THESIS

LEAF--HISTOLOGY OF CONIFERAE

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Preliminary Remarks.

The classification of coniferous plants, especially of the pines and spruces, has been, in years past, a very difficult task. This has been due, in part, to a lack of distinguishing characters used in their descriptions, and in part, to the very close resemblance that certain species bear to each other, making it very difficult to distinguish the different species by a written description. It is due chiefly to Dr. Engelmann that these difficulties have been greatly lessened. In his treatment of the conifers of the United States, he bases his classification partly on the structure of the reproductive organs, especially the characters of the cones, and partly on leaf-structure. The difficulty of distinguishing different species of pines by their coarser external characters led J. W. Coulter and J. Rose in '86 to prepare a "Synopsis of North American Pines," based on Leaf Anatomy, following more or less in detail the line laid out by Engelmann. This classification is so arranged as to agree with the system as based on general structure of the plants, and as is of double advantage, furnishing both...
natural and an easy key for determination of species.

Whether it was due to the difficulty of distinguishing different species, or to a lack of knowledge, or otherwise, or all combined, the nomenclature has been badly mixed and uncertain. At present, however, it seems to have reached a more settled state. This is due in part to Dr. Engelmann's investigations, which were spoken of above. This nomenclature is the generally followed today. Some idea of the former confusion may be gained when we consider that most of these plants have four or five synonyms, while some, according to Gordon, have as high as eighteen. A great deal of confusion has also been caused by the misusing up of the two genera Picea and Abies, the characters of one genus frequently being given under the name of the other. Some authors also seem to have placed the species of both of these genera under the one genus Abies. They are now placed under the four genera Abies, Picea, Tsuga, and Pseudotsuga. From what we have seen of the leaf structure of some of the different species, it seems to bear out these divisions. It was with the idea of gaining some knowledge of leaf
structure, as a method of distinguishing species of coniferous plants that the present thesis was undertaken. The species examined, except two, are those that are cultivated on the grounds of the University of Illinois, and they represent all the genera of coniferous plants as given by Gray's Manual as native to the United States, except Tordium and Chamaecyparis. These are represented in this paper nine genera and fifteen species. Of these but four are natives of the state, while of those introduced four are European, and the remainder are from different parts of the United States. There are, taking the native and cultivated conifers into account, some twelve genera and thirty-eight species found in this state. Of these seven genera, represented by eleven species, are native. There seems to be no native apricot, although there are three native pines.

We have tried to examine sections from as many different individuals as possible, also from different parts of the same individual, so as to see within what range the species are variable. What difference an examination of individuals from different regions, or under different climatic influences, would reveal, we can
not state, as our specimens have all been taken from the University grounds, and our opportunity for literature treating especially on this subject has been limited. The method of procedure was to take transverse sections made by cutting them leaf imbedded in paraffine, and examine them imbedded in water or glycerine, the latter seeming to be the better mounting fluid. Transverse sections from different parts of the leaf were taken to see what differences of structure, if any they would reveal, but unless otherwise stated, the description of the sections is that of those taken from the central part of the leaf. Again, we have only studied transverse sections, as these are the ones on which specific characters are based, and least likely to show variation. Longitudinal sections would vary a good deal, according to what parts of the leaf they passed through. As a rule the same elements are found through the entire length of the leaf.

It would be presumption to attempt to draw any fixed conclusions of generic characters from an examination of two or as species, especially in the case of Pine, which contains some seventy species. Still in the examination of species of the same genus, we have
noticed certain constant characters or peculiarities. We give elsewhere under "Distinguishing Characteristics" these observations on genera and species. Perhaps a more extended study would reduce these peculiar characteristics. We give them as applicable only as far as we have examined.

In general, we find three different regions in sections of coniferous leaves. 1st. The epidermis, consisting of the epidermis, and usually the hypoderma. Here, also, we find the stomata. 2nd. The mesophyll, consisting of a band of parenchymatous cells containing chlorophyll, and in which the resin passages are situated. 3rd. The fibro-vascular system, usually in the center of the leaf surrounded by a special row of cells called the bundle sheath, and containing one or two bundles composed of two kinds of tissue called xylem and phloem and with parenchymatous cells and tracheids between bundles and sheath.

Among the generic peculiarities of the pine, the infolding of the cell walls of the mesophyll seems to be the most prominent. We found this infolding of cell walls in no other genus, except
in Laxí, where some of the cells have irregular infoldings or bending.

So in the case of Taxodium distichum, Walter represents the walls of the mesophyll as having irregular infoldings. In the different species of pines, we find quite definite characteristics by which they can be distinguished, a peculiarity much more prominent in this genus than in the others. In the case of the pines, Picea, we find certain generic characters, but distinguishing specific characters are not so very prominent. The close resemblance of the species in this respect, however, points strongly to the validity of the genus. As stated by Boulter and Rose, we find certain relations between the shape of the sections, and the number of leaves in a bundle in the genus Pinea. Thus, when we have two leaves, their opposing sides are flat, while the outer surfaces are rounded, and with leaves in threes or fives the sections are triangular. It seems to me that the shape of leaf sections could be made quite a factor in distinguishing different species of the conifers, if diagrams were used as references. Again in flat leaves, we are pretty sure to find a
layer of palisade cells on the upper side, and an absence or scarcity
of stomates on this side. We find great diversity of hypodermal structure.
In some species, as *Achis falcanea*, this is entirely wanting. In
others, as *Pinus strobus*, it is composed of a row of thin walled
cells. Others have a row, or groups, of thick walled, or sclerenchymatous
cells. In the matter of stomates, we always find them
situated below the surface. Reain passages are also an almost uni-
form occurrence, according to *LeBaron* being found in all the
genera, except *Taxus*, which was the case so far as we investigated.
In the position of the elements of the bundles, we always find the
zygumen on the upper, or inner side. This is explained when
we considers that the bundles spring from the circular bundle
of the stem, which has the phloem on the outside and the xylem
within.

The key for classification given in the latter part of this
paper is based on the possession of these peculiar generic and specific char-
acteristics. Of course such a key must be imperfect and unnatural to a great
extent, but we have arranged the genera in the order given in the latest
edition of Grajs Manual. The method of discussion of the different parts of
the leaf will be similar to that followed by Bower and Nire in their treatment
of Pinus sylvestris in the "Practical Botany." We have taken one species,
Pinus Austriaca, and have treated it in detail. In the treatment
of the others, reference will be had more particularly to the differences. Among
the spruces, Picea excelsa is treated more in detail. The drawings were
made by outlining and getting the size of the different elements with
a camera lucida, and then, by comparison with sections as seen in
the microscope, completing the drawings free hand. The drawings repre-
sent magnifications from fifty-six to three hundred six diameters. We
also give at the end a list of the references that we have been able to find
as relating to this subject.

1. Pinus Austriaca, Hoss. Austrian Pine. (P. laricis Austriaca, P. nigra &)
Leaves two in each bundle, 4-5½ inches long, stiff and furgent. A section
shows the upper side flat, and the lower convex with highest point of points
middle of upper side. The ratio of base to altitude is about 5:3, the upper side

*We give only the more commonly knowns!
being the base. If we were to view the flat side of an entire leaf under a low power, we would find that the margin has fine, somewhat distant teeth, pointing toward the apex of the leaf. Also that the stomata are arranged in quite regular rows running lengthwise of the leaf. There are usually from 8-15 of these rows on the upper side, and from 11-13 on the lower, though at the ends there are fewer rows. A section will not always show as many stomata as there are rows, since even if it were cut perpendiculary across, the stomata are not arranged in regular rows across the leaf.

**Epidermal System.**

Epidermis. The general shape of the cell is flattened, circular though with parallel diameters usually a little longer. The two or three end cells are enlarged. There is outside of the cells a cuticle which follows around them, being somewhat thickened at the end cells. Below this and appearing like the outer side of the cell wall is a thickened layer having a granular appearance. This runs down between the cells. This inner layer is more deeply colored by staining re-agents. The cells themselves are nearly or entirely filled with a tissue, called by Bowers the pitted tissue.
because in this are seen fit-like markings. These fits are most easily seen in the end cells. The majority of cells have still other markings. These are generally in the shape of an X (X), or they have the appearance of a broken H (H). This fleshy tissue seems to be made up of concentric layers.

Stomata. These are depressed below the epidermis, the guard cells being in the first row of the hypodermal tissue, and having a little cup-shaped depression in the epidermal row above. These guard cells are two in number, and if closed each has the shape of a right triangle with the altitude sides opposing, and the common apex directed toward the midst of the depression. If open, the cells are more oval, and touch each other only at the tip, if at all. The outer cell wall of the guard cells is thickened. At the basal acute angle is a small cell without sclerenchyma matrix filling, and along the upper side is another cell somewhat larger and longer. These two cells connect the guard cell with the hypodermal layer. If the section is just above or below a stoma, in place of the guard cells, etc., we find two larger thin-walled
along cells, end to end, connecting the hypodermal cells. Below
the guard cells is a regular \( U \)-shaped space, stomatic cavity,
surrounded by one or two of the mesophyll cells. In the sections
examined, we found the number of stomates to vary from 4-13
on the upper, and 8-14 on the lower side. If the section is taken
near the apex or the base, the number is less.

Hypoderma. This consists of white sclerenchymatous cells
Engelmann objected to the name hypoderma, as cells similar
to these are found in other places, so he called them strengthening
cells. They are somewhat polygonal, and are from
nearly empty to two-thirds filled with sclerenchymatous tissue,
which seems to be in concentric layers. The inner row, which
is the only continuous one, has but little sclerenchymatous fill-
ing. The cells are absent at the stomates. The stomates, in
fact, divide the hypodermal layers into little bands, the cells
being arranged in from two to four rows deep midway between
the stomates, and tapering down to one or two near the sto-
mates, or else two or three cells deep all the way between the
stomata. The cells next the stomata and the epidermis are not as completely filled as the others.

Mesophyll System.

Chlorophyll cells. This is made up of a band of parenchyma motar cells running around the leaf, and having in its center the fibro-vascular system. It is usually three or four cells wide, and is widest at the corners. These cells are the largest in the leaf, and contain the chlorophyll, which gives the green color to the leaf. The cells are peculiar because of their infolding cell walls. The contiguity of the cells makes their walls double. The inner of these cell walls sends into the cell projections by folding upon itself. These projections vary from short infoldings, to slender projections extending half way across the cell. Those from the sides of the cells next the bundle sheath and the hypodermis, especially the latter, are usually the longest. The cells consequent from their infoldings, have a somewhat wavy outline. The infolding of the cell wall is best shown by pickling the sections in alcohol, and then mounting them in glycerine.
Resin passages. These are parenchymatous, that is, are entirely within the mesophyll. They consist of a row of sclerenchymatous cells, similar to those forming the hypoderma, surrounding a central intercellular space. This space is immediately surrounded by a row of very thin walled cells with granular contents, to which is given the name, epithelial cells. The intercellular space is from \( \frac{1}{3} \) to \( \frac{2}{3} \) the diameter of the passage. The number of resin passages vary from 2 - 8. The two near the ends are the largest, and as far as I know are always present. According to LeBey it is the epithelial cells of the resin passage that secrete the resin, the intercellular space acting as the reservoir.

Fibro-Vascular System.

Sheath bundle consists of a row of oval cells, with longer diameters end to end, surrounding the central fibro-vascular system. The cells have starch and granular contents, but little chlorophyll. Sometimes the number of these cells is taken as one of the specific characters.
running around the sheath. The former have usually starch grains or other contents, and are much like the sheath cells. The tracheids are inclined to be a little narrower than the other cells here, and are destitute of contents, but have pits, or areolated dots on their cell walls.

Bundles are two, slightly separated by a band of small thin-walled empty cells, which are spread out above the upper, gyeny side of the leaf. The bundles are connected on the lower, flobiin side by a row of sclerenchymatous or thick-walled cells, similar to the hypoderma cells, which passes from the outer end of the flobiin of one bundle to the outer end of flobiin of the other bundle. The bundles are slightly oblique to each other, approaching nearest on flobiin side. The flobiin is made up of thick-walled white cells. These cells are oblong or square. The gyllem forms the upper part of the bundle, and is made up of less bright, more polygonal cells. The cells are larger than the flobiin cells, but not in so regular rows.

De Bary says that the tracheids spring from the gyllem
and, outer end of bundles, and form a sort of band above
and below the bundles. He considers these as taking the place of
the branches of the bundles. The tracheides do seem to spring from
the xylem, and the cells going from the xylem towards the
sheath bundle have their cell walls cut so as to show the areo-
lated dots or lenticular openings in the cell walls. I noticed
that the parenchymatous cells seemed in like manner to spring
from the phloem end of the bundles, and go around like the
tracheides, for the cells at the end of the xylem are enlarged and
and extend into cells similar to, but smaller than, the parenchyma-
tous cells with which they are connected.

Section at Base of Leaf.

If the scales are cleared away from the base of the leaf bundles,
there will be seen the naked fibre vascular bundle. This fibre-vascular
bundle is circular with the band of phloem on the outside, then the
xylem, and at the center a few small chlorophyll cells. Now as the
bundle comes to where the leaves separate, half goes up one leaf
and half the other, and the half in each leaf also in turn separates
into two bundles. Taking a section across the two leaves near where they are joined together, we find some differences from a cross-section near the middle of the leaf. The epidermal layer is similar to the hypodermal. Its cell walls are only moderately thick, and are without vitality filling. The hypodermal layer differs from that further up by having thinner cell walls. It is also of a more uniform thickness, consisting of two or three rows of cells. Stomata are absent. The mesophyll is reduced to a narrow band, with rounded cells without unfolding cell walls, and but loosely put together. A number of reserve passages are present. The fibre-vascular system occupies nearly all the leaf, and the close approach of the bundles of one leaf to those of the other, shows their common origin. The two bundles of each leaf have on the phloem and xylem sides, and are connected by cells resembling the xylem. As sections are taken further up, the epidermal cells become more filled, the end cells showing thick first. Stomata appear first on the lower side, and after the two leaves are fairly separated on the upper side. The band of mesophyll
becomes wider, the fibrovascular system smaller. The xylem-like cells between bundles and on xylem side become somewhat thinner walled, while on the phloem side sclerenchymatous cells begin to appear. The mesophyll cells also begin to show infoldings of their walls. And so as we take sections farther up, we reach the normal state.

If we take a section from near the tip of the leaf, we find that the hypodermal layer is thick, and continuous, there being no stomata. This gives the rigidity and sharpness to the point of the leaf. The vascular system is reduced to a few elements, and the resin passages are not as numerous.

I. Pinus sylvestris, L. Scotch Pine

Leaves in twos, 2½-3 inches long, sections similar in outline to P. Austriaca, but with face to altitude as 2:1.

Epidermis: cells similar, though smaller, to those of P. Austriaca. Stomata less depressed, and not quite as numerous. Hypodermal layers of one row of small, oval to oblong, thin
to fairly thick walled cells. The cells at corners show inclination to sclerenchymatous filling, and there are here perhaps a few cells out of the row. The absence of sclerenchymatous tissue in the hypodermis accounts for the lack of rigidity in the leaves. Néosphyll is not essentially different from that of P. Austriaca. Resin passages vary from 7-11 (1-22 according to Lé Bœuf). They differ from those of P. Austriaca in being peripheral, that is, having connection with the hypodermal layer, but consist of similar sclerenchymatous cells and epithelium. Sometimes one or two passages are found to be parenchymatous. They are most numerous (3-6) on the lower side, with 1-4 on the upper, and one near each corner.

Vascular system. The space is distitude of chlorophyll, and elongated in direction of base, so becoming oblong rather than oval. Sheath cells present, containing starch granules, and some seem to have a little chlorophyll. Pitted tracheides and parenchymatous cells also present. Bundles two, smaller than in P. Austriaca, and much farther apart. They are connected on phloem side.
by one or two rows of sclerenchymatous cells below this row between the bundles generally have quite thick walls. Gymn
directed toward the flat, or upper side.

Sections at base similar to those of P. Austriaca, except space
between bundles is entirely filled with thick walled cells which also
send bands around on upper and lower sides of the bundles
so as to nearly or quite surround them. Resin passages
reduced to a few sclerenchymatous cells.

S. Pinus resinosa, Ait. Norway Pine
Leaves in twos, 5-6½ inches long, quite limber. Sections with
outline as in preceding, but with face to altitude as 8:2.
Epidermal cells similar to P. sylvestris, but with markings
of felled layer not as plain as in P. Austriaca.
Hypodermal layer without sclerenchymatous filling, similar to
that of P. sylvestris.
Mesophyll normal.
Resin passages 2-5 generally, peripheral, sometimes parench
matous. Cells of resin passage without sclerenchymatous filling found in P. Austriaca and P. sylvestris, but with thick walls.

Stomata generally 4-6 on upper 8-12 on lower side.

Fibro vascular system. With ovul sheath cells generally without chlorophyll. Bundles two close together. Without the row of sclerenchymatous cells on phloem side. Pitted tracheids and parenchymatous cells present. Cells between bundles small, empty and thin walled.


Leaves usually in fives, 3-4 inches long. Cross sections equilateral triangular, with corners sometimes truncated.

Epidermal layer consists of cells smaller than those of other pines described. Markings of felled layer not as prominent as in P. Austriaca. General shape of cells oval, with longer diameter touching. Like P. Austriaca with end cells enlarged.

Stomata generally two or three on two sides, lower side without stomates. Not deeply seated. If entire leaf is viewed with low power as opaque object, stomates show as bright dots usually in three
row, and two fainter continuous lines show position of serein passages lower side. The rows of stomates are close together and near the center of the side, while the lines of the serein passages are toward the ends of the side. It is the lines of stomates on the two sides that give those sides the whitish streaks that are seen by the naked eye.

Hyphodermal layer is composed of one row of oval cells, without sclerenchyamatosus filling.

Serein passages generally two (1-3 according to Boulder & Rose) toward ends on phloem side. "When three, the odd one is on one of the central faces." Peripherally, with cells similar to those of the hyphodermal layer, except perhaps a little larger. Epithelial cells present. Mesophyll similar to that of other pines examined.

Fibro-vascular system circular. With normal bundle sheath, and one bundle, fairly filling the space. Tracheida with areolated dots, and parenchymatous cells with granular contents and some chlorophyll cells just above pylem thin walled and empty.
5. *Picea excelsa*  Norway Spruce. (*Abies excelsa*)

Leaves separate, on all sides of stem, from 1/2 - 1 inch long. Sections from oblong to square (rounded at corners).

Epidermis with cuticle and thick cuticularized layer. Cells in one row, without fited filling. Oval to obovate.

Stomates arranged in somewhat irregular rows running lengthwise of leaf. From 5 - 8 stomates generally in a section. Repelled below surface. Similar to those of *Pinus Austriaca*.

Hyposdermis consists of one or two rows of cells. Row next epidermis continuous, and with cells at corners filled with sclerenchymatous tissue, while cells at sides may be without this filling. Generally part of second row of sclerenchymatous cells at corners.

Sclerenchymatous cells polygonal; thin walled cells more obovate.

Resin passages vary from 0 - 2; even in the same leaf. Generally near the line of shorter diameter. Peripheral, with cells somewhat more elongated than the unfilled hypodermal cells.

Mesophyll is without the infoldings of the cell walls peculiar to pines. Cells vary in shape from irregular circular to obovate.
Somewhat wavy in outline. Filled with starch granules, chlorophyll.
Fibro-vascular system central and circular, with oval to oblong sheath cells, containing starch and some chlorophyll.

Bundles, two, quite close together, separated by thin-walled cells.
Sometimes appear as one bundle. Phloem and xylem well developed, with a row or mass of sclerenchymatous cells connecting bundles on phloem side. With firmed tracheids and parenchymatous cells. Bundle sheath and some of the parenchymatous cells seem to contain some chlorophyll.

6. Picea fargesii, Eng. Blue Spruce,
Leaves 1/2-1 inch long. Very stiff and furred, with white streaks along sides. Sections square, rounded at corners. Very similar to P. excelsa, though shape more constant.

Epidermis without-fitted layer. 1-4 stomates on a side in rows of 3-6 generally.

Hydrodermis chiefly of sclerenchymatous cells. These sclerenchymatous cells seem to be more continuous than in P. excelsa, though
the sclerenchymatous filling is absent near stomata. Frequently double row of cells at corners.
Mesophyll similar to P. excelsa, walls plainly double.
Resin passages generally two, through sometimes one or more, few peripheral cells generally thicker than in P. excelsa.
Fibre-vascular system circular, with or long sheath cells containing some chlorophyll. Bundles apparently two, or else one with dividing cells in center. Without sclerenchymatous cells on phloem side, though sometimes one or two such cells are found with fitted tracheids and parenchymatous cells.

7. Picea mariesii Link. Black Spruce
Leaves 1/3 - 1/2 inches long. Shorter and without the sharp point of P. firsens. Sections nearly square, with rounded corners, in shape of sections resembling P. firsens, but smaller. Histological structure shows very close resemblance to P. firsens, in fact hard to find permanent characters in which it differs from that species. Epidermis with cells without filling. Generally 1-4 stomata on
as sides
Hydrophobic with cells having sclerenchymatous filling, except those near stomatae, and almost confined to one row.
Mesophyll normal.
Vessels passages two, constant as far as I examined. With cells from thin to thick walled. Peripheral fibro-vascular system probably with two bundles very close together, though at times looks like one only. Sometimes one or two or a band of sclerenchymatous cells found on phloem side of bundle. Tracheides with fited dots, and parenchymatous cells present.

P. Pseudotsuga "Douglasii" (Bass. "Douglas" Spruce)
Leaves flat, somewhat two ranked, ½-1 inch long. They are larger and stronger than those of this subalpine section approaching shrub, with depression in middle of upper side, and with somewhat of an elevation in middle of lower side.
Epicormic with circular polygonal cells, without filaments, cuticularized layers thick.
Stomata on lower side entirely, on each side of ridge, 4-6 in a section. Usually with 4-6 rows on each side of ridge of leaf.

Hypodermal layer sometimes barely present by a few elements, and sometimes an almost continuous row of thick walled or sclerenchymatous cells. These cells are a little larger and thicker walled than the epidermal cells.

Resin passages two, peripheral, toward end on lower side of leaf. Cells similar to hypodermal cells, though more elongated and thinner walled. With usual lining of epithelial cells.

Mesophyll with two or three rows of palisade cells on upper side, extending down to resin passages at ends and bundle in center. Cells from resin passages and upper side of bundle to lower side of leaf more rounded and not as closely packed, leaving numerous small intercellular spaces except the cells just below the bundle which are closer together.

Fibro-vascular system is circular. Sheath cells oval with chlorophyll, enclosing fitted tracheids and parenchymatous cells. Bundle one.
Tuscarora (Tsuga Canadensis), bar's hemlock spruce (Abies Canadensis)


Altitude to base 1 3/4.

Epidermis consists of rounded cells with upper half filled with white tissue.

Stomates absent on upper side, 3-6 usually on each side of bundle on lower side. Not deeply set. Irregulars space beneath the guard cells which are without basal cells.

Hydodermis absent.

Resin passage one, peripheral, immediately below bundle on lower side. Cells similar, though a little smaller, to the mesophyll cells. With usual thin walled epithelium. Sometimes there seems to be a membrane covering the inter-cellular space of the resin passage. This is colored by aniline red. It may be the secretion of the cells.

Mesophyll with about two rows of palisade cells on upper
side. Cells on lower side more circular, and not as closely packed, showing intercellular spaces. Central cells show more elongation in direction of longer axis of leaf.

Fibrous vascular system is central, approaching circular. Bundle sheath irregular, of indefinite larger and smaller chlorophyll cells. Bundle fine, nearly filling space. With parenchymatous cells, but no tracheids. With scattered dots, as far as I could find.

10. Abies balsamea, Mill. Balsam Fir.

Leaves flat, two ranked, 1/2-3/4 inch long. Sections approaching along with elevation in central lower side and depression above on upper side. Shorter diameter to longer about as 2:5. Under side of leaf with stomates arranged in 4-8 irregular rows on either side of ridge. These give the whitish appearance to the under side. From 6-8 irregular rows of stomates on upper side.

Epidermis consists of oval to elliptical cells placed longer diameter end to end. With cuticle and upper side of cell thickened. Cells without filling.
Stomates without basal cell, somewhat depressed, generally two or so on upper side, and from four to five on lower.

Hypodermis wanting.

Mesophyll of oblong to circular cells, with chlorophyll and numerous oil-like globules, which may have escaped from the resin passages. On upper side, cells are arranged in one or two rows of palisade cells, the cells on lower side being more nearly circular.

Resin passages two, parenchymatous, toward ends of section. The cells are generally oblong, thin walled, and contain chlorophyll with lining cells, and oil-like globules in resin passage.

Fibro-vascular system circular. With oval sheath cells containing chlorophyll. Traeheid with incised dots few, if any. Parenchymatous cells present, and with some chlorophyll. Bundles two, farther ends near the sheath, separated by, and having on phloem side, empty thin walled cells.

Numerous leaves in a fascicles (from 1-1 1/2 inches long. Sections oblong, with swelling in center on lower side.

Epidermis with cells circular to oval. Moderately thin walls.

Generally with two or 20 stomates on upper side, and 2-6 on lower.

Hyphodermis present above and below bundle, and at ends, cells with more or less sclerenchymatous filling. Some young leaves that were examined did not show the sclerenchymatous filling, so it must have been a later addition as the older leaves seemed to have it.

Resin passages small or abortive, frequently resembling a group of hyphodermal cells, peripheral.

Mesophyll with oval or oblong cells around margin, and with irregular larger cells, having irregular infoldings, filling central part.

Fibro-vascular system central, circular. Sheath cells without chlorophyll, oval to circular. Bundle one. No associated tracheids observed. Dr. Bay says that tracheids were absent alone in this.
of the species of coniferous known to him.


Leaves flat, small, scale-like, two-ranked, adnate and equitant at base on the flat leaf-like stem. Between the two ranks of leaves, the stem has, on either side, a second row of scale-like tips just free at their end. The whole branch might be taken for the leaf, but if we look at the dried part of the stem, we find that we can trace the dry scales into the green scale-like leaves and the stem into the green central portion on which the leaves are ranked. Again, if we look, we shall see that the divisions arise from the axils of the scale-like leaves, the proper origin of the branches. So the anatomical characters point to the central part as the stem, as it has in its center a circular bundle. In none of the coniferous leaves, I have examined have I found a circular bundle, that is, with the xylem within and the phloem as a circular band surrounding it. A section through the central part of the leaves shows the leaves on either end of
the longer diameter of the stem, somewhat clamping the end, and
joined to it at center of end of contact.

Epidermis of leaves is made up of oval to oblong cells. Outer
walls of cells rather thick.

Hypodermis consists of an incomplete row of sclerenchyma-
tous cells. Sometimes in more than one row. Vary greatly in
number of cells, generally forming a complete row at end, nearly
complete row on upper side, and more or less on lower side.

Stomata as far as found limited to lower side. Not deep
set, and rather numerous.

Mesophyll with palisade cells on upper side, cells on
lower side more rounded, with central cells still more circular,
looser, and with numerous large empty cells or spaces.

Fibrovascular system situated at center of end of the leaf
joining the stem, with phloem pointing toward free end of leaf.
The bundle is small, has on each side numerous aroclated
tracheids, and surrounded by small chlorophyll cells.

The stem has similar tissues except at its center is a
circular bundle.

If the section is taken so as to cut near the tip of the leaves, we find they are free from the stem. Further down, they become united to the stem, and we usually find here a large resin passage, or intercellular space. This is situated in the mesophyll toward the outer end of the leaf, and is probably spherical as it does not run down very far. It seems to have no specialized bounding cells. In the stem, we find also two similar resin passages on either side of the bundle on shorter axis of stem. They show from the outside as a small blister at base of the small scales.

Sections in different parts would show relative different sizes of stem and leaves. We can see that the leaf bundle springs from the bundle of stem. In places, we might find the stem with bundle surrounded by thick-walled cells full of starch, and occupying almost entire diameter of stem. Again we might find an abundance of tracheids with isolated dots around bundle of stem, these not usually being seen there.

Leaves of two kinds, viz. scale-like, and awl-like, the latter the ones examined. They are generally in two, opposite, and adnate to the stem at their base. A section of the free end of leaf is triangular.

Epidermis is composed of oval to circular cells, with cuticle and thick outer walls.

Hypoderma is composed of sclerenchymatous cells, forming a complete row, except on upper side, it being found there only at the corners. Sometimes secondary row less complete, present.

Stomates found only on the upper side, where the hypodermal row is absent.

Mesophyll has palisade cells on its lower side, with those of central and upper parts more nearly circular, and not as closely packed together.

Resin passages more found in free portion of leaf, but near juncure of leaf to stem.

Fibro-vascular bundle one, central, surrounded by small chlo-rophyll cells with usual phloem and xylem.
If we take sections from near the juncture of leaf to the stem, we find a large resin passage joined to the epidermis in the center of the lower side. This resin passage is probably spherical or nearly so, as it extends only a short distance. It occupies a good part of the leaf, and is peculiar because bounded by several rows of small elongated chlorophyll cells. The bundle here is toward the upper side of the leaf, it eventually joining the bundle of stem. A section of leaf and stem where they are joined together is shown in Fig. XIII, B. This shows two small leaf-like projections of the stem between the two leaves, one on either side of stem.

Leaves somewhat two-ranked, about one half inch long. Sections oblong, upper side convex, lower concave, both with swelling above and below bundle, though upper more prominent. Base to altitude as 4:1.
Epidermis with thick cuticle. Cells similar to those of mesophyll, but smaller. From circular to oval, with longer axes touching. Thin
"Made examination from dried specimen soaked in water."
walled, with granular contents and chlorophyll.

Stomates absent on upper side, from 3-5 on each side of swelling on lower side. Not deeply set, and with irregular intercellular face.

Hyphodermal layer absent.

Mesophyll with about two rows of palisade cells on upper side, lower side having cells smaller and oval. Cells in center of leaf running from bundle to ends, oval to oblong, larger and looser than the others. Resin passages absent.

Fibro vascular system with no definite or regular bundle sheath.

Bundle one well developed, surrounded by small thick walled chlorophyll cells. Isolated trachide not present as far as I could find.

Distinguishing Characteristics:

**Pinus**: Leaves in bundles 2-5, 2-15 inches long. Epidermal cells having the two diameters about equal, and nearly or quite filled with marked or pitted tissue. Hyphodermal cells from thin walled to sclerenchymatous, and in one complete row to several incomplete. Mesophyll with infolding cell walls. Resin passages generally two or more.
Bundles one or two.

P. Austriaca. Leaves in twos, very stiff and fragrant, 4-5½ inches long. Hypodermal sclerenchymatous, in several incomplete rows, thickest at corners. Resin passages parenchymatous, with sclerenchymatous cells, 2-8. Bundles two, connected by row of sclerenchymatous cells on phloem side.

P. sylvestris. Leaves in twos, not stiff, 2½-3 inches long. Hypodermal cells in one row, without sclerenchymatous filling. Resin passages 7-11, usually peripheral, consisting of sclerenchymatous cells. Bundles two, widely separated, and connected on phloem side by band of sclerenchymatous cells, with thick walled cells running down between bundles.

P. resinosa. Leaves in twos, lustrous, 5-6 inches long. Hypodermal cells in one row, without sclerenchymatous tissue. Resin ducts 2-5, usually peripheral, without sclerenchymatous filling. Bundles two, very close, without sclerenchymatous band.

P. palustris. Leaves in threes, triangular in section, 10-15 inches long. With several incomplete rows of sclerenchymatous cells. Row
next epidermis without filling. Resin passages internal, thin walled, though sometimes with one or two sclerenchymatous cells. Bundles two, connected on both sides by sclerenchymatous cells, those on phloem side more numerous.

**P. strobus.** Leaves in fours, sometimes in threes, 3-4 inches long, slender and very limber, triangular in section. Hypodermal cells in one row, thin walled. Resin passages 1-3, generally two, thin walled, peripheral. Bundle one.

**Picea.** Leaves separate, all around, stem, less than two inches long. Sections inclined to be square. Epidermal cells without filling. Hypodermal cells with one complete row, and sometimes second incomplete row. Cells at ends with sclerenchymatous filling. Mesophyll without unfolding cell walls. Resin passages 0-2. Bundles, if two, close.

**P. excelsa.** Leaves green, ½-1 inch long. Sections oblong to square. Bundles with hypodermal cells with sclerenchymatous filling, generally a second row there. Resin passages 0-2; near line of shorter axis. Bundles two, close, connected by row or band of sclerenchymatous cells.
P. fungens. Very similar in histological characters to P. excelsa. nigra. Leaves ½-1 inch long, strong and furred, with whitish sides. Sections more nearly square than in P. excelsa. Sclerenchymatous cells of hypoderma more nearly continuous, and cells of resin passages somewhat thicker. Resin passages 1-2, more constantly two than in P. excelsa. Without-sclerenchymatous cells on phloem side of bundle.

P. nigra. Leaves flatter, with whitish sides, ½-¾ inch long. Sections square, but smaller than those of P. fungens. Sclerenchymatous cells of hypoderma almost continuous, and mostly confined to one row. Resin passages two. Bundle, if two, are so close together as to oppose as one, without or with a few sclerenchymatous cells on phloem side.

Pseudotuega Douglasii. Leaves flat, ¾-1 inch long, two-ranked. Sclerenchymatous hypodermal cells forming incomplete row. Stomata on lower side only; with palisade cells on upper. Resin passages two, peripheral, toward ends of lower side. Bundle one.

Tiega Canadensis. Leaves flat, about ½ inch long, two-ranked.
No hypodermal layer. Upper side with palisade cells, fat no stomates. Resin passage one, peripheral, just below bundle. Bundle one. No sclerenchymatous cells in leaf.

abies falcata. Leaves flat, ¼- ¾ inch long, two ranked. No hypoderma, Resin passage two, parenchymatous, toward end of leaf. Palisade cells on upper side, and but few stomates on this side. Bundle two. Leaves whitish on under side.

Larix Euro-paea. Leaves numerous in a fascicle, 1- 1½ inches long. Hypodermal sclerenchymatous cells present above and below bundle and at ends of leaf. Resin passages peripheral, at end, small, or rudimentary. Bundle one, central, without tracheids.

Thuja occidentalis. Leaves flat, scale-like, imbricated in two rows, stacked for greater part of length to stem, and sheathing it at base. Stem flat. Incomplete row of sclerenchymatous hypodermal cells. Palisade cells on upper side. Resin passage near tip of leaf, spherical.
Bundle one, at juncture of leaf and stem, with numerous isolated tracheids.

*Juniperus Virginiana*. Leaves small, of two kinds, needle-like, and scale-like, former triangular and adnate to stem at base. With incomplete row of aerenchymatous hypodermal cells. Upper side with palisade cells and without stomates. Resin passage one, spherical, peripheral on outer side, at base of leaf, with several rows of oblong small chlorophyll cells as boundary. Bundle one, central, approaching side of leaf next to stem at base of leaf.


Key to the analysis of the above species based on leaf structure.

I With at least one complete row of hypodermal cells. With resin passages.

A. *Pineus*. Mesophyll with infolding cell walls. Leaves in bundle of two to five.
a. Fibro-vascular bundle two.

! Leaves in two's.

1. With sclerenchymatous hypodermis none to several rows.

P. austriaca. Bundle close, connected on phloem side by row of thick-walled or sclerenchymatous cells. Resin passages parenchymatous. 2-5.

2. Hypodermal cells in one row, not sclerenchymatous.

P. resinosa. Resin passages peripheral, 2-5. Bundles close, without row of sclerenchymatous cells connecting them.

P. sylvestris. Resin passages peripheral, 7-11. Bundles far apart, connected by band of sclerenchymatous cells.

!! Leaves in three's.

P. falunensis. Resin passages internal, about six. With row of sclerenchymatous cells on both phloem and xylem sides of bundle with groups of sclerenchymatous hypodermal cells.

b. Fibro-vascular bundle one. Leaves in fives.

P. etruscus. Hypodermal row of cells not sclerenchymatous. Resin passages peripheral, usually two.
B. *Picea*. Epidermal cells without marked or fitted filling. Sections ollong to square (rounded at corners). Leaves separate on stem. Resin packages peripheral, 0-2.

*P. excelsa*. Sections vary in shape from irregular ollong to square. Bundles two, very close, connected on phloem side by mass of sclerenchymatous cells. Leaves green, ½-1 inch long.

*P. nigra*. Sections square. Generally with few, if any, sclerenchymatous cells on phloem side of bundle. Resin passages two. Leaves ½-¾ inch long, rather blunt, whitish along the sides.

*P. fergusii*. Sections square. Without sclerenchymatous cells on phloem side of leaf. Leaves with white along sides, very firm, ½-1 inch long.

II. Hypodermal row absent, or incomplete. Leaves flat, two ranked.

A. Hypodermis of an incomplete row of thickened or sclerenchymatous cells. *Pseudotsuga Douglasii*. Resin passages peripheral, two, on lower side toward ends. Stomates absent on upper side.
8. Hypodermis completely absent.

Tilia camadensis. Resin passage one, peripheral, on lower side below bundle. Epidermal cells with upper half filled. No stomata on upper side. Bundle one.

Abies lalsamea. Resin passages two at ends in mesophyll. But few if any stomata on upper side. Bundle two.

III. Numerous leaves in a fascicle. Hypodermal row incomplete.

Resin ducts very small or rudimentary, peripheral at ends of leaf.

Larix Europaea. Hypodermal cells mostly with sclerenchymatous filling, present above and below bundle, and at ends of leaf. Some of the mesophyll cells with irregular in folding.

IV. Leaves inconspicuous, two or three ranked, united toward base with stem. Incomplete row of sclerenchymatous cells.

Palisade cells. Resin passage spherical.

Thuja occidentalis. Leaves scale-like, flat. Resin passage
at apex of leaf, and without special boundary cells. Bundle one, at end of leaf next the stem.

Juniperus Virginiana. Leaves of two kinds, scale-like and awl-like, triangular. Resin passage at base of leaf, peripheral on lower side, with several rows of specialized strong chlorophyll cells. Bundle one, central, except at base of leaf.

V. Leaves flat, with palisade cells, and without hypodermal cells. No resin passages.

Taxus Canadensis. Epidermal cells with chlorophyll and very thick cuticle. Bundle sheath indefinite, bundle one.

Literature.

We give below a partial list of the literature on this subject.

1. Dr. MacRad in the Proceedings of Royal Irish Academy for '75, '76, '77.
2. Botanical Works of Engelmann, published by Shaw. Article on
the conifers of the U. States. Treats more of coarser externals than minute anatomy.


7. De Bary's Comparative Anatomy of Phæanerogamæ and Ferns (Eng Ed). In general like Sachs.


Explanations of Drawings.

Fig. I. Transverse section of Pinus Austriaca.

A. Transverse section of entire leaf of P. Austriaca. x 56.
   1. Epidermis - a cuticle, b. cuticulared layer, c. fritted layer.
   2. Stomata - d. stomatic depression, e. guard cell, f. basal cell,
      g. hypostome cell, h. intercellular space.
   3. Hypodermis.
   5. Resin passage - k. bounding cells, l. epithelial cells.
   6. Fibrovascular system - m. sheath cells, n. parenchymatous
      cells, o. tracheids, p. sclereenchymatous cells. R. bundle.
      q. phloem, r. xylem.

B. Corner of A. magnified still more. x 306.
C. Side of A. ...
D. Showing mesophyll and resin passage. x 806.
E. Showing bundle and surrounding cells. x 255.

Fig. II. Transverse section of leaf Pinus sylvestris. x 56. Explanations same as in Fig I.

Fig III. ... " " " " Pinus resinosa. x 56. ... " " " " " 
Fig. V. A. flat leaf, B. square leaf of Picea excelsa. x 56. Explanations same as Fig. I.

Fig. IV. Transverse section of leaf Picea abies. x 56.

Fig. VI. " " " Picea pungens. x 56.

Fig. VII. " " " Picea nigra. x 56.

Fig. VIII. " " " Pseudotsuga Douglasii. x 56.

Fig. IX. " " " Tsuga canadensis. x 56.

Fig. X. " " " Abies falsamea. x 56.

Fig. XI. " " " Larix Europea. x 56.

Fig. XII. " " " Thuya occidentalis.

A. Showing stem with leaves, on either end. x 56.
B. Showing resin passage in leaf and stem. x 56 (diagram).
C. Showing portion of leaf more highly magnified.

Fig. XIII. Transverse section of leaf of Juniperus Virginiana.

A. Showing section of leaf where it is free from stem. x 56.
B. Showing stem with leaves on sides. (diagram) x 56.
C. Showing portion of leaf more highly magnified. x 56.

Fig. XIV. Transverse section of leaf of Taxus Canadensis. x 56.

FINIS.