COMPARATIVE ANATOMY OF THE SPECIES OF THE

GENUS POPULUS

by

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INTRODUCTION

To the student interested in any of the many branches of
natural science, there is open an almost illimitable field for
original investigation. To the botanist, a particularly attrac-
tive field is that of comparative anatomy. While the anatomy
of certain families of the great groups is generally known,
no great amount of work has ever been conducted upon the in-
dividual genera; and of that—but a small per cent from a com-
parative point of view. Our classification of plants is based
chiefly upon external features; or in other words, we classify
plants upon gross external characteristics rather than upon
fundamental or anatomical differences.

In the light of our present scientific knowledge, it seems
plausible—in fact, indisputable that the species of any of the
various plant genera have risen from a common ancestral form.
Forms apparently closely related and yet having gross differ-
ences sufficient to place them in different species of a genus
must have been produced thru mutations, hybridization of mutants,
and possible further mutations and cross breeding.

A comparative anatomical study of the species of a given genus should reveal first of all whether there are sufficient anatomical similarities to warrant the assumption of a common ancestral form. Or, assuming the common ancestor as inevitable, the study should reveal (1) in what ways the existing species differ anatomically, (2) whether species isolated geographically are less similar anatomically than those not so isolated, and (3) whether the species can be distinguished by their anatomical characters. These, then, have been the purposes of this study of the comparative anatomy of the species of the Genus Populus.

Previous work with the Genus Populus has, with few exceptions, been motivated by a different purpose. Von Hildegard Hermann (3) in her extensive work with the wood of Salix and Populus, prepared a systematic table for classification based on the structural differences of several species of each genus.

The anatomy of the petiole of certain species of Populus was investigated by Morvillez (5) and later by Leach((4) whose purpose it was to show the relation of the anatomical structure of tne petiole to the chief physiological functions of the blade.

The work of Ursprung (6) also involved the structure of the petioles--certain species of the genus Populus being included with many other dicotyledons studied. His chief concern was of an architectural nature--the torsion capacity and its relation to the anatomy of the

leaf.

The foregoing studies have all dealt with the
species of Populus found in the Old World. The present
study includes three of the Old World forms: P. nigra,
P. alba and the so-called Chinese Lombardy[*]; and in
addition, three forms native to America: P. deltoides,
P. grandidentata, and P. tremuloides.

Moreover, it will be noted that these previous
studies have dealt with only one feature of the plant
such as the petiole, the stem, or the wood. Anyone of
these features furnishes an ample field for extensive
investigation. However, in the present research, an
attempt was made to include all important features and
to extend the comparative study to the six species
mentioned above, with the result that it proved too
vast a field for one calendar year's work. In every
feature touched upon, the work could be carried out in
much finer detail; in fact, so broad is the field and
so numerous are the points of interest which present
themselves that the subject would lend itself well to
research leading to a Doctor's thesis.

[*]This form has only recently been introduced into
the United States, and its scientific name could not
be located.

ANCESTRY OR GEOLOGICAL HISTORY

We learn from Berry that the poplars were widespread
in early geologic times. Besides the now existing forms--
about 25 in number--some 125 fossil forms have been de-
scribed. During the Lower Cretaceous period when dina-
saurs still inhabited the earth, and forms of ferns,
cycads, and conifers of the older Mesozoic Era still
survived, so far as our fossil record shows, the first
poplars made their appearance. It is interesting to note
that a poplar of this period found in the Kome beds of
Greenland was for a long time the oldest known dicotyledon.
Another form of this early period is found in the
Potomac River Valley. Thirty species of poplar have been
found in the deposits of the upper cretaceous period.
They were then common in Greenland, and widespread
thruout North America. During the Eocene period which
followed, 50 species are known to have existed. Leaves
of poplars are the most abundant fossils of the contin-
ental deposits of this period. At this time they seem
to have covered all plains and mountain countries of the
West and to have encircled the globe in high latitudes.
Records are found in Greenland, Siberia and Manchuria.
Apparently but few species occured in central Europe,
the great bulk being American and Arctic. The 30 species
of the succeeding Miocene, flourished from Greece west
to Spain and thruout the western United States and Canada.
Following this came the Pliocene which has contributed

16 species, several of which are close to or identical with existing forms, such as the European Aspen and the silver poplar. Fossils have been found in deposits from Asia Minor to Spain. Of the 10 existent species of the Pleistocene, only 2 are extinct. Of the forms studied, for this thesis, Pleistocene fossils are found of P. nigra in Italy, P. alba in both England and France, and P. deltoides in the river terrace deposits of Alabama and Western Kentucky.

At the present time, species of the Genus Populus are well distributed thruout the boreal and temperate regions of the northern hemisphere. Great forests composed of Populus occur in the extreme north. In the New World, they are scattered southward to Northern Mexico and Lower California; in the Old World, to Northern Africa and the southern slopes of the Himalayas, upon which Populus ciliata and Populus microcarpa are found. According to Sargent (7): "9 species now inhabit British America and the United States where they are found from the Atlantic to the Pacific and the Artic Circle to Mexico, lining the banks of streams in the northern and central regions of the continent and growing on high mountain slopes. In the eastern hemisphere they extend north to the Artic Circle; abound in northern and central Europe and northern and central Asia, where they are often the most conspicuous forms of vegetation."

The species of Populus presented in the anatomical research of this thesis are distributed as follows: P. alba, the silver leafed or white poplar, is of European origin. There it is distributed from eastern and southern England all over central and southern Europe to northern Africa. It is found in western Siberia, Syria, Asia Minor and the foot hills of the northwestern Himalayas. In eastern America it has become sparingly naturalized from the valley of the lower St. Lawrence to northern Alabama.

The fastigiate form of the Black Poplar of Europe-- P. nigra Italica had its origin in Afghanistan and is thought to have been introduced into Europe by the Arabs. It is found growing wild in the forest at Shakhabad near Cabul at an altitude of 7500 feet. It is cultivated quite extensively thruout eastern and central North America where it has found favor with the landscape designer.

The Chinese Lombardy is a fastigiate form recently introduced into the United States from Asia.

Populus tremuloides or American Aspen, is the most widely distributed tree of North America, being found from Labrador to Alaska, south to Pennsylvania and Missouri, as well as in California and on the mountain slopes of Colorado, Arizona and New Mexico.

Populus grandidentata, the Large-toothed Aspen, occurs in rich woods and stream borders from Nova Scotia to the mountains of North Carolina, west to

Ontario, Minnesota and Iowa.

Populus deltoides, sometimes known as the Necklace Poplar--and also designated as the Common Cottonwood in this region is found along stream borders from western Quebec and New Hampshire south to Florida and west to the Rocky Mountains.

METHODS

The preparation of materials for this research involved only ordinary processes as explained in Steven's "Plant Anatomy".(9) One of the most important steps in preparation for embedding--either in paraffin or celloidin--is the removal of air from the plant tissue by means of a suction pump. All leaf material from both petiole and blade was found very satisfactorily prepared when embedded in paraffin, sectioned on the rotary microtome, mounted, and stained in safranin.

Stems and other woody material could be more easily and satisfactorily sectioned if first desilicified by soaking in a 50 % hydrofluoric acid solution for a week or two and then embedding in celloidin. Such material was of course sectioned on the sliding microtome.

It was found that fresh material--both leaves and stems--or material which had been preserved in 4 % formalin could be satisfactorily sectioned on a sliding microtome if first dipped in paraffin (heated just above the melting point) to protect the epidermis, and then placed between pieces of pith.

Good sections were made from older wood if the wood was first boiled and then placed for some time

in a mixture of equal parts alcohol, glycerine, and water.

In the maceration of woody material, a combination of two well-known processes was used. Small tangential sections were first treated by the Mangin process; that is, were placed for 48 hours in a mixture of four volumes of alcohol and one volume of hydrochloric acid. Then they were rinsed in water and placed for a few minutes in a saturated solution of chromic acid. When mounted in a drop of water, the fibers could be teased apart easily.

All drawings were made under a microscope projector, illuminated with an automatically regulated arc light.

DESCRIPTION AND COMPARISON OF SPECIES

The variation in the external appearance of the leaves of the various species of the genus Populus is marked. In the six forms studied there is not an outstanding characteristic applicable to the leaves of all species.

P. deltoides (Fig. 5) and P. nigra (Fig. 6) resemble each other most closely. P. deltoides is usually characteristically deltoid in shape and rather abruptly acuminate. P. nigra varies considerably in form but usually is broader than long, is often cuneate at the base, and is more pronouncedly three-nerved from the base of the blade than P. deltoides. P. tremuloides (Fig. 3) is generally ovate or semi-orbicular in form and slightly cordate at the base. The margin is finely serrate, whereas the margins of the former two are rather coarsely crenate. Leaves of P. grandidentata (Fig. 1) are ovate and very coarsely crenate. These four forms are much alike ih texture; and all four have elongated petioles which are compressed laterally. No difference of color on the upper and lower surfaces of P. deltoides is noted: the other three seem slightly lighter on the lower surface. The aspens, particularly P. grandidentata, seem more papery in texture.

The upper surface of P. alba (Fig. 2) is smooth dark green—sometimes slightly pubescent along the veins; in sharp contrast the lower surface is woolly-white—tomentose. The petiole is not so definitely elongated nor so markedly compressed laterally, as will be noted in the diagram of the cross section. The margin is deeply toothed and on the younger twigs the leaves are quite distinctly 5 lobed.

The leaf of the Chinese Lombardy (Fig. 4) is leathery in texture, dark green above; and glabrous and slightly lighter below. In decided contrast with the other forms are its obovate shape, its very short ridged petiole, and its prominent pinnate venation.

BLADE

The anatomical variations in the leaves of the different species is less prominent, though marked differences do occur. The outstanding and perhaps most distinguishing feature noted in an examination of the cross section of the leaves is the amount and arrangement of palisade tissue. In all species, two rows of palisade cells occur next the upper surface of the leaf. The rest of the space between the upper and lower epidermal layers is taken up, ordinarily, by spongy parenchyma tissue.

However, this does not hold true in P. deltoides (Fig. 7). In this species, two additional rows of palisade cells lie next the lower epidermis. The external likeness of the two leaf surfaces is indicative, or at least suggestive of internal similarity and such proves to be the case. The average thickness of a P. deltoides leaf measured in cross section is .15 mm. The palisade cells vary considerably in length, but the average within a species appears to be quite constant; the average for P. deltoides being .023 to .03 mm.

The two other native species, P. grandidentata (Fig. 11) and P. tremuloides (Fig. 9) resemble each other greatly in their anatomy. Both are characterized by peculiarly thickened epidermises, the irregularity of which appears most marked in a surface study of the leaf of P. grandidentata. This feature will be mentioned again in connection with the descriptions of stomata. The tissues of both are arranged in the type manner; that is, with two rows of palisade cells above, and spongy parenchyma next the lower epidermis. The blade of P. grandidentata averages .12 mm. in thickness. The palisade tissue composed of cells approximately .023 mm. long occupies about one half the space between epidermises. The rest of the space is occupied by three or four rows of spongy parenchyma cells with frequent air spaces.

The blade of P. tremuloides averages slightly
more-- about .15 mm. in thickness. Here the palisade
cells, which are more compactly arranged than those of
P. grandidenlata, but are also .023 mm. long, take up
less than one-half the inter-epidermal space, with the
result that one or two more rows of spongy parenchyma
cells occur. The spongy parenchyma of P. tremuloides
is more compact than that of any other species studied.

The leaf of Chinese Lombardy (Fig. 8) an Old
World form, is the thickest of all species in cross
section. Its average thickness is .22mm., half or
sometimes less than half of the inter-epidermal thick-
ness being composed of palisade cells which average
.045 mm. in length and often are longer. The cells
of the spongy parenchyma are loosely arranged with
numerous large intercellular spaces.

In P. nigra (Fig. 10) also, about half the inter-
epidermal thickness of the leaf--.15 mm.--is occupied
by palisade tissue, but the individual cells average
only .025 or .03 mm. in length since the thickness of
the leaf is less. Their length is comparable to those
of P. deltoides, but they are broader. Comparative-
ly large air spaces are found among the parenchyma
cells.

P. alba (Fig. 12) resembles the aspens in its
leaf thickness, often measuring scarcely .12 mm. wide,
in cross section, though it appears heavy in external

aspect due to the numerous hairs which arise from the lower epidermis. (The hairs are not shown in the drawing, Fig. 12). The palisade tissue occupies over one-half, often two thirds, of the inter-epidermal area, and is composed of two, occasionally three, very compact rows of cells, averaging .034 mm. in length. The three or four rows of spongy parenchyma cells are rather compactly arranged.

Various other anatomical differences are noted in the leaf blade; but along with these differences is such a marked variation of individuals within the same species that they carry little value for the purposes of this thesis.

EPIDERMIS

In this connection, the study made of the epidermises and the arrangement and number of stomata seems worthy of mention. Here again, P. deltoides, the most common species in this region may be taken as a standard for comparison. Fig. 15 shows the comparative largeness of its epidermal cells, the regularity of their arrangement, and something of the frequency of stomata as well as the variation in their size. By actual count, P. deltoides was found to have an average of 62 stomata per sq. mm. on its upper leaf surface, and 145 per sq. mm. on the lower.

The lower epidermis of P. grandidentata (Fig. 18)
shows a marked contrast to that of P. deltoides. The
irregular thickening mentioned before, gives an un-
dulating effect which makes it almost impossible to focus
well enough on the epidermis to make an accurate drawing.
The drawing serves merely to show this irregularity
of cell outline and the comparative smallness of the
stomata. No stomata occur in the upper epidermis of P.
grandidentata, but a proportionately larger number--
approximately 330 per sq. mm. are found in the lower
epidermis.

P. tremuloides (Fig. 17) more closely resembles
P. deltoides in a surface drawing. For some reason
which the writer is unable to explain, the irregular
epidermal thickening, so similar to that of P. gran-
didentata in cross section, fails to produce the same
irregularity in surface outline. As in P. grandidentata
there are no stomata in the upper surface, and the aver-
age in the lower is considerably smaller--about 225 per
sq. mm.

Of the Old World forms, both P. nigra (Fig. 16),
and the Chinese Lombardy (Fig. 13) resemble P. deltoides,
though the arrangement of cells in each is more irregular
and variable. P. nigra has an average of 126 stomata
per sq. mm. in the lower epidermis and of 90 per sq. mm.
in the upper. The Chinese Lombardy has fewer stomata

per unit area of leaf surface than any other species studied; an average of 90 per sq. mm. occur in the lower surface, and 50 in the upper.

The epidermal cells of P. alba (Fig. 14), as well as the stomata, are smaller than in any species except P. grandidentata. No stomata appear in the upper surface, and as might be expected, a correspondingly larger number occurs in the lower--340 per sq. mm. being the average count.

PETIOLE

The petiole is, perhaps, the most characteristic feature of the Genus Populus. With one exception, the species studied have petioles which are definitely compressed laterally from below the central portion to the blade of the leaf. Cross sections of this portion of the petiole are definitely oval in shape; and since this is an important region of the petiole from the physical standpoint, sections of this region were studied in detail .

The outermost layer is, of course, the cutinized epidermis, the similarity of which among the various species necessitates little comment. It appears comparatively thicker in the Chinese Lombardy but varies too greatly with the individual to draw definite conclusions.

Just beneath the epidermis, as in all petioles, lies the collenchyma, occupying comparatively the same region in all species. The chief difference noted is the degree of thickening of the outer rows of cells, and the definiteness of the boundary between the collenchyma and parenchyma cells.

In P. deltoides (Fig. 23) the outer rows of cells show only a moderate thickening, and the change from collenchyma to parenchyma is so gradual that it is almost impossible to determine where the collenchyma ceases. The collenchyma region of P. grandidentata (Fig. 20) is practically identical with that of P. deltoides. However, P. tremuloides (Fig. 21) shows a marked thickening of the 3 or 4 outer rows of collenchyma, with the same gradual change to the thin walled parenchyma cells of the cortex.

In the Chinese Lombardy (Fig. 25) the thickness of the cell walls is outstanding--so marked in fact that in places scarcely any cell cavity remains. The corresponding cells of P. alba (Fig. 22) are conspicuously thickened, and there is a definite boundary between the collenchyma and parenchyma. P. nigra (Fig. 24) resembles P. deltoides in the moderate thickening of the cell walls, and the gradual change to thin walled parenchyma.

The parenchyma beneath the collenchyma appears like a matrix in which the vascular bundles--the very vitals

of the petiole--lie imbedded. Three bundles, or ag-
gregates of bundles compose the leaf trace which enters
the petiole from the stem. In cross section the base
of the petiole is ovoid or oval, having one surface--the
upper one--flattened. The three bundles or groups of
bundles constituting the trace lie in a slightly curved
plane following the curve of the section. Fig26 shows a
basal section of P. tremuloides which gives the arrange-
ment of tissues typical in all species. Differences in
tissues are comparable to those in the flattened portions
of the petioles.

A series of cross sections cut consecutively thru
the length of the petiole of any species having the
laterally compressed type shows that as the petiole be-
comes more definitely rounded above the basal portion and
below the upper and flattened portion the bundles are
divided and tend to form a circle of bundles which are
bordered toward the center and on the sides by funda-
mental tissue. Sections from the flattened portion
show the bundles again arranged in one plane, but now
perpendicular to the plane of the surface of the blade.
The number of bundles in corresponding regions varies
within the species. As the bundles pass from the petiole
into the midrib of the blade they again tend to arrange
themselves in a circle, finally merging to form only
one large bundle surrounded by hard bast. The drawing

of P; nigra (Fig. 19) shows a section through the mid-
rib where this merging has been effected.

It was noted that the comparative amount of tissue
composing the bundles varies according to the age of the
leaf. For example, cross sections of petioles as well
as of the blades made from P. deltoides specimens col-
lected early in the spring and soon after the leaves had
reached full size, shows scant development of phloem
and no hard bast. Sections made from material gathered
two months later shows marked increase in the amount of
phloem, and prominent regions of hard bast have develop-
ed.

The most prominent difference between the species
noted in cross sections of the petiole is in the amount
and arrangement of the hard bast. With the exception of
an occasional isolated strand, it is found just out-
side the phloem, forming a protective ring--either con-
tinuous or composed of separate strands. This ring may
surround either a single bundle, as is commonly the case
with the bundles in the upper side of the petiole (the
narrower portion as seen in cross section) or it may
surround a group of two or more bundles.

The discontinuity in the ring of hard bast is un-
doubtedly useful to the plant in allowing for inter-
change of food and other materials. As already noted
by Ursprung (6) and Leach (4), this breaking up of the
hard bast and xylem into strands also provides for the

twisting and bending movements of the mechanical strands
in the petiole without injury to the soft living tissue.

In P. deltoides (Fig. 23) the hard bast rings sur-
rounding the upper and lower bundles are distinctly
segmented, while those around the center bundles tend
to be continuous. In P. grandidentata (Fig. 20) the
arrangement is remarkably like that of P. deltoides
with the exception of that which surrounds the two
small upper bundles that lie in adjacent positions;
here it is nearly continuous. In p. tremuloides (Fig. 21)
the hard bast zones are in most cases continuous.

In P. nigra (Fig. 24) there is more of a tendency
for the hard bast to be broken into segments than is the
case in other species. P. alba (Fig. 22) shows a
noticeably smaller amount of hard bast developed, and
while the hard bast occupies the corresponding region,
its segments are much more widely separated and con-
sequently offer less protection to the adjacent phloem
but provide for better interchange of materials. In the
Chinese Lombardy (Fig. 25) the most marked difference
occurs. Since the petiole is not laterally flattened
and is relatively short, no scattering of the vascular
strands occurs. The entire vascular system is sur-
rounded by a ring of hard bast composed of narrow
separated strands.

THE STEM

In cross section, the one year stems likewise uphold the assumption of a common ancestor. All species are alike in some respects. Immediately below the epidermis lie several rows of cork cells, an average of four being found in twigs picked about three months after growth had started, and the inner layer being meristematic in nature and known as cork cambium. Next lie a few rows of collenchyma, then parenchyma, and finally a broken ring of bast surrounding the vascular cylinder which may or may not be five-angled. In all species studied, the pith is at least obscurely five-angled.

P. deltoides (Fig. 27) is distinct in having a relatively larger amount of collenchyma. Its cork cells are squarish. The vascular cylinder, particularly on its inner border, is definitely five-angled. Stone cells occur only rarely in the primary cortex and pericycle, usually in scattered groups but sometimes adjacent to the hard bast. The phloem area is comparatively larger than in any other species; and the hard bast ring is more segmented though the segments lie in close proximity. Crystals of calcium oxalate are numerous.

Compared with P. deltoides, the collenchyma of P. grandidentata (Fig. 28) is poorly developed—only

two or three rows of cells appearing between the cork and stone cells. The early and very pronounced development of stone cells may account for the fact that a more extensive development of collenchyma has not occurred. Practically continuous hard bast surrounds the vascular region which is prominently five-angled.

P. tremuloides (Fig. 32) differs from P. deltoides as does P. grandidentata. It, too, is unique in having large and irregular masses of stone cells in the primary cortex separated from the cork cells by two or three rows of collenchyma. The pith and wood are five-angled as in P. grandidentata. The continuity of its hard bast is intermediate between that of P. deltoides and P. grandidentata.

All three Old World species vary from P. deltoides in having a comparatively smaller amount of collenchyma, and a very obscurely five-angled vascular region. The hard bast ring is segmented in all, but the segments are less numerous than in P. deltoides. The first cork cells which are definitely squarish in P. alba (Fig. 31) and P. nigra (Fig. 30) tend to elongate radially in the Chinese Lombardy (Fig. 29). Intercellular spaces of the primary cortex are most numerous in this species-- particularly just within the collenchyma.

In the study of the two-year stems, care was taken to obtain sections from the same internode by

counting from the terminal bud scar of last year's growth. In a section thus taken P. deltoides (Fig. 33) shows little change with the exception of the addition of the second year's zone of wood and phloem. No stone cells appear in the secondary thickening.

A corresponding section of P. grandidentata (Fig. 37) shows that a ring of secondary, hard bast has been deposited by the cambium early in the season's growth. A study of a like section from P. tremuloides (Fig. 36) shows that here, too, a ring of hard bast is being laid down but is slower in developing than in the previous species.

Likewise, in the Old Word forms, little change has taken place; the only variation here also being in the deposit of hard bast by the cambium. P. nigra (Fig. 36) shows an almost continuous ring of hard bast laid down, with the second year's deposit of phloem still very scant. P. alba (Fig. 35) as yet shows no deposit of secondary bast. Stone cells are still lacking in all these forms.

There is a marked similarity of the wood of all species. It is composed of medullary ray cells, water tubes, tracheids, wood fibers and various intermediate forms. No xylem parenchyma occurs. With two exceptions, sections for the comparison made were cut from wood produced the third or fourth

year. Sections of P. tremuloides and P. grandidentata were made from small two year stems, so that in this respect the basis for comparison is not so accurate as might be desired.

In all species the medullary rays are distinctly narrow, being but one cell in cross section. Von Hildegard Hermann (3) found two rows of cells in P. alba but this distinction does not occur in my material representing the American form. The radial extent of the medullary ray cells varies with the individual within a species as well as among the species. The water tubes lie adjacent to the medullary ray cells or are separated from them by one or more rows of schlerenchyma.

There is a noticeable difference between the early and late growth of wood as seen in cross section. Figures 39 to 44 show the early growth of each species. In P. deltoides (Fig. 39) the tubes thruout the season's growth average larger than those of any other species studied. They usually lie singly; aggregates of two or more water tubes occur but are not common. A decrease in the number of tubes is apparent in the late growth.

The tubes in P. grandidentata (Fig 43) are very much smaller than those of P. deltoides, but are more numerous, particularly in the early growth. Aggregates of two, three, or more tubes frequently occur.

The Chinese Lombardy (Fig. 40) ranks next to P.

deltoides in size of water tubes. The tubes are more numerous per unit area in cross section. Aggregates of two or three tubes are found more commonly than single tubes in the early growth, though the reverse is true for the late growth.

The water vessels of P. nigra (Fig. 41) also are smaller than those of P. deltoides. Tubes either single or in pairs are most common in the early growth. In the late growth they are smaller and commonly occur in groups of three or four.

P. alba (Fig. 43) produces the smallest vessels of any Old World species. However, they are more numerous and occur in groups of three or more, more often than singly. The late growth shows a decrease in number as well as in size of the vessels.

Figures 51 to 56 show the distribution of medullary ray cells as seen in tangential section. The frequency per unit area is practically the same in all species. A variation in the length of the rays of P. deltoides (Fig. 51) and P. grandidentata (Fig. 52) and in the breadth of the Chinese Lombardy (Fig. 55) are the only differences noted.

A microscopic study of the tangential sections reveals a fairly constant average for all species in the number of cells in vertical extent.

In P. deltoides as many as 34 superimposed cells are found, though on an average there are but 14 or 15 cells. The average in P. grandidentata, is slightly larger, as many as 35 cells occurring in the

length of a ray. The average of P. tremuloides is smaller--
8 or 10--and no extremely long rays are noted.

The Chinese Lombardy reveals a few moderately long
rays of about 25 cells, but the rays have an average
length less than that of P. deltoides. P. nigra averages
12 to 14 cells in the vertical row of a ray, and P. alba
the least of all--8 to 10 cells.

Figures 45 to 50 show the extremes in length as
well as an average of wood fibers from the various
species. So similar are they that they might well have
been taken from the same species.

DISCUSSION AND CONCLUSIONS

The first purpose of this research was to deter-
mine in what ways the existing species of the Genus Popu-
lus differ anatomically. This has been accomplished--
superficially perhaps to some extent but at least in
enough detail to reveal the principal differences.

Despite the fact that most of the description has
served to bring out these anatomical differences, the
thing which most impresses one is not the difference in
the species but rather their apparent similarity of
structure; the striking likeness of all features.
These likenesses are sufficient evidence, it seems, to
waive any doubt there may have been concerning the
existence of an ancestral form. Certainly a common
ancestry is strongly indicated.

The apparent external differences contrasted
with the rather obscure internal differences is evidence
that anatomical changes have come about very slowly--
far more so than external changes. The indication is
that in their anatomical structure the species of the
Genus Populus are still remarkably like their common
ancestor.

The second purpose was to determine whether species
isolated geographically are less similar anatomically
than those not so isolated. The comparative study
has revealed that in general this is not the case.

First considering the external features of the leaves: P. deltoides and P. nigra, the forms most nearly alike, are isolated geographically; and as many or more differences are apparent among the three Old World species--P. alba, P. nigra and the Chinese Lombardy--than occur between them and the forms from which they are isolated.

Considering the leaves anatomically there is less negative evidence though but little positive indication in favor of the less similarity of isolated forms. P. deltoides, of course, differs from all forms in the arrangement of its tissues. In two respects-- in the type of epidermis and in the arrangement of tissue. P. grandidentata and P. tremuloides resemble each other more closely than do any isolated forms. The three Old World species strongly resemble each other, but considering only the arrangement of tissues the resemblance is scarcely more striking than between anyone of these forms and either of the aspens of the New World.

In consideration of the petiole, the cross sections of the three New World forms reveal a striking likeness; but a like similarity is existent between them and P. nigra, an Old World species. Here again, the difference between Old and New World forms is not greater than that found among species of the Old World.

In one year stems, a more prominently 5 angled pith occurs in the American species than in the Old World forms. However, this difference does not hold true in 2 year stems. It appeared first from sections being considered that the presence of stone cells in the primary cortex was characteristic of all the American species, but investigation showed that only rarely do they occur in P. deltoides.

However, it may be of some significance that the two forms most closely related--considering all anatomical features--are two forms not separated geographically-- P. tremuloides and P. grandidentata. The existence of two non-isolated forms which resemble each other more closely than any isolated forms, may be considered the one exception to our general conclusion that forms isolated geographicall y are not less similar than those not so isolated.

And so we arrive at what may be the most outstanding fact revealed by this research. In considering the marked anatomical similarity of the now existent isolated forms we can arrive at only one conclusion. Without a doubt the mutations which gave rise to the present species of the Genus Populus took place early in the history of the genus and before a separation of the land masses had taken place. Particularly is this true of the anatomy of the stems and also of the petioles, with one exception. The petiole of the Chinese Lombardy is so distinct in its structure that

it seems likely it has developed since the separation
of the continents. In the leaf structure, too, there
is indication of less stability of structure. In
general though we may conclude that in recent times
the Genus Populus has been a remarkably stable one
particularly in America. There is, in fact, little
evidence that hybridization is taking place among
species of this continent, tho Sargent (7) speaks
of the "hopelessly confused" forms of the Old World.

An interesting observation which might be
mentioned in this connection is the apparent difference
between P. alba of Europe and P. alba which is cul-
tivated in the United States. Two indications of
this difference have been noted: Hildegard Von
Hermann (3) classified the European form on the basis
of its having two rows of medullary ray cells. No
trace of this distinguishing feature was found during
the present research. Neither could Solereder's
statement (8) that in P. alba "the stone cells of the
primary cortex unite to form a ring" be verified.
In no case were any stone cells found in the primary
cortex of P. alba.

The last point to be considered in this research
is whether the species can be distinguished by their
anatomical characters. With the petioles and stems
this can not be done, but the writer believes it is

possible on the basis of leaf structure, and after
careful study has prepared the following key based
on the anatomical characters of the leaves.

I. Epidermis thin or if thickened, regularly thickened
   A. Leaf more than .15 mm. thick in cross section--
      often .2 mm. or more------Chinese Lombardy
   B. Leaf .15 mm. or less in cross section
      (1) Lower epidermis having hairs---P. alba
      (2) Lower epidermis without hairs
          a. Having 2 rows palisade cells--P. nigra
          b. Having 4 rows palisade cells--2 rows
             next each epidermis---P. deltoides

II. Epidermis irregularly thickened
   A. Having only 3 or 4 rows spongy parenchyma
      cells; palisade tissue occupying at least
      half inter-epidermal space--P. grandidentata
   B. Having 5 or more rows of spongy parenchyma
      cells; palisade tissue occupying less than
      half the inter-epidermal spaces--P. tremuloides

ACKNOWLEDGMENT

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criticisms made this study possible.

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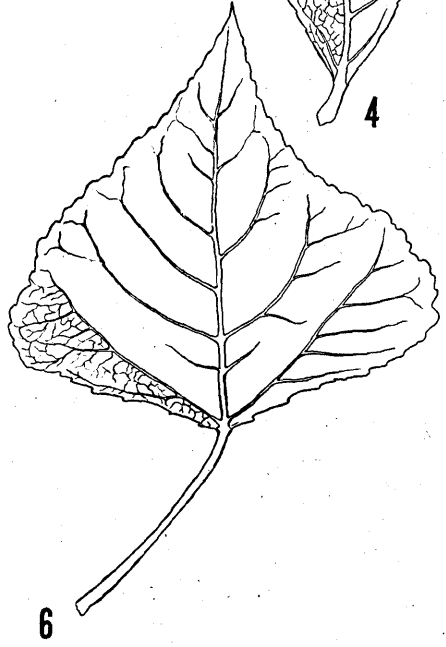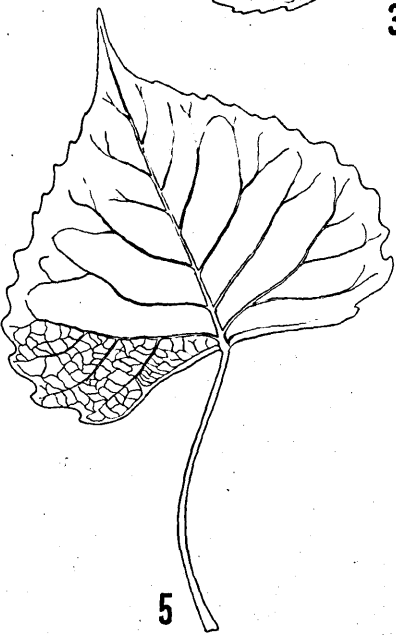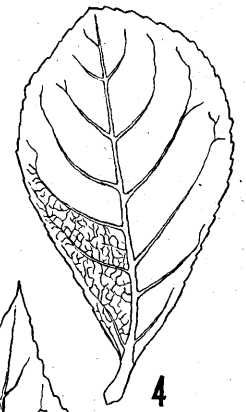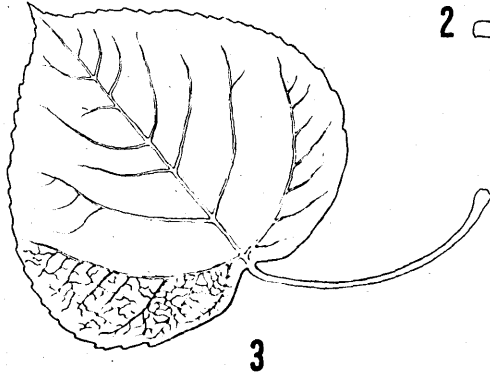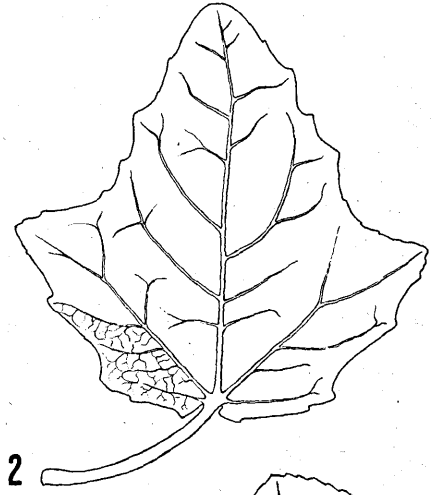
PLATE I

Fig. 1. Leaf of Populus grandidentata.

Fig. 2. Leaf of Populus alba.

Fig. 3. Leaf of Populus tremuloides

Fig. 4. Leaf of Chinese Lombardy.

Fig. 5. Leaf of Populus deltoides.

Fig. 6. Leaf of Populus nigra Italica.
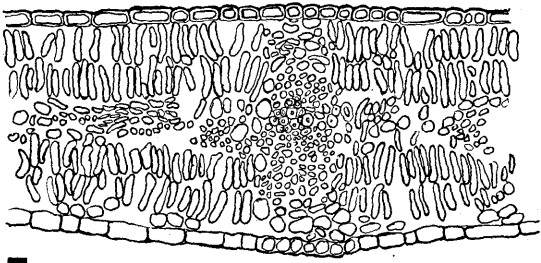
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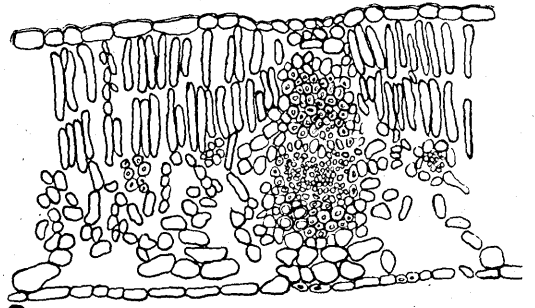
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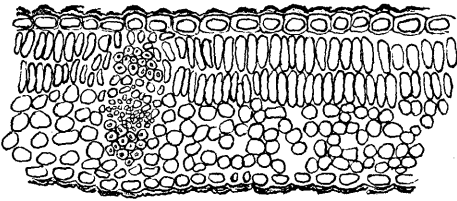
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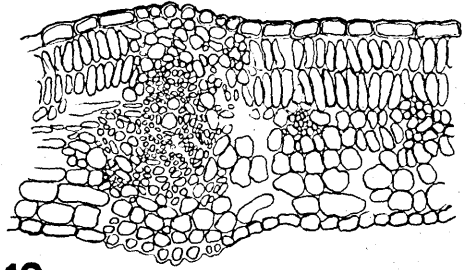
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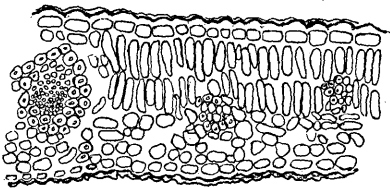
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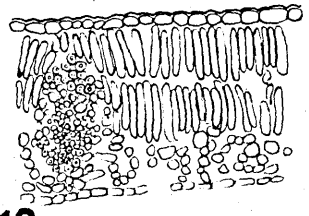
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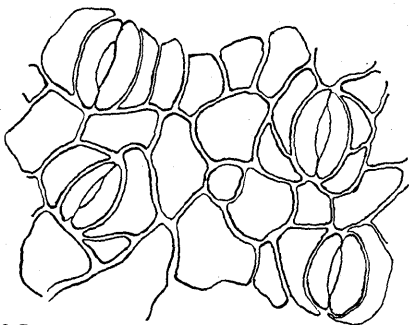
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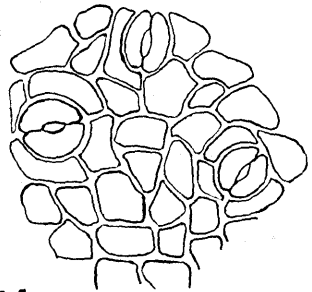
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PLATE II

Fig. 7. Cross section of a leaf of P. deltoides. x153

Fig. 8. Cross section of a leaf of Chinese Lombardy. x153

Fig. 9. Cross section of a leaf of P. tremuloides. x153

Fig. 10. Cross section of a leaf of P. nigra Italica. x153

Fig. 11. Cross section of a leaf of P. grandidentata. x153

Fig. 12. Cross section of a leaf of P. alba. (Hairs of lower epidermis not shown.) x153

Fig. 13. Lower epidermis of leaf of Chinese Lombardy. x375

Fig. 14. Lower epidermis of leaf of P. alba. x375
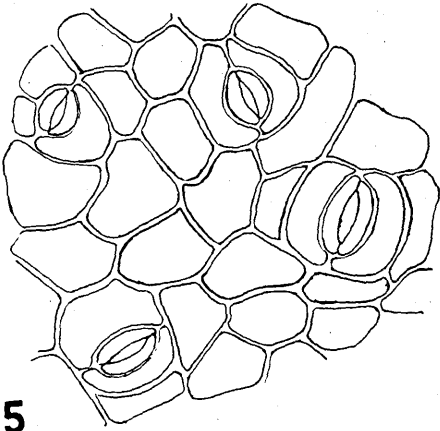
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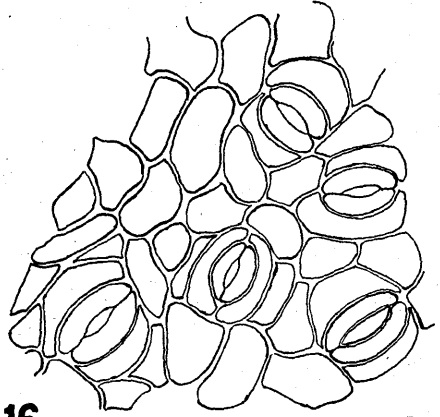
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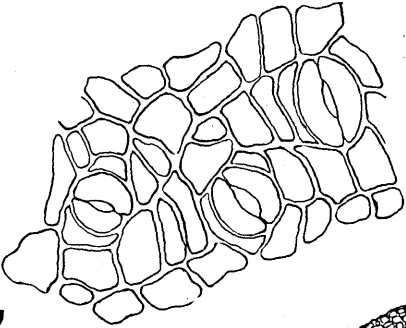
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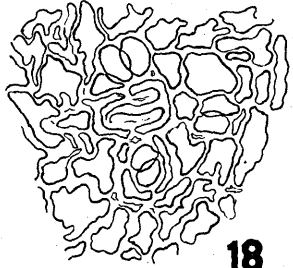
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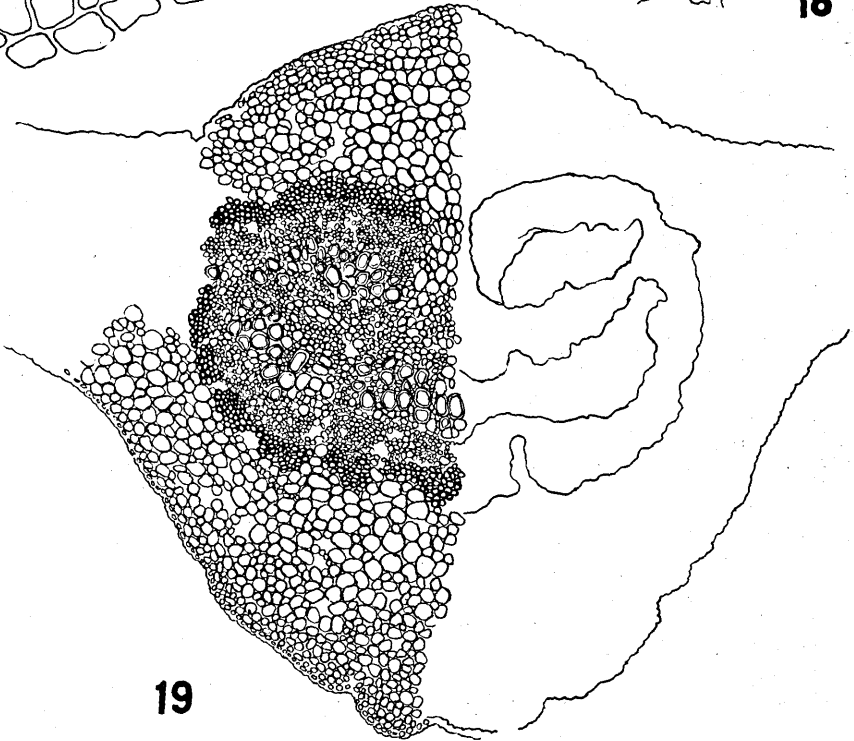
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PLATE III

Fig. 15. Lower epidermis of leaf of P. deltoides. x375

Fig. 16. Lower epidermis of leaf of P. nigra Italica. x375

Fig. 17. Lower epidermis of leaf of P. tremuloides. x375

Fig. 18. Lower epidermis of leaf of P. grandidentata. x375

Fig. 19. Cross section showing detail of cells of midrib from leaf of P. nigra. x72
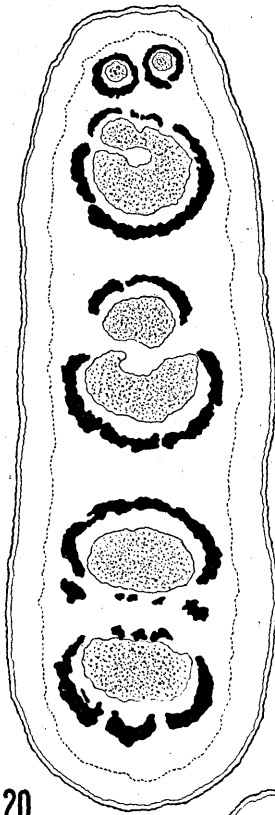
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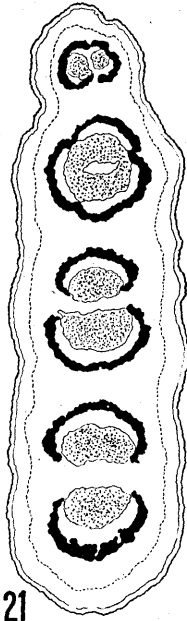
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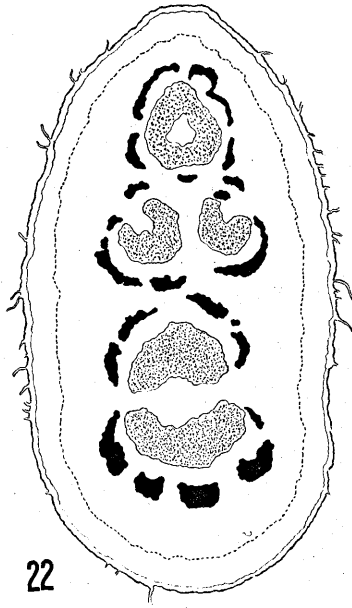
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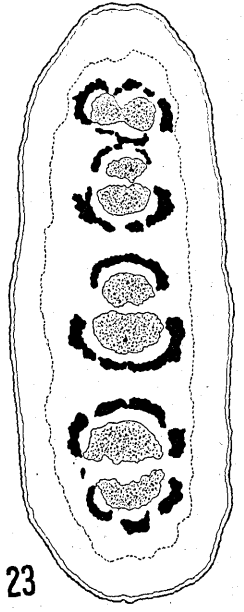
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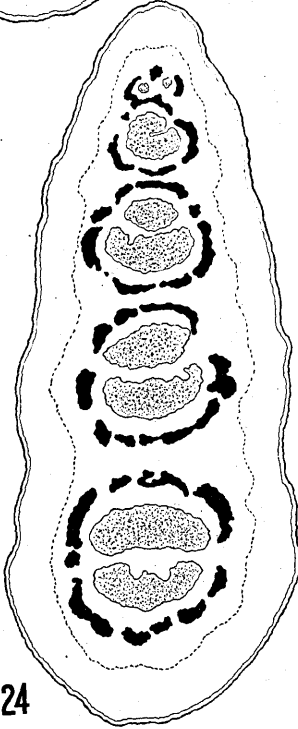
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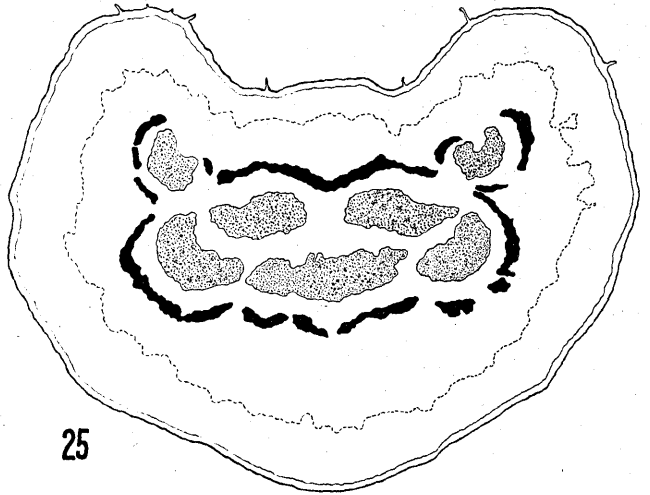
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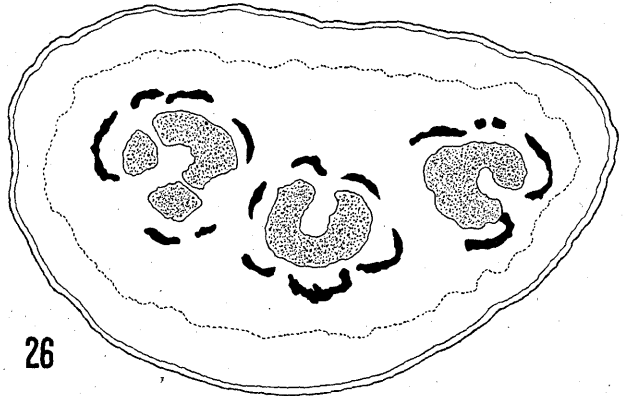
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PLATE IV

Fig. 20. Cross section* from upper central portion of P. grandidentata petiole. x40

Fig. 21. Cross section from upper central portion of P. tremuloides petiole. x40

Fig. 22. Cross section from upper central portion of P. alba petiole. x40

Fig. 23. Cross section from upper central portion of P. deltoides petiole. x40

Fig. 24. Cross section from upper central portion of P. nigra Italica. x40

Fig. 25. Cross section from upper central portion of Chinese Lombardy. x40

Fig. 26. Cross section from the base of P. tremuloides petiole. x40

* Outer region represents the epidermis; dotted line indicates the inner boundary of the collenchyma; solid black represents hard bast areas; shading indicates phloem tissue; and stippling indicates xylem.
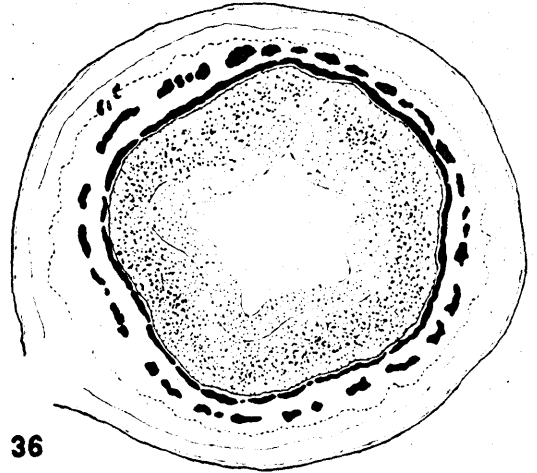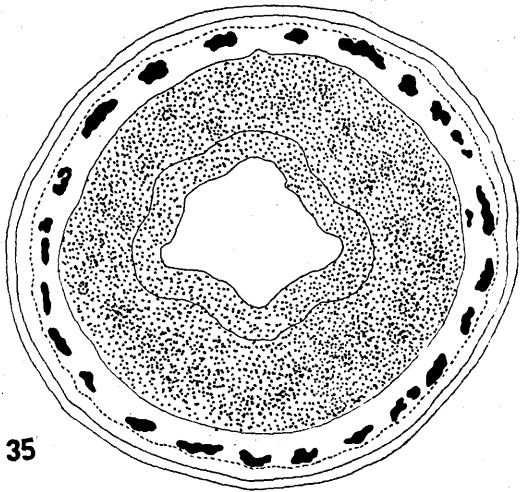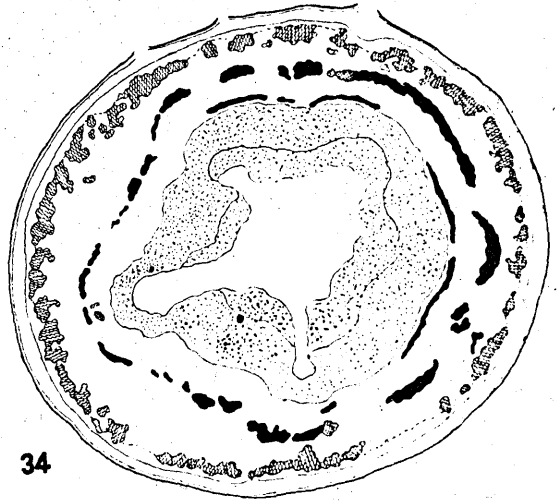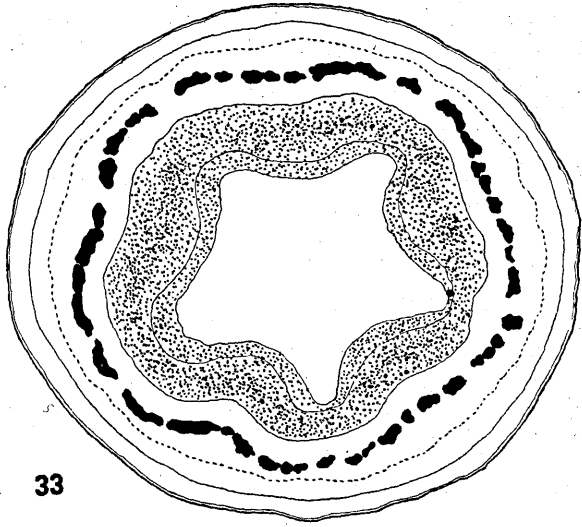
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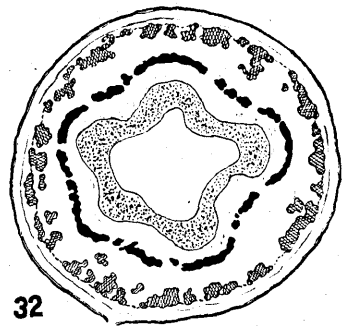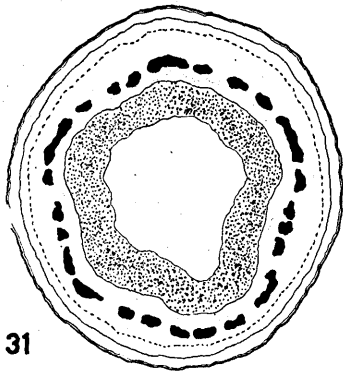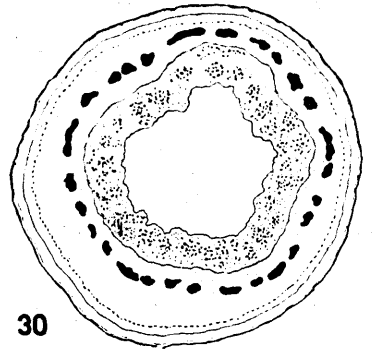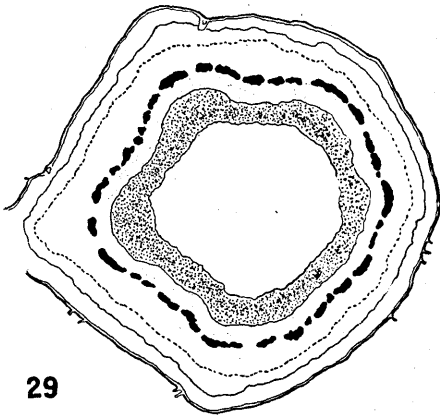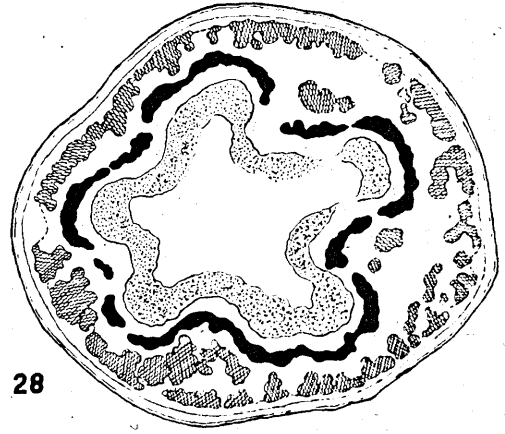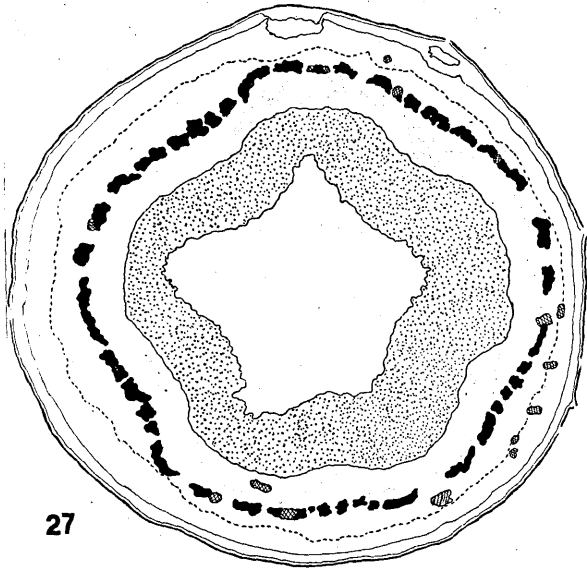
PLATE V

Fig. 27. Cross section* of one year old stem of
P. deltoides. x22

Fig. 28. Cross section of one year old stem of
P. grandidentata. x22

Fig. 29. Cross section of one year old stem of
Chinese Lombardy. x22

Fig. 30. Cross section of one year old stem of
P. nigra Italica. x22

Fig. 31. Cross section of one year old stem of
P. alba. x22

Fig. 32. Cross section of one year old stem of
P. tremuloides. x22

* Regions represented as in petioles except that a
cork region lies just inside the epidermis, and that
stone cells are represented by diagonally-lined areas.

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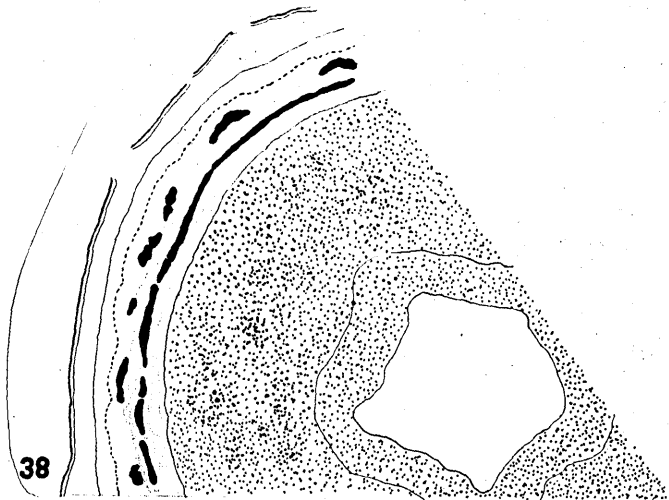
PLATE VI

Fig. 33. Cross section of two year old stem of P. deltoides. x22

Fig. 34. Cross section of two year old stem of P. tremuloides. x22

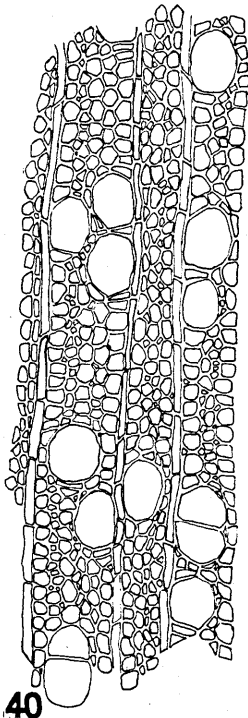Fig. 35. Cross section of two year old stem of P. alba. (Epidermis not shown) x22

Fig. 36. Cross section of two year old stem of P. nigra Italica. x22

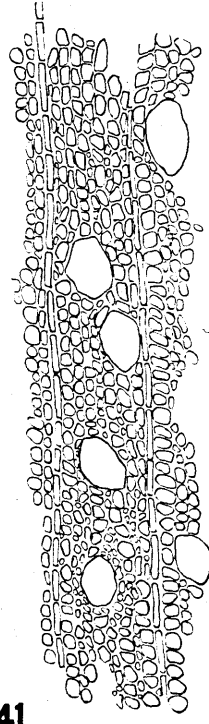Fig. 37. Cross section of two year old stem of P. grandidentata. x22

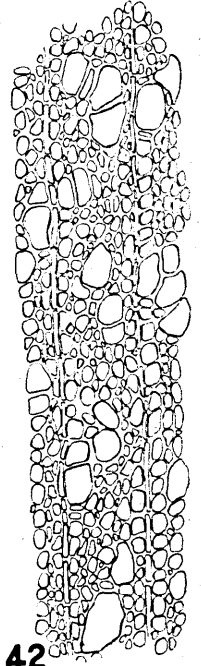Fig. 38. Cross section of two year old stem of Chinese Lombardy. x22.
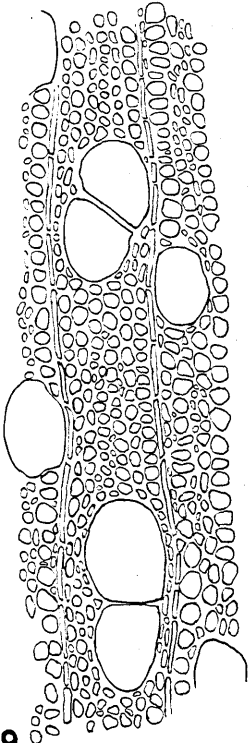
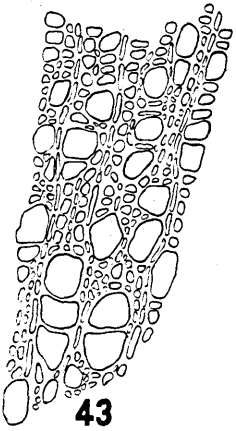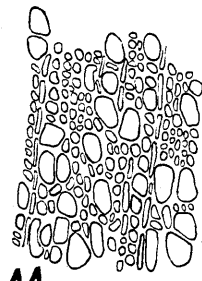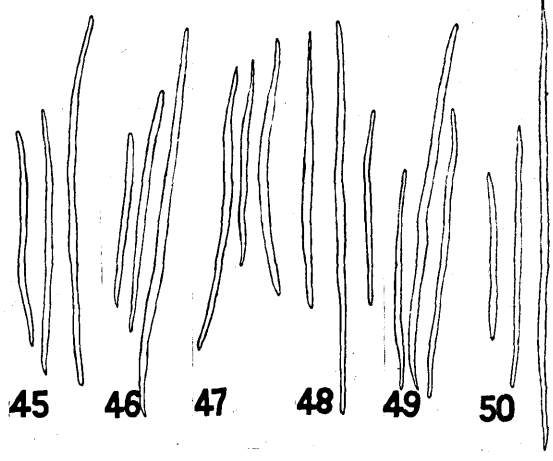**39**

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PLATE VII

Fig. 39. Cross section of early growth of wood of P. deltoides. x150

Fig. 40. Cross section of early growth of wood of Chinese Lombardy. x150

Fig. 41. Cross section of early growth of wood of P. nigra Italica. x150

Fig. 42. Cross section of early growth of wood of P. alba. x150

Fig. 43. Cross section of early growth of wood of P. grandidentata. x150

Fig. 44. Cross section of early growth of wood of P. tremuloides. x150

Fig. 45. Wood fiber of P. deltoides. x60

Fig. 46. Wood fiber of P. grandidentata. x60

Fig. 47. Wood fiber of Chinese Lombardy. x60

Fig. 48. Wood fiber of P. tremuloides. x60

Fig. 49. Wood fiber of P. alba. x60

Fig. 50. Wood fiber of P. nigra Italica. x60

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PLATE VIII

Fig. 51. Tangential section of P. deltoides, showing the number and size of medullary rays. x72

Fig. 52. Tangential section of P. grandidentata, showing the number and size of medullary rays. x72

Fig. 53. Tangential section of P. tremuloides, showing the number and size of medullary rays. x72

Fig. 54. Tangential section of P. nigra, showing the number and size of medullary rays. x72

Fig. 55. Tangential section of Chinese Lombardy showing the number and size of medullary rays. x72

Fig. 56. Tangential section of P. alba, showing the number and size of medullary rays. x72