cross section, (Fig. 96). The epidermal cells of the margin have both radial and tangential walls thickened. Below the epidermis is a layer of collenchyma with extremely thick walls reenforcing the margin.

#### Midrib.

Sections of the midrib measure 1.75 mm. from the upper to the lower surface and are 1.5 mm. broad. The midrib is rounded in cross section and extends above the leaf blade, (Fig. 109), where it is composed of collenchyma, the cells of which are prominent

because of their walls being so thick that in many cases the cell cavity is almost obliterated. Here the walls measure as much as .035 mm. in cross section.

Thin-walled parenchyma cells enclose a main ectophloic concentric vascular bundle, above which and to either side are very subordinate bundles with xylem entirely surrounded by phloem.

#### Petiole.

Sections of the petiole taken midways between the base and the leaf blade measure 3mm. in thickness and 2 mm. in width. In cross section it is ovate with two thin extensions above to a height of .6 mm. (Fig. 141).

The epidermis has a cuticle .002 mm. thick and below the epidermis is thick-walled collenchyma 5-6 cell layers wide, adjoining which is the ground tissue where numerous crystal sacs are found filled with crystals of calcium oxalate. The petiole midway its length has a main vascular arc and above this on either side are two subordinate bundles. These split up before entering

the blade and we discern that the main vascular arc of the midrib already spoken of is formed by the fusion of the five bundles from the petiole.

Venation.

From the midrib run 14 lateral veins which pass outwards and upwards to within 2 mm. of the margin, the marginal veins near the leaf base being especially prominent. The midrib extends through the acuminate apex to the extreme tip. An average of 3 meshes and 2.3 free vein endings per sq. mm. obtains 3 mm. back from the apex.

KEY TO SPECIES FROM CROSS SECTIONS  
OF MIDRIBS.

A. Midrib scarcely thicker than the leaf blade.

H. petiolaris.

B. Midribs extending above and below the leaf blade.

1. Upper projection of midrib acuminate.

a. One vascular arc subtending a smaller  
bundle, H. arborescens urticifolia.

b. The vascular tissue in one arc only.

H. quercifolia.

II. Upper projection of midrib not acuminate.

a. Vascular tissue in two arcs; the  
lower subtending the smaller and the  
edges of both arcs joining.

1. Midrib obovate in cross section.

H. radiata.

2. Midribs ovate.

a' Lower surface of midrib  
rugose.

H. xanthoneura setchunensis.

b' Lower surface of midrib smooth.

1' Midribs large, 2-3 mm.

from upper to lower  
surface.

(a). Collenchyma on  
upper side extending  
below the surface  
of the midrib.

H. Bretschneideri.

(b) Collenchyma on upper  
surface extending  
no farther downward  
than the leaf blade,

H. Bretschneideri glabrescens.

2' Midrib much smaller, .75mm.  
to 1.5 mm. from upper to  
lower surface.

H. Bretschneideri lancifolia.

b. Vascular tissue in one large arc.

1. Portion of midrib above leaf blade  
in cross sections projecting into  
several points. H. arborescens.

2. Upper portion of midrib uneven but  
not pointed. H. arborescens grandiflora.

c. Vascular tissue in one large arc  
subtending a small bundle.

1. Midribs large, 2-3 mm. from upper to lower surface.
  - a. Upper projection of midrib quite wavy in cross section.

H. paniculata praecox.

- b. Upper projection of midrib only slightly wavy.

H. cinerea sterilis.

2. Midribs smaller, .75 mm. to 1.7 mm. from upper to lower surface.

- a. Collenchyma at lower surface extending upward to the leaf blade.

H. paniculata.

- b. Collenchyma not extending upwards as far as the lower surface of the leaf blade.

H. cinerea.

KEY TO SPECIES USING CROSS SECTIONS  
OF THE PETIOLES.

A. Petioles obovate in cross section.

1. Petioles with two winglike projections on upper side.

a. Vascular tissue in two arcs, the lower subtending the smaller and the extremities joined.

H. xanthoneura setchuenensis.

b. Vascular tissue in one arc and subtending a smaller bundle.

1. Wings extending .5 mm. above the general surface.

a' Upper surface of petiole concave between the wings.

H. paniculata.

b' Upper surface of petiole convex between the wings.

H. paniculata grandiflora.

2. Wings extending only slightly above the petiole.

a' Petioles large, 2-3.5 mm. from  
the upper to the lower surface.

1'. 7-8 cell layers of  
collenchyma on upper  
surface between the  
winglike projections.

H. paniculata praecox.

2' Only 3-4 cell layers of  
collenchyma on upper  
surface between the winglike  
projections.

H. Bretschneideri glabrescens.

b' Petioles smaller, 1-2 mm. from  
the upper to the lower surface.

1' Wings of petiole pointed  
in cross section.

H. Bretschneideri.

2' Wings of petiole rounded  
in cross section.

H. Bretschneideri lancifolia.

B. Petioles ovate in cross section.

I. Both upper and lower surface of petiole rugose. H. arborescens grandiflora.

II. Only upper surface of petiole rugose.  
H. arborescens.

III. Neither the upper nor lower surface of the petiole rugose.

H. arborescens urticifolia.

C. Petioles lunate in cross section.

I. Petiole covered with tufted trichomes.

H. quercifolia.

II. Petiole with microscopic multicellular trichomes.

a. Vascular tissue grouped into 10-12 bundles arranged in an arc subtending two large bundles. H. radiata.

b. Vascular tissue similar to above but all the bundles arranged in an arc.

H. cinerea.

D. Petioles rounded but truncate above in cross section.

I. Petiole with multicellular microscopic trichomes. H. cinerea sterilis.

II. Petiole without such trichomes.

H. petiolaris.

#### SUMMARY OF LEAVES

Only the leaves of *quercifolia* are lobed; the leaves of the other species range from broad-ovate in *peltolaris* to lanceolate in *Bretschneideri lancifolia* and have serrate margins; the apices are acuminate in the majority of the species studied and the bases usually rounded. The leaves vary in length from 3 cm. in *peltolaris* to 20 cm. in *Bretschneideri lancifolia*, and from .18 mm. in thickness in *quercifolia* to .32 mm. in thickness in *peltolaris*, the average thickness is about .24 mm. The leaves of *peltolaris* have a strikingly different texture, being quite leathery, while the leaves of the other species are finer and more soft.

Trichomes of the simple clothing-hair type are found on the majority of the leaves, varying from .3 to 2 mm. in length throughout the genus; the trichomes found on the lower surface of *Bretschneideri lancifolia* are finer than the average and measure about .5 mm. in length. *Quercifolia* alone has ligulate trichomes on the lower surface which are much smaller than those of the other species and lack the calcium

carbonate encrustation found on the trichomes of the other species. *Arborescens* and its varieties *grandiflora* and *urticifolia*, and *peticolaris* are glabrous on the lower surface. *Cinerea* and variety *sterilis* are villous, the numerous trichomes forming a dense mat on the lower surface. *Paniculata* and varieties and *xanthoneura setchuenensis* are pubescent along the veins on the lower surface, those on *paniculata* being bristlelike. *Bretschneideri* and its varieties are glabrous above but villous beneath; variety *glabrescens* seems to have as many trichomes as the species *Bretschneideri*.

As seen from the surface, the lateral walls of all the lower epidermal cells are undulated, excepting those of *Bretschneideri lancifolia* and *xanthoneura setchuenensis*, while the lateral walls of the upper epidermal cells of *radiata*, *cinerea* and variety *sterilis*, *paniculata* and varieties *praecox* and *grandiflora*, *quercifolia*, and *arborescens* are undulated. Stomata were found on the upper epidermis of only *paniculata praecox* and the upper epidermal cells of this variety are very similar to those of the lower epidermis, (Figs. ).

The cells of the upper epidermis are distinctly larger than those of the lower, averaging

.052 mm. tangentially, while those of the lower epidermis average .04 mm. There is very little difference in the thickness of the outer and inner cell walls, but the outer walls near the margin are slightly thicker and serrate in *peltolaris*, (Fig. 94), *Bretschneideri* and variety *lancifolia*, (Fig. 85). A very thin cuticle averaging .002 mm. in thickness is found on the upper surface and the lower surface near the margin.

The mesophyll generally consists of one row of palisade cells, but two rows are found near the margin in *peltolaris* and *Bretschneideri*. The palisade cells are usually .1 to .12 mm. long and .02 mm. wide; they vary from 2800 per sq. mm. in *paniculata* to 6000 per sq. mm. in *Bretschneideri*.

The spongy parenchyma consists of a layer of irregularly-shaped cells with large inter-cellular spaces; the spongy parenchyma occupies about half the collenchyma column. Numerous crystal sacs lying parallel to the leaf surface are commonly found in the spongy parenchyma.

The margins are all reinforced with collenchyma excepting those of *paniculata praecox*, (Fig. 92) and *arborescens*, (Fig. 82). The normal leaf structure extends to within .8 mm. of the margin.

The midrib of petiolaris is distinctly different from those of the other species, being scarcely thicker than the leaf blade. Sections of the midribs taken midways of the blade vary from 1-2 mm. in thickness and from .7 mm. to 1.5 mm. in breadth. Such sections, excepting those of petiolaris, are obovate to rounded and usually extend above the leaf blade, where they are composed of thick-walled collenchyma. This collenchyma is also found on the lower surface of the midrib, where it is prominent because of its thick walls, measuring as much as .035 mm. in thickness and almost occluding the cell cavity in many cases.

The ground tissue enclosing the vascular tissue is composed of thin-walled parenchyma cells containing starch and tannin in most cases. Here, too, are found numerous crystal sacs similar to those of the spongy parenchyma.

The vascular tissue, as seen in cross section, is generally composed of two arcs, the lower the larger and subtending the upper. Above these arcs are usually found smaller bundles, with phloem surrounding the xylem.

The petioles vary in length from 2 cm. in petiolaris to 8 cm. in quercifolia, radiata and paniculata.

The petioles also vary greatly in thickness. The petiole of *paniculata grandiflora* is the smallest, measuring .9 mm. in breadth and 1.1 mm. in depth; *quercifolia* has the largest petiole, measuring 3 mm. in breadth and 2 mm. in depth.

The petioles of the following species are obovate in cross section and have winglike projections from the upper side: *Bretschneideri* and varieties *glabrescens* and *lancifolia*, (Figs. 130, 131 and 132), *paniculata* and variety *grandiflora*, (Figs. 135 and 136), and *xanthoneura setchuenensis*. The petiole of *cinerea* is luneate as seen in cross section (Fig. 133), while the petiole of variety *sterilis* is more rounded and slightly larger, (Fig. 134). The petiole of *arborescens* and varieties *grandiflora* and *urticifolia* are ovate as seen in cross section, (Figs. 127, 128 and 129).

The petiole of *quercifolia* is covered with clusters of ligulate trichomes similar to those found on the young stem, (Fig. 25). Microscopic multicellular trichomes are found on *cinerea* and *arborescens* and its varieties *grandiflora* and *urticifolia*. The trichomes found on the petioles of the other species are of the simple clothing-

hair type like those found on the blades.

Three vascular bundles enter the petioles, and in their upward course divide and redivide so that in the median portion of the petiole there are from 6 to 12 small bundles. Near the blade, the bundles again fuse to form a vascular arc as the section of *arborescens* shows (Fig. 127). The arrangement of the vascular tissue in *xantheneura setchuenensis* is a little different; the upper bundles form a small arc which is subtended by a larger arc formed by the lower bundles, (Fig. 141).

The venation varies little within the species studied. The midrib extends into the apices and lateral veins are given off and pass outward and upward along the margins. The veinlet meshes are relatively quite large, varying from 1-3 per sq. mm. while free veinlet endings average 1-2 per veinlet mesh. (Figs. 36 to 50).

KEY TO LEAVES

A. Leaves lobed ----- *H. quercifolia*

B. Leaves not lobed.

1. Leaves villous beneath.

a. Leaves lanceolate--*Bretschneideri lancifolia*

b. Leaves not lanceolate.

1. Blade 7-12 cm. long. *Bretschneideri*

2. Blade smaller, 4-9 cm. long; leaves

more deeply serrate-- *Bretschneideri*

*glabrescens*.

II. Leaves not villous.

a. Leaves glabrous beneath only.

1. Leaves dark green and lustrous above;

blade 5-10 cm. long. *H. petiolaris*

2. Leaves larger, 6-20 cm. long; more

dull green above.

a' Margin curving downwards

*H. arborescens*

b' Margin straight.

1' Tip with long acuminate apex-

*H. arborescens urticifolia*

2' Tip only slightly acuminate-

*H. arborescens grandiflora*.

b. Leaves glabrous above-

L. Normal leaf structure

continuing to the margin.

a. Margin deeply serrate.

*H. paniculata praecox.*

b. Margin slightly serrate; a few trichomes along veins on lower surface.

*H. paniculata grandiflora.*

2. Normal leaf structure replaced by parenchyma and collenchyma 1.5 mm. from the margin.

*H. paniculata.*

c. Leaves not glabrous on either surface.

1. Leaves abruptly acuminate at apex and cuneate at base; green above and with yellowish veins beneath.

*H. xanthoneura setchuenensis.*

2. Leaves with acuminate apices, but rounded bases.

a' Upper epidermis with trichomes

*H. cinerea.*

b' Upper epidermis glabrous.

*H. cinerea sterilis.*

3. Bases subcordate; white tomentose beneath; reticulate veins. *H. radiata.*

PLATE I  
DRAWINGS OF XYLEM ELEMENTS.

X 162

- Fig. 1 - *Hydrangea arborescens*  
Fig. 2 - " " *grandiflora*  
Fig. 3 - " " *urticifolia*  
Fig. 4 - " *Bretschneideri*  
Fig. 5 - " " *glabrescens*  
Fig. 6 - " " *lancifolia*  
Fig. 7 - " *cinerea*  
Fig. 8 - " " *sterilis*  
Fig. 9 - " *paniculata*  
Fig. 10 - " " *grandiflora*  
Fig. 11 - " *peltolaris*  
Fig. 12 - " *quercifolia*  
Fig. 13 - " *radiata*  
Fig. 14 - " *xanthoneura setchuenensis*

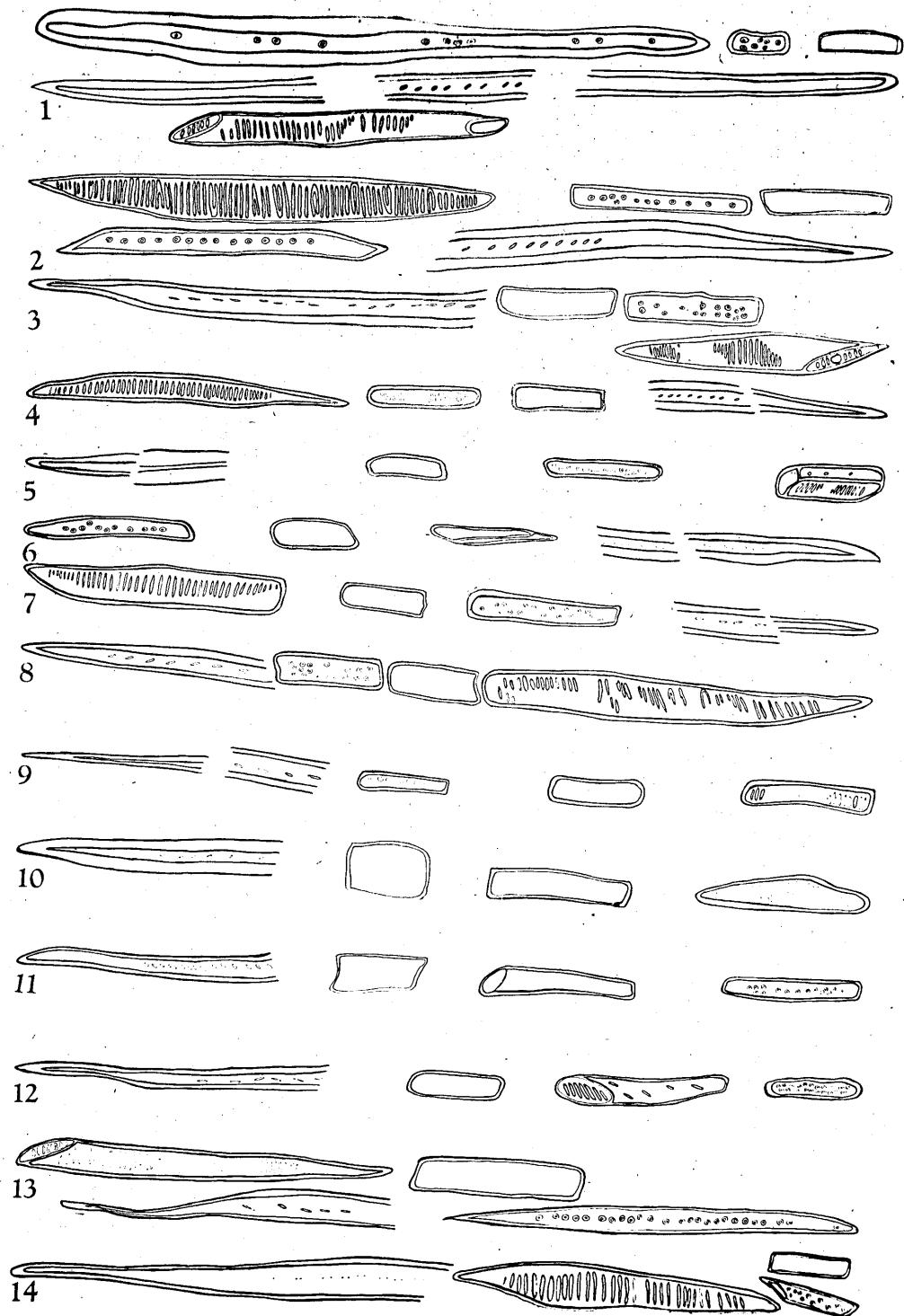


PLATE III

DRAWINGS OF STEM EPIDERMISES AND TRICHOMES

X 162

- Fig. 15 - Trichome on stem of *cinerea sterilis*  
Fig. 16 - Epidermis of *H. arborescens*  
Fig. 17 - " " *grandiflora*  
Fig. 18 - " " *urticifolia*  
Fig. 19 - Trichome on stem of *Bretschneideri*  
Fig. 20 - Epidermis of *H. Bretschneideri*  
Fig. 21 - " " *glabrescens*  
Fig. 22 - " " *lancifolia*  
Fig. 23 - " *panículata*  
Fig. 24 - " " *grandiflora*  
Fig. 25 - Trichome on stem of *H. quercifolia*  
Fig. 26 - Epidermis of *H. cinerea sterilis*  
Fig. 27 - " "  
Fig. 28 - Trichome on stem of *cinerea*  
Fig. 29 - Epidermis of *H. paniculata praecox*  
Fig. 30 - " *quercifolia*  
Fig. 31 - " *radiata*  
Fig. 32 - Trichome on stem of *Bretschneideri*  
Fig. 33 - Epidermis of *H. petiolaris*  
Fig. 34 - Epidermis of *H. xanthoneura setchuenensis*  
Fig. 35 - Trichome on stem of *H. radiata*

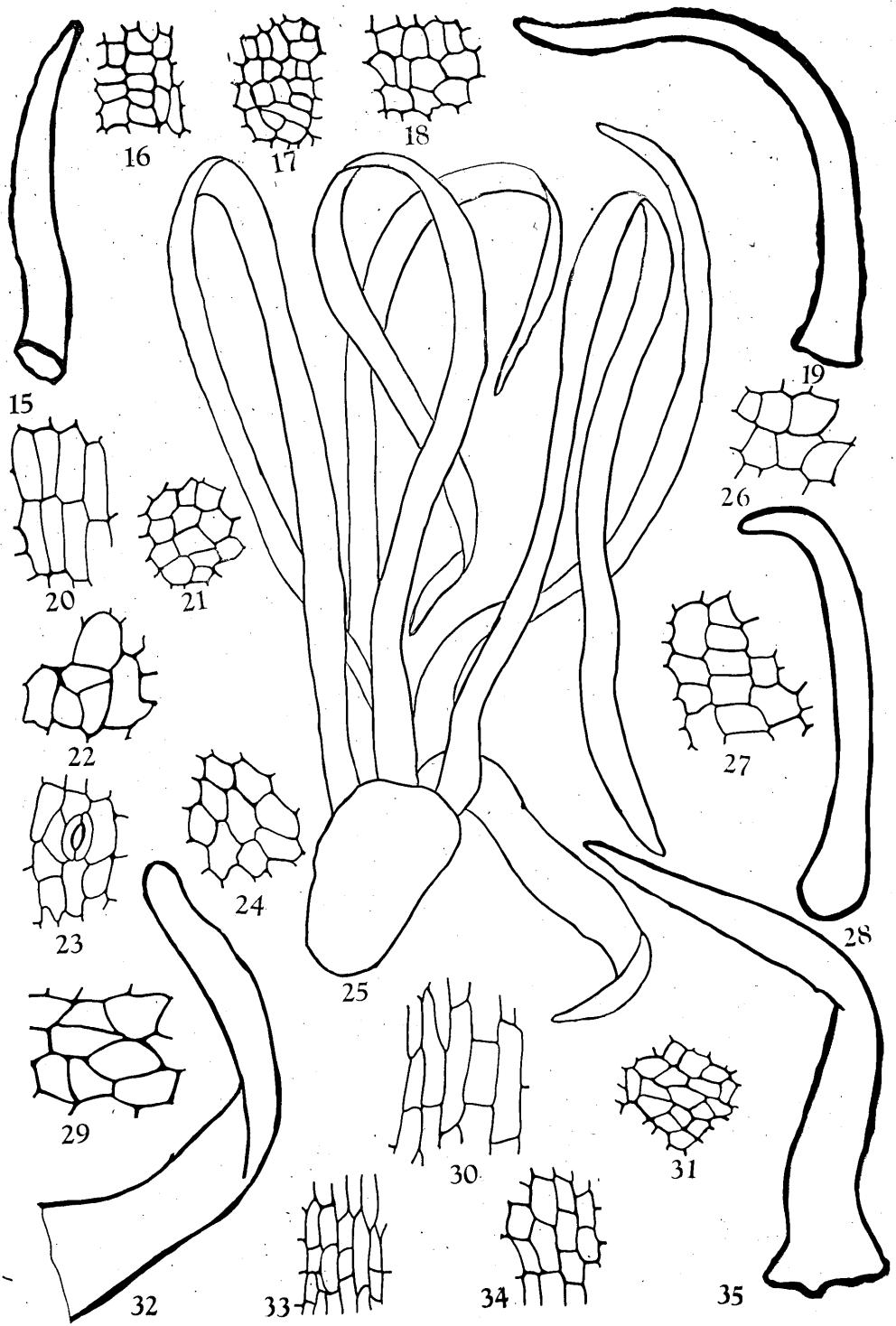


PLATE III

VENATION

X 28

Fig. 36 - *Hydrangea arborescens*

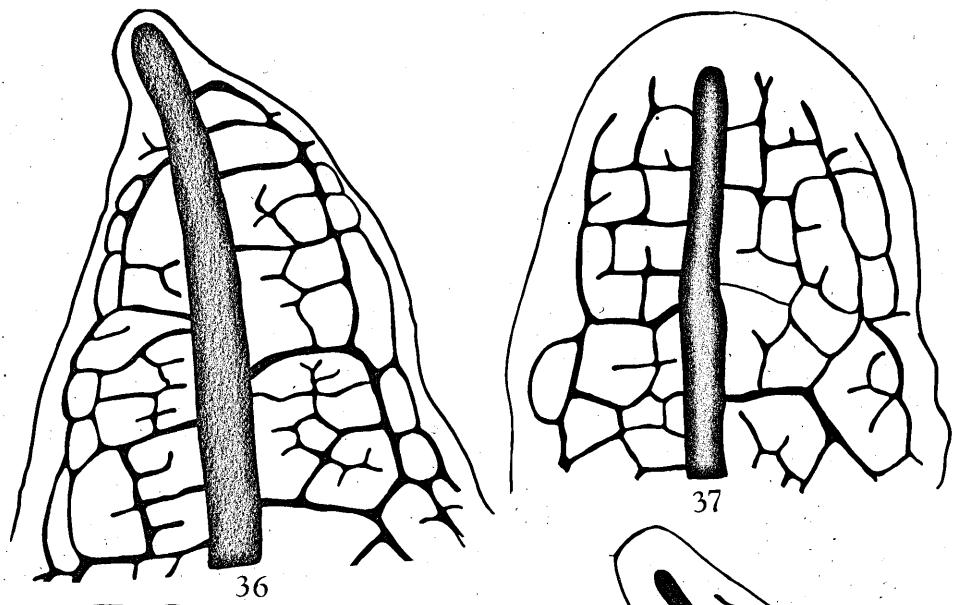
Fig. 37 - " *Bretschneideri*

Fig. 38 - " " *glabrescens*

Fig. 39 - " " *lancifolia*

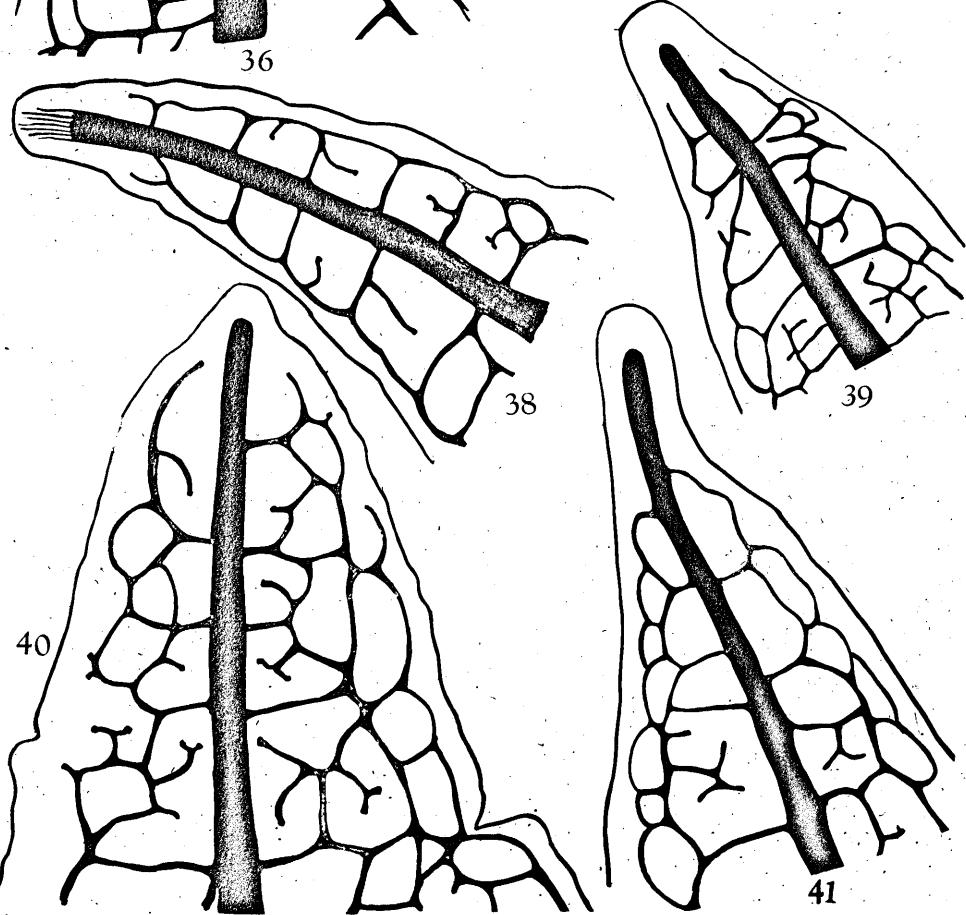
Fig. 40 - " *arborescens grandiflora*

Fig. 41 - " " *urticifolia*



36

37



38

39

40

41

PLATE IV

VENATION

X 28

- Fig. 42 - *Hydrangea paniculata grandiflora*  
Fig. 43 - " *cinerea*  
Fig. 44 - " " *sterilis*  
Fig. 45 - " " *paniculata grandiflora*  
Fig. 46 - " " *quercifolia*

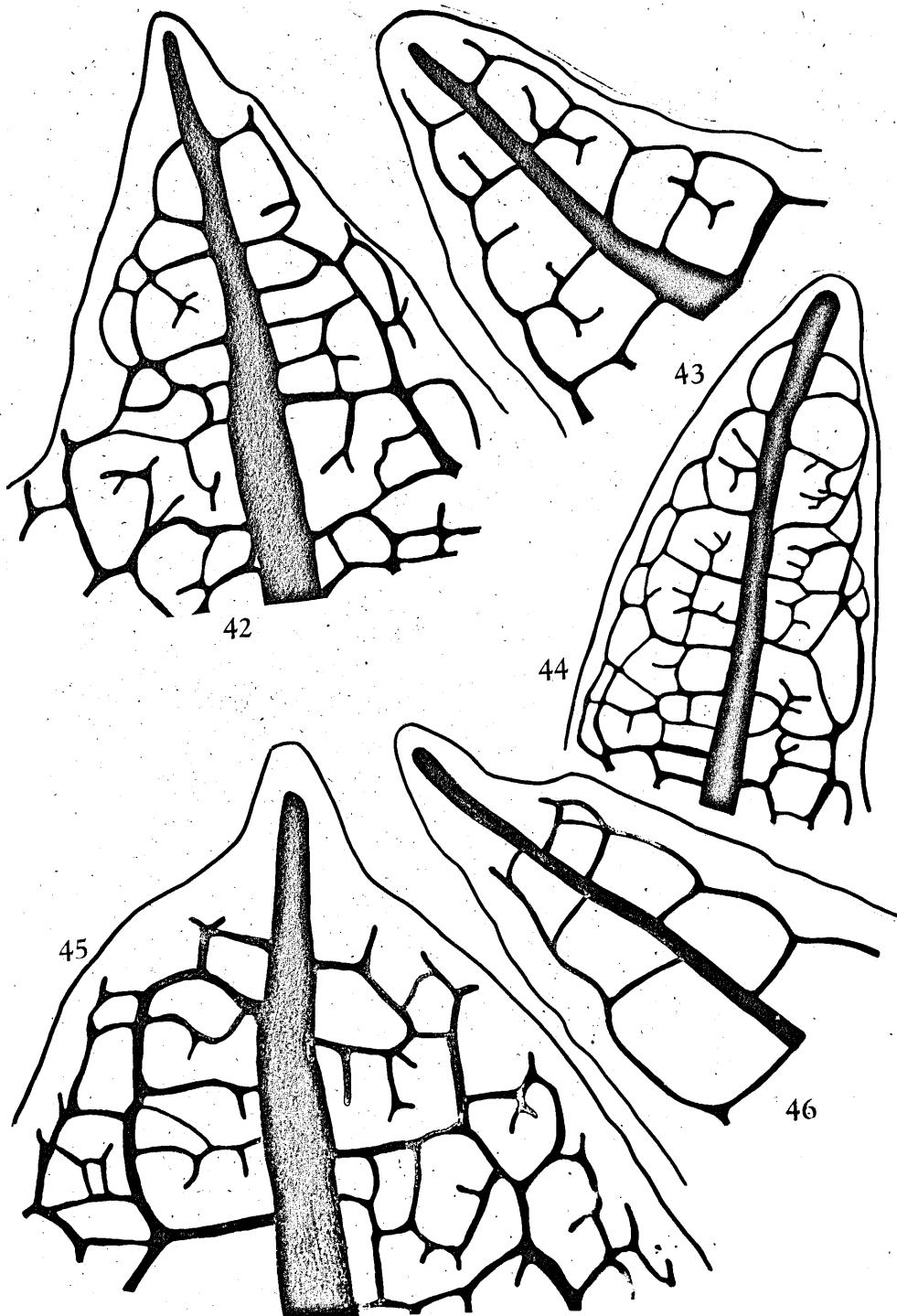


PLATE V

VENATION

X 28

Fig. 47 - *Hydrangea paniculata*

Fig. 48 - " *peticolaris*

Fig. 49 - " *xanthoneura setchuenensis*

Fig. 50 - " *peticolaris*

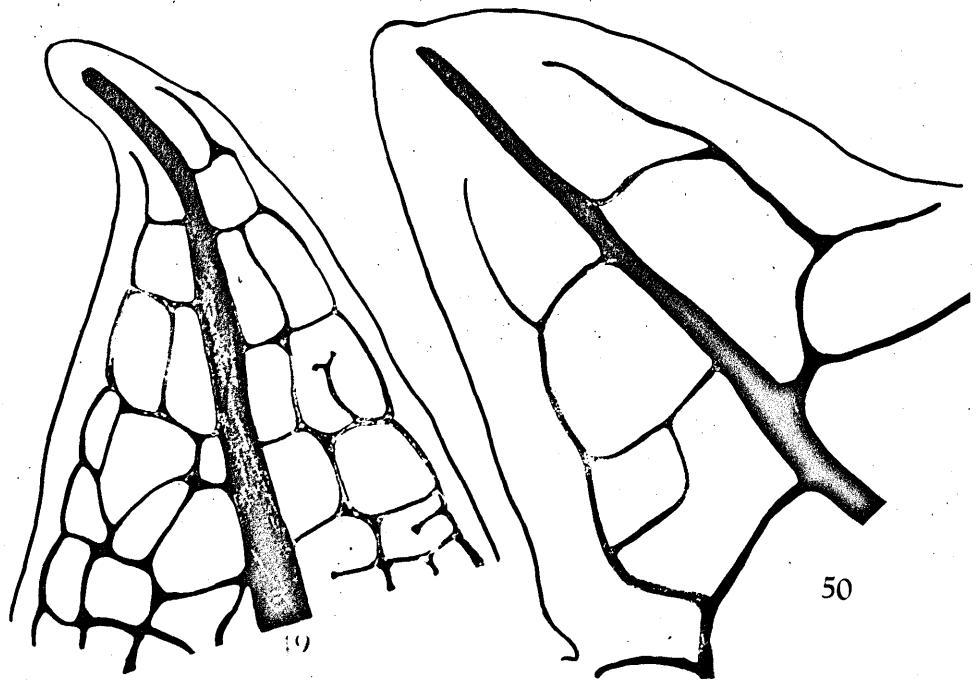
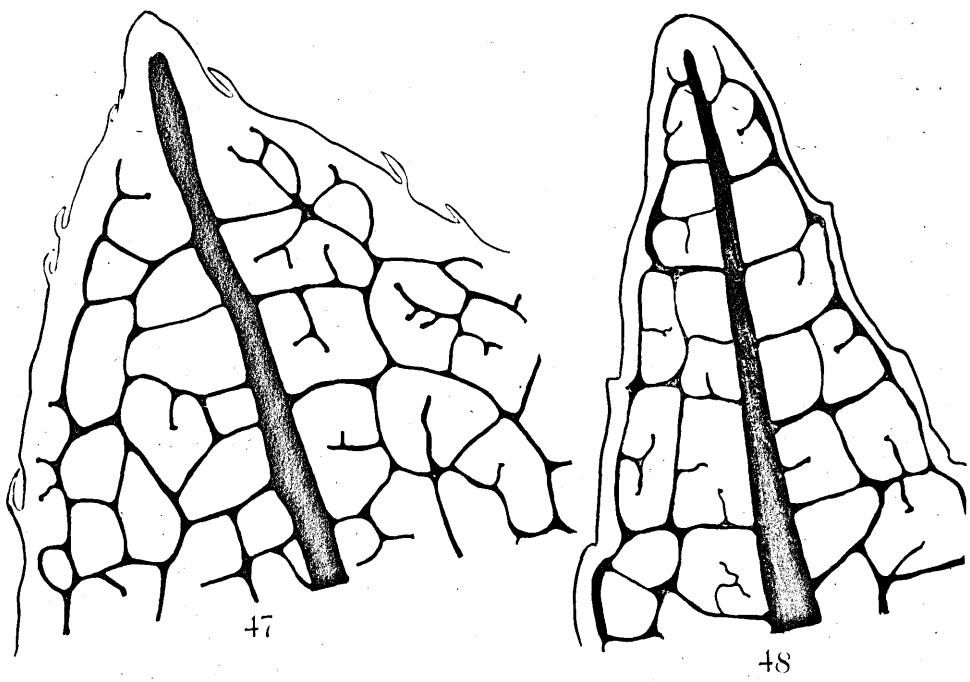


PLATE VI

LEAF EPIDERMISES AND TRICHOMES

X 182

- Fig. 51 - Upper epidermis of *H. arborescens*
- Fig. 52 - Lower " "
- Fig. 53 - Upper " " *grandiflora*
- Fig. 54 - Lower " " "
- Fig. 55 - Upper " " *urticifolia*
- Fig. 56 - Lower " " "
- Fig. 57 - Upper " " *Bretschneideri*
- Fig. 58 - Lower " " "
- Fig. 59 - Upper " " *glabrescens*
- Fig. 60 - Lower " " "
- Fig. 61 - Upper " " *lancifolia*
- Fig. 62 - Lower " " "
- Fig. 63 - Upper " " *cinerea*
- Fig. 64 - Trichome on upper epidermis of *cinerea*
- Fig. 65 - Lower epidermis of *H. cinerea*
- Fig. 66 - Upper " " *sterilis*
- Fig. 67 - Lower " " "

PLATE VI (Continued)

- Fig. 68 - Upper epidermis of *H. paniculata*  
Fig. 69 - Lower " " "  
Fig. 70 - Upper " " " grandiflora  
Fig. 71 - Lower " " " "  
Fig. 72 - Upper " " " praecox  
Fig. 73 - Lower " " " "  
Fig. 74 - Upper " " petiolaris  
Fig. 75 - Lower " " "  
Fig. 76 - Upper " " xanthoneura setchuenensis  
Fig. 77 - Lower " " "  
Fig. 78 - Lower " " radiata  
Fig. 79 - Upper " " "  
Fig. 80 - Lower " " quercifolia  
Fig. 81 - Upper " " "

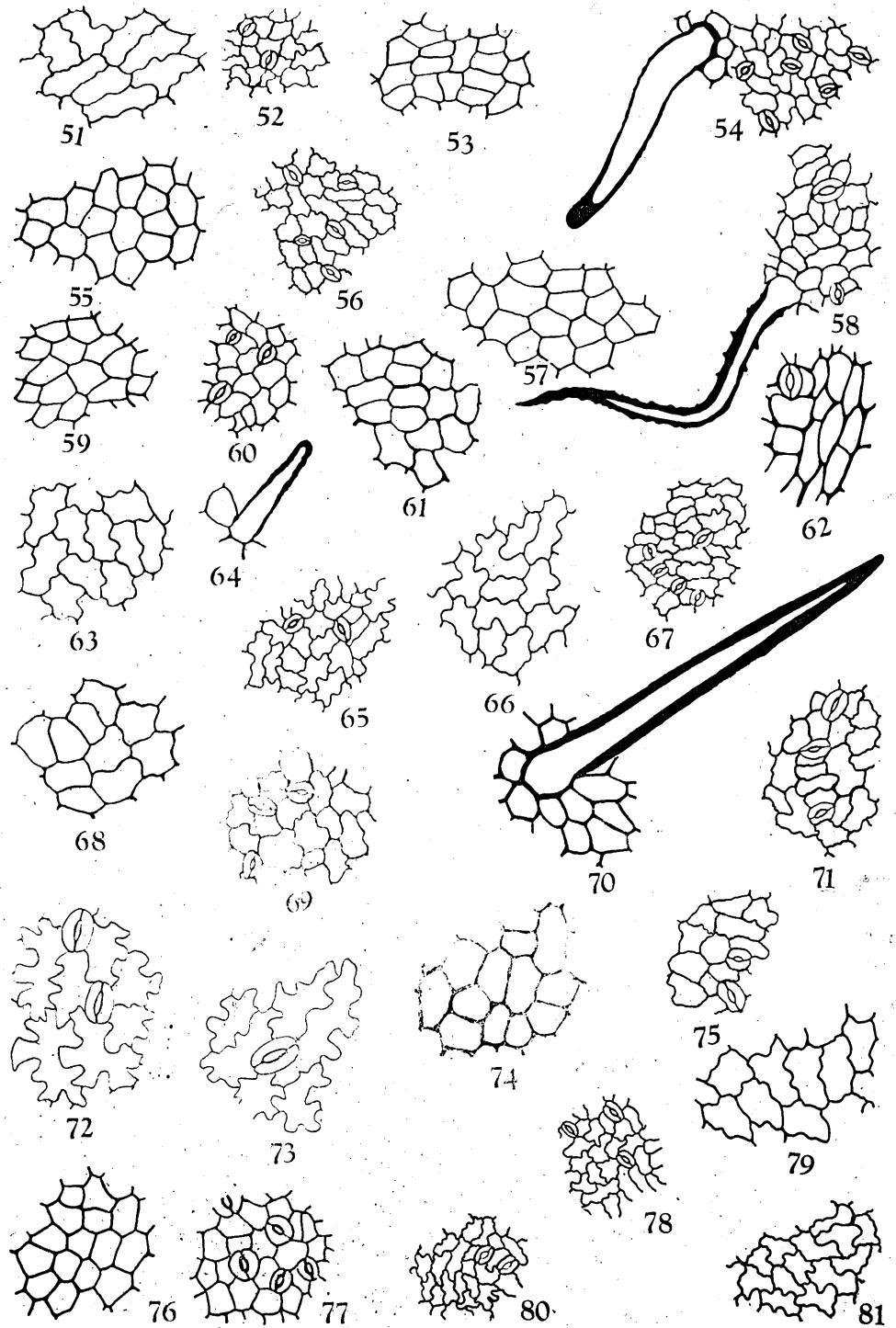


PLATE VII

CROSS SECTIONS OF LEAF MARGINS

X 182

- Fig. 82 - *Hydrangea arborescens*
- Fig. 83 - " " " *grandiflora*
- Fig. 84 - " " " *urticifolia*
- Fig. 85 - " " " *Bretschneideri*
- Fig. 86 - " " " *glabrescens*
- Fig. 87 - " " " *lancifolia*
- Fig. 88 - " " " *cinerea*
- Fig. 89 - " " " *sterilis*
- Fig. 90 - " " " *paniculata*
- Fig. 91 - " " " *grandiflora*
- Fig. 92 - " " " *praecox*
- Fig. 93 - " " " *quercifolia*
- Fig. 94 - " " " *peltolaris*
- Fig. 95 - " " " *radiata*
- Fig. 96 - " " " *xanthoneura setchuenensis*

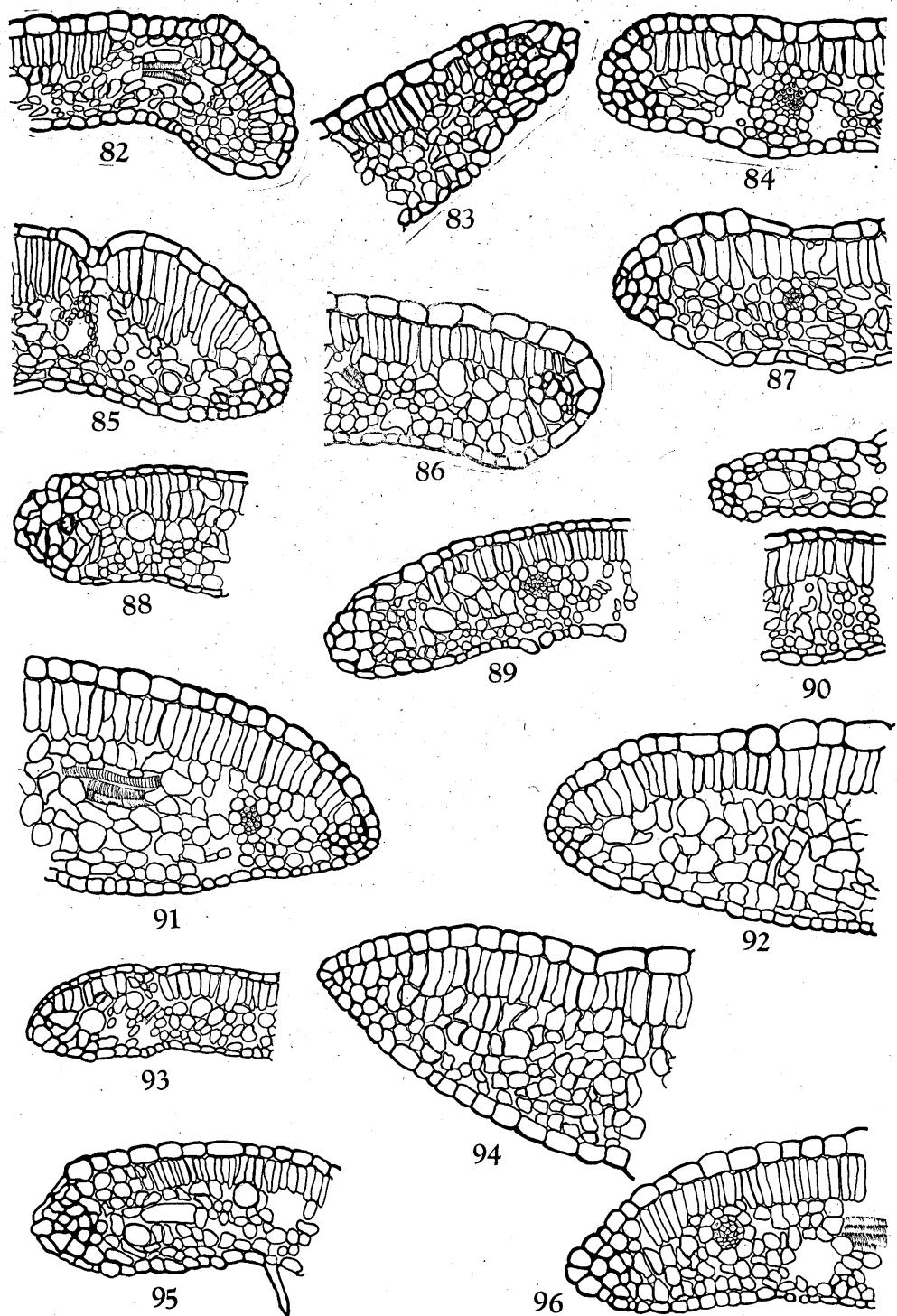


PLATE VIII

DRAWINGS OF CROSS SECTIONS OF MIDRIBS

( Vascular tissues solid; collenchyma shaded)

X 28

Fig. 97 - *Hydrangea arborescens*

Fig. 98 - " " *grandiflora*

Fig. 99 - " " *urticifolia*

Fig. 100 - " *Bretschneideri*

Fig. 101 - " " *glabrescens*

Fig. 102 - " " *lancifolia*

Fig. 103 - " *cinerea sterilis*

Fig. 104 - " "

Fig. 105 - " *paniculata*

Fig. 106 - " *paniculata praecox*

Fig. 107 - " *peltiolaris*

Fig. 108 - " *paniculata grandiflora*

Fig. 109 - " *xanthoneura setchuenensis*

Fig. 110 - " *quercifolia*

Fig. 111 - " *radiata*

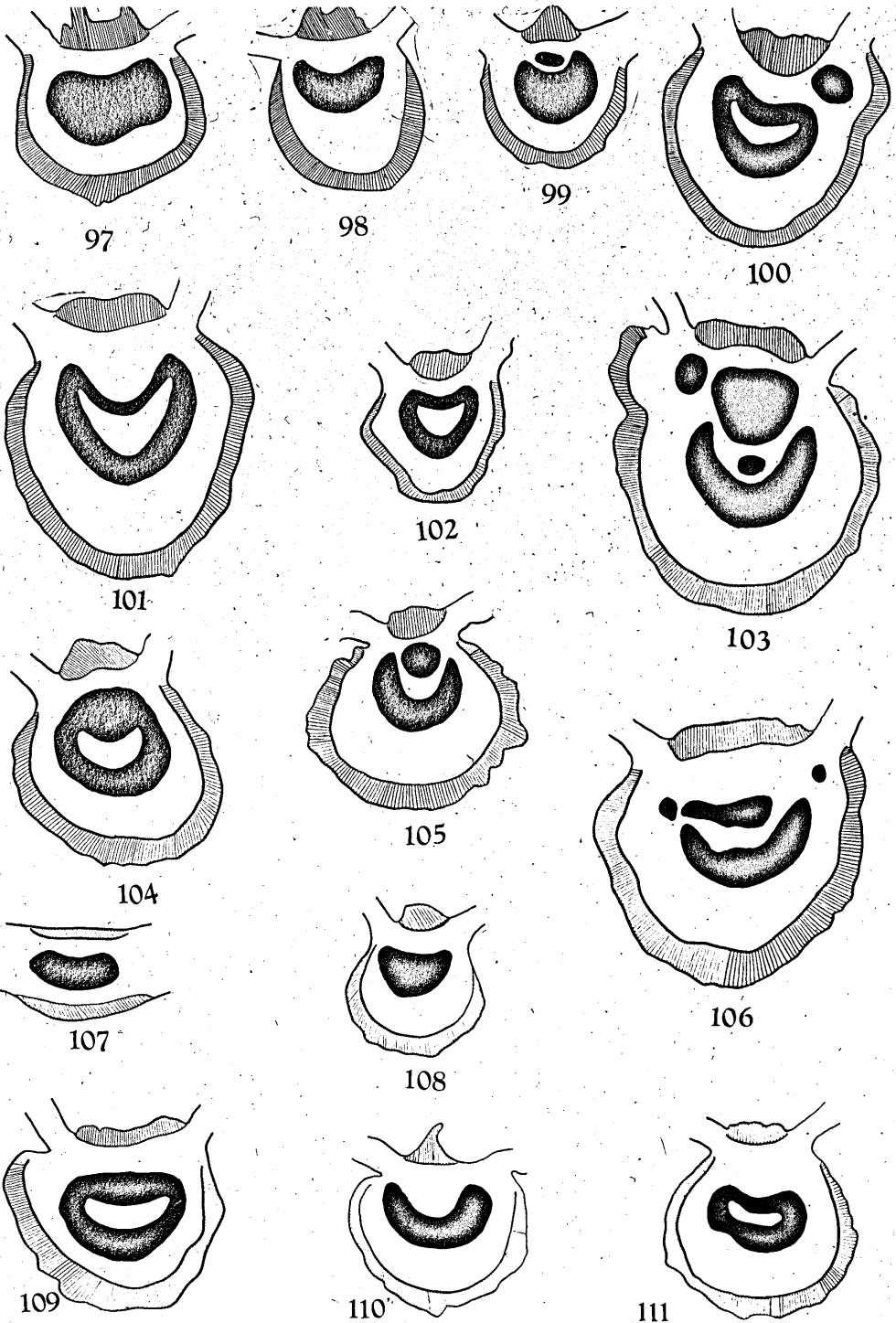


PLATE IX

CROSS SECTIONS OF STEMS

X 48

Fig. 112 - *Hydrangea arborescens*

Fig. 113 - " " " *grandiflora*

Fig. 114 - " " " *urticifolia*

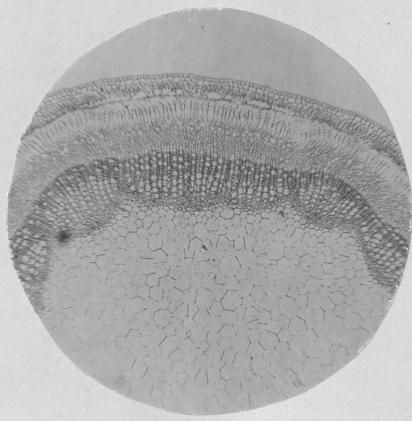


FIG. 112

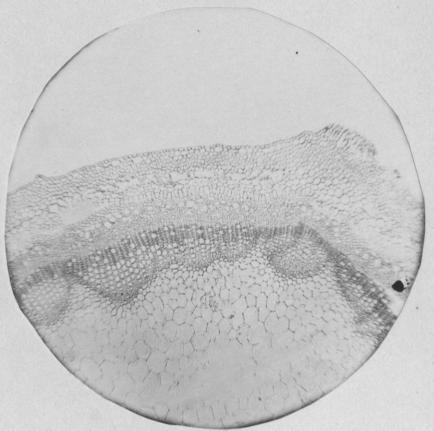


FIG. 113

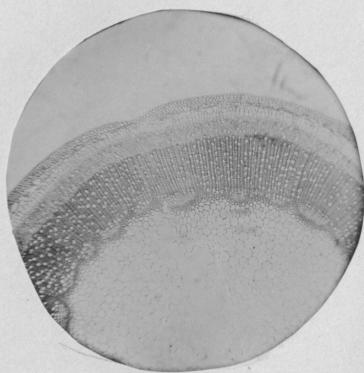


FIG. 114

PLATE X

CROSS SECTIONS OF STEMS

X 48

Fig. 115 - *Hydrangea Bretschneideri*

Fig. 116 - " " " *glabrescens*

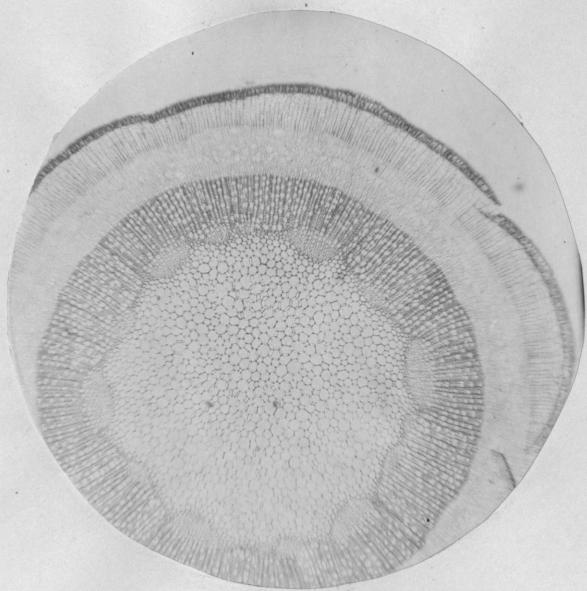


FIG. 115

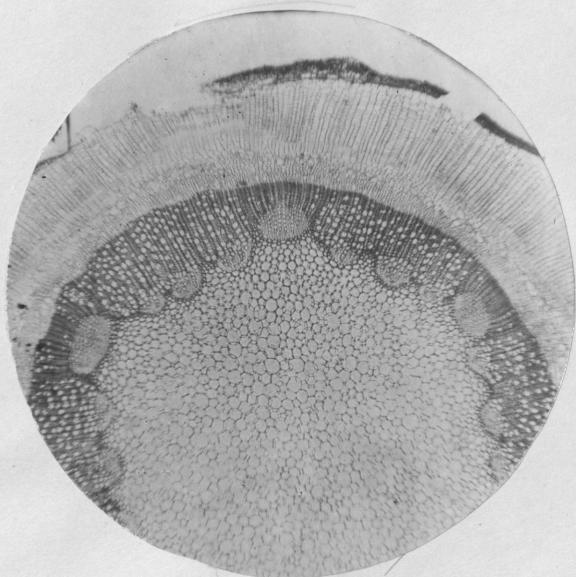


FIG. 116

PLATE XI

CROSS SECTIONS OF STEMS

X 48

Fig. 117 - *Hydrangea Bretschneideri lancifolia*

Fig. 118 - " *cinerea*

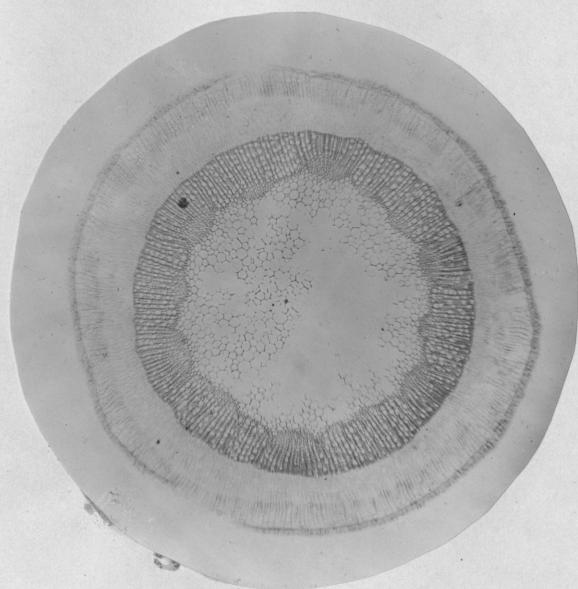


FIG. 117

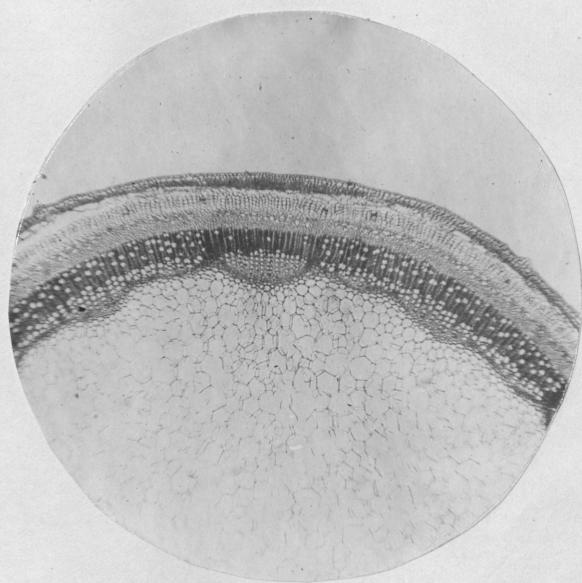


FIG. 118

PLATE XII

CROSS SECTIONS OF STEMS

X48

Fig. 119 - *Hydrangea cinerea sterilis*

Fig. 120 - " *paniculata*



FIG. 119

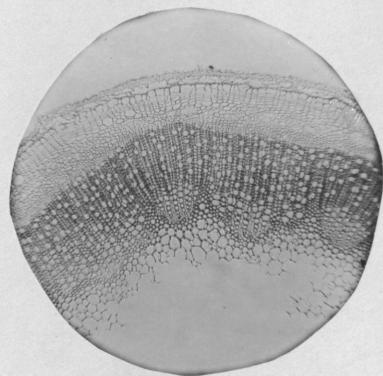


FIG. 120

PLATE XIII  
CROSS SECTIONS OF STEMS  
X 48

Fig. 121 - *Hydrangea paniculata grandiflora*

Fig. 122 : " " praecox

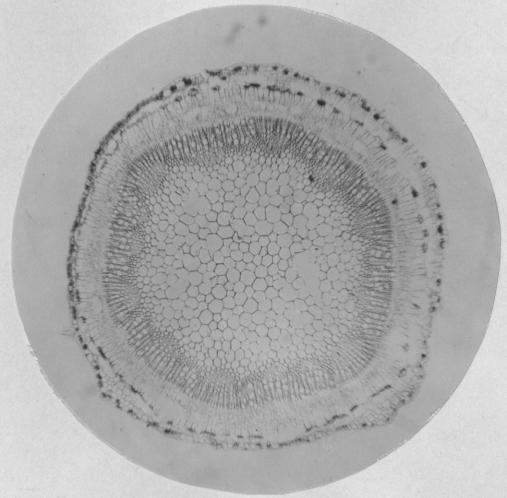


FIG. 121

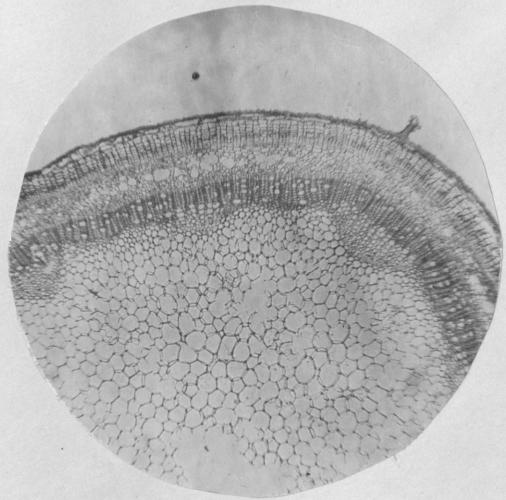


FIG. 122

PLATE XIV

CROSS SECTIONS OF STEMS

X 48

Fig. 123 - *Hydrangea petiolaris*

Fig. 124 - " *quercifolia*

Fig. 125 - " *radiata*

Fig. 126 - " *xanthoneura setchuenensis*

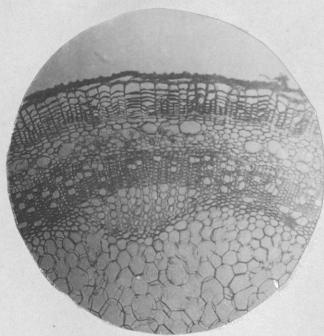


FIG. 123

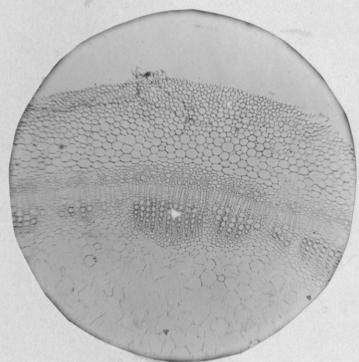


FIG. 124

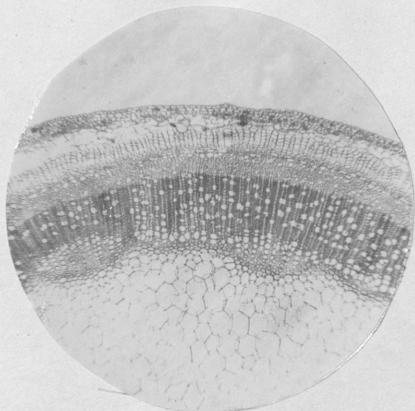


FIG. 125

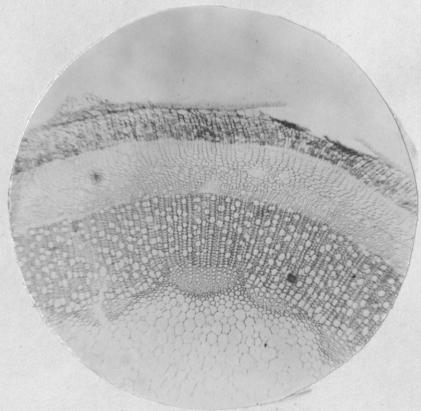


FIG. 126

PLATE XV  
CROSS SECTIONS OF PETIOLES  
X 48

Fig. 127 - *Hydrangea arborescens*

Fig. 128 - " " " *grandiflora*

Fig. 129 - " " " *urticifolia*



FIG. 127

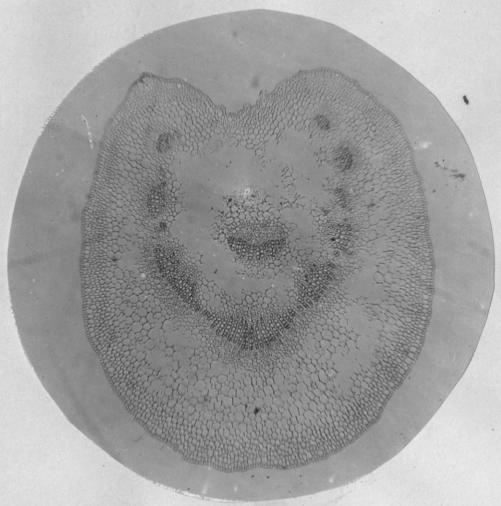


FIG. 128

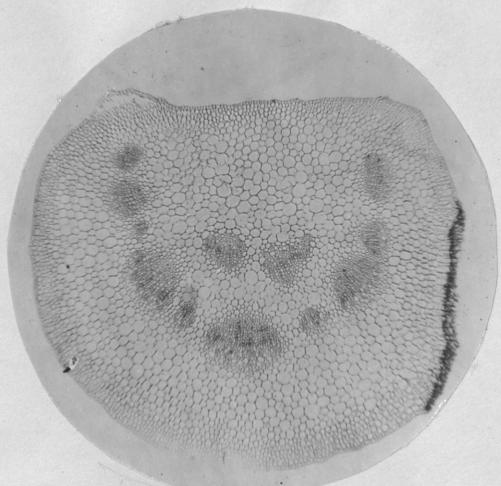


FIG. 129

PLATE XVI

CROSS SECTIONS OF PETIOLES  
X 48

- Fig. 130 - *Hydrangea Bretschneideri* glabrescens
- Fig. 131 - " " " *lancifolia*
- Fig. 132 - " " " *cinerea*
- Fig. 133 - " " " *sterilis*

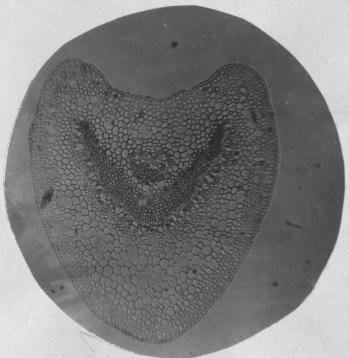


FIG. 130



FIG. 131

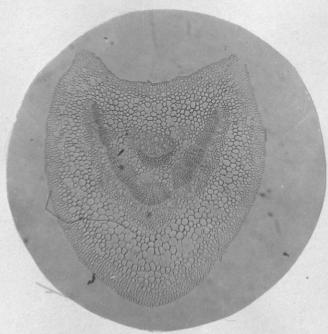


FIG. 132



FIG. 133



FIG. 134

PLATE XVII

CROSS SECTIONS OF PETIOLES

X 48

Fig. 135 - *Hydrangea paniculata*

Fig. 136 - " " " *grandiflora*

Fig. 137 - " " " *praecox*

Fig. 138 - " " *petiolaris*

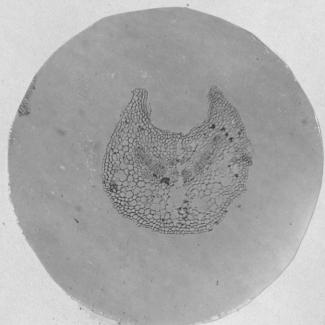


FIG. 135

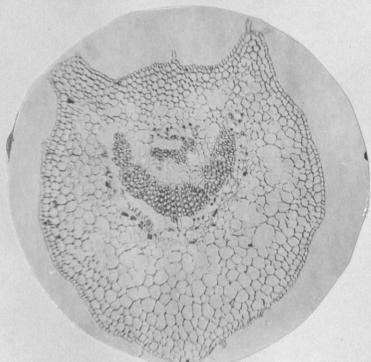


FIG. 136



FIG. 137



FIG. 138

PLATE XVIII

CROSS SECTIONS OF PETIOLES

X 48

Fig. 139 - *Hydrangea quercifolia*

Fig. 140 - " *radiata*

Fig. 141 - " *xanthoneura setchuenensis*

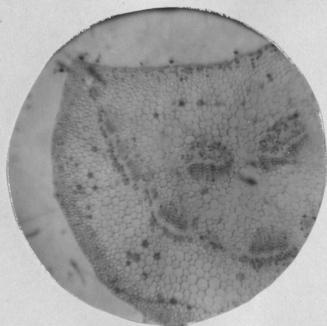


FIG. 139



FIG. 140



FIG. 141

PLATE XIX

CROSS SECTIONS OF MIDRIBS

X 48

Fig. 142 - *Hydrangea arborescens*

Fig. 143 - " *Bretschneideri*

Fig. 144 - " *cinerea*

Fig. 145 - " *petiolaris*

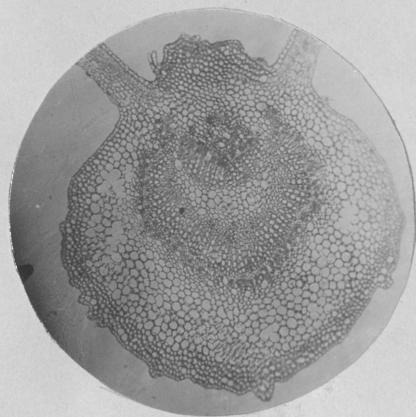


FIG. 142



FIG. 143

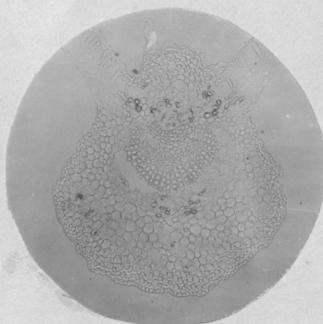


FIG. 144

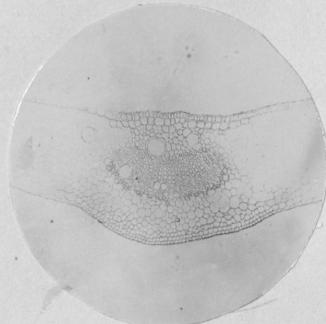


FIG. 145

## MICROCHEMICAL TESTS

In the species of *Hydrangea* used in this study, the microchemical tests show quite common features, such as storage of starch. However, some of the tests show various stored materials in interesting combinations.

Raphide crystals of calcium oxalate, stored in large crystal sacs, are common in the cortical parenchyma and pith of the majority of the species. No mucilage was found in the crystal sacs, as is commonly reported.

Sudan III shows suberin in varying amounts in different species of the genera; an especially large amount of suberized cork is characteristic of the species of *Bretschneideri*, and its varieties, while a very small amount of cork is found in the species *quercifolia*.

A very thin layer of cuticle, as evidenced by Sudan III, is characteristic of the various species. More water-proofing is not needed since cork is formed early the first growing season.

Nitric acid and ammonia, and iodine in a solution of potassium iodide were used to test for proteins. These tests show protein stored in those cells which are rich in protoplasm, or mainly the phloem and phelloderm.

Sudan III shows oil in great amounts in some of the species, especially in *Bretschneideri* and its varieties, but oil is entirely absent in other species. When found, the oil is stored throughout the pith, phelloderm, and medullary rays.

As evidenced by the ferric chloride test, tannin is commonly found throughout the stem tissues. Large numbers of tannin bodies are found in the epidermises of some species; generally in the collenchyma, commonly in the phelloderm, often in the phloem parenchyma, and occasionally in rays and pith.

Fehling's test shows very little reducing sugar to be present in any of the species; however, upon standing in Fehling's solution over night in the paraffin oven, a great amount of cuprous oxide crystals have been formed, which shows that some sugar has been hydrolyzed from some more complex substance.

It is interesting to note that the greater amounts of cuprous oxide crystals are in cells which formerly contained tannin. This seems to show that tannin, by some considered to be a complex glucoside, is broken down into simpler glucosides which in turn are hydrolyzed to glucose; it is the glucose which gives the positive test with Fehling's solution.

Equally as interesting as the great amount of sugar hydrolyzed from tannin or other substances is the association of tannin and starch in the same cells.

To show this close association, stem sections of *H. quercifolia* were treated with ferric chloride, others with K II. From the chart we see that tannin and starch are found associated in the same cells.

This close association of tannin in the same storage cells with starch is itself suggestive at least that tannin, aside from its protective functions, is one form of stored food.

## CONCLUSION

The primary object of this research has been to compare the anatomy of the various species studied and to point out anatomical features by which the various species could be identified.

The anatomy of the various species has been set forth in the preceeding pages, and now I shall attempt to compare the family characteristics set forth in Solereder with the genus landmarks as I have found them in this study, and also to point out new features which I have noticed in the genus as a whole or unique characters of a species.

Solereder speaks of subsidiary cells lying parallel to the stomatal slit. In the various species studied, no such subsidiary cells were noted. Solereder also states that stomata were found only on the lower leaf surface; however I found a few stomata on the upper surface of *H. arborescens*.

Again, in Solereder's and also Holle's descriptions it is stated that the cork is produced

internally in the genus *Hydrangea*, even as deep as the cortical parenchyma cells near the phloem. I find that in the genus *paniculata* and its two varieties a definite starch sheath occurs and that here the phellogen originates in the parenchyma cells immediatley below the starch sheath. With these exceptions the cork cambium in all of my hydrangeas originates in the parenchyma cells immediately below the collenchyma.

In another feature my findings are in disagreement with Holle's where he reports that the superficially formed cork consists of radially compressed cells. I find such cells in *Bretschneideri* and its two varieties, measuring .005 mm. to .01 mm. radially, but in all the other species studied the cork cells were much wider radially, measuring from .015 mm. to .03 mm. in that direction.

The hairy covering was especially interesting in the genus. Simple clothing-hair trichomes appeared in the majority of the species, such as are described by Solereder, but nowhere does he mention the tufted trichomes found on *H. quercifolia*. He does, however, mention that by the association

of simple unicellular hairs tufted hairs arise ~~such as~~ occur in the genera *Broussaisia*, *Calicoma*, *Cornidia* and *Pileostegia*. These hairs more closely resemble those of *H. quercifolia* than any other found in the genus *Hydrangea*.

Holle states that the rays vary in breadth, but does not mention the fact that the ray is quite uniform for a species. For example I will cite the following cases. In *H. arborescens* and its varieties *grandiflora* and *urticifolia* both uniseriate and multiseriate rays are found, the multiseriate rays being either three or four cells wide. *H. quercifolia* has outstanding rays which are 7-8 cells wide and extend vertically for a length of 16 mm. Contrasted with the large multiseriate rays of *H. quercifolia* are the relatively small uniseriate rays of *H. paniculata praecox* which extend vertically for a depth of about 1 mm.

Quoting Mentivoch, Solereder reports that the pith is heterogenous in *Hydrangea* and *Deutzia*. Such pith was absent in the various species studied by me, but tannin was found only in the pith of *H. quercifolia*.

Mention is made by Solereder of the absence of secondary bast in the family. My hydrangeas are in agreement with this excepting that a few scattered fibers were found in the stem of *H. quercifolia*.

The raphide sacs spoken of by Solereder were noted in the leaves of the majority of the species studied, but in all cases the crystal sacs were lying parallel with the leaf surface and not at right angles as stated by Solereder.

In all other respects my study confirms the previous reports on the anatomy of the genus *Hydrangea*.

In all cases a marked similarity was noted in the anatomy of a species and its varieties. This would tend to show that there is a close relation between gross external features which have been primarily used in classification and internal anatomical features.

Another matter inviting attention is a comparison of the various features of the species native to a geographic region, and then lining up such species against those that are geographically isolated from them to show by this

comparison the relation of the American to the Asiatic forms. One of the first things noted in such a comparative study is that the native American forms have an inferior type of ovary and that the Asiatic forms have both an inferior and a partly superior type of ovary. This fact was noted by Engler and Prantl and also by Rehder in separating the American and Asiatic forms. Since the inferior type of ovary is common to both the Asiatic and the American forms, we would think that the common ancestor of the Hydrangeas had the inferior type of ovary, and that the superior type has been developed later even though it be considered the most primitive type by the systematic Botanists.

The type of inflorescence is very interesting in a comparison of the Asiatic and American forms. In both Asia and America we find one native species having a paniculate type of inflorescence while the remaining species have their flower clusters in a corymb.

*H. quercifolia*, the American form having the paniculate type of inflorescence has been very interesting in other ways also; in fact, it varies so much from the other species that we might well

think it is the result of a series of mutations, and that since <sup>the</sup> only other species having the paniculate type of inflorescence is *H. paniculata*, a native of Japan and Chine, it would seem that this species is the one from which *quercifolia* has mutated. However, one could hardly assume that the tufted trichomes and the lobed leaves of *quercifolia*, which are found on no other species of *Hydrangea*, are the result of a series of mutations. It would seem more highly probable that not only is *H. quercifolia* a mutant but also a hybrid, and possibly between genera.

Since we find members of this genus in both Asia and America showing such marked similarities, such as the inferior ovaries and a native species in each Asia and America having a paniculate type of inflorescence, I think that we might well suspect that in preglacial times the genus *Hydrangea* was well distributed over what we now call North America and Eastern Asia, and that at the present time the genus is quite limited in its range by climatic conditions. I think we might also reasonably suspect that Asia, with its greater number of species and it having such a complete representation of the genus as a whole, is the original home of the *Hydrangeas*.

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