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LEAF DAMAGE IN DICOTYLEDONS

[Following is a translation of a French-language book by A. Tison entitled Memoires de la Societe Linneenne de Normandie (Reports of the Linnaean Society of Normandy), Caen, Vol XX, 1899-1901, pages 125-327.]

Introduction

Most of the trees in the countries in our area lose their leaves each year in the fall; this is a rather striking phenomenon which has never failed to attract the attention of botanists. However, as we shall see in the historical review of this topic, there are very few authors who covered this subject specially and scientifically; those authors who did write about the subject did so in a rather incomplete fashion and their conclusions do not agree. Most of them confined themselves to a more or less detailed study of a specific case and to a summary of the observations reported on other individuals.

On the basis of the differences of opinion found in the works of these authors, we concluded that we actually have very little information on this topic and that a detailed study of numerous individuals, primarily from the anatomic viewpoint and checked over several successive years, would be necessary in order to understand this phenomenon fully. With this purpose in mind we undertook the research project contained in this report.

The study we are presenting here today is therefore primarily an anatomic study of the changes which occur in the foliar (leaf) pulvinus [pulvinus folii] before and after the leaves fall; as its title indicates, our study involves only the dicotyledons with deciduous leaves. We thus confined the study of the phenomenon to those species where it occurs periodically and regularly. A similar study for species with persistent (indeciduous) leaves would undoubtedly be very interesting at least for purposes of comparison; we expect to undertake such a study later on.

In order to learn more about the mechanism involved in the falling of the leaves in autumn, we thought that it would not be enough to examine the region of separation, by itself, before the leaf falls and each of the two surfaces of dehiscence afterwards; we thought that it would be necessary to study the operations involved in separation from life, in other words, to observe it at the very moment when this separation takes place. However, the extreme ease with which the petiole is separated from the stem under these conditions constitutes a major obstacle to the longitudinal sections required for such observations; besides, in each of the cases studied, we tried -- by trial and error and by making many tests -- to obtain samples in which the detachment of the leaf has already been partly begun but where, nevertheless, the petiole was still sufficiently attached to enable us to make longitudinal sections without isolating it from the leaf pulvinus.

On the other hand, we were quite aware that we had to adhere to the natural conditions of defoliation; we therefore always protected our specimens from the tree, without artificially hastening the fall of the leaf by putting detached branches in a box, as was done by some of the predecessors.

We did not take any species of glass house plants; we concentrated on individuals freely growing in the Botanical Garden of the city of Caen, around the Botanical Laboratory. In addition, we chose our species from among the largest possible number of genera and families.

Since it had been found that the fall and cicatrization of the folioles on the complex leaves revealed the characteristics of leaf cells, although on a small scale and with not as much constancy; we therefore believed that we should include a study of these folioles after we studied the leaves; this second study will therefore be found in the second part of this report.

The research project contained in this report was conducted at the Botanical Laboratory of the School of Sciences of Caen under the very kind over all direction of Professor O. Lignier.

[Cf. Table of Contents, pages 163-166, below.]

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Historical Review

The assumptions made by the first authors who discussed the fall of leaves were more or less unfortunate. Many of them based their statements on simple outward appearance or on excessively superficial observations. Botanists did not begin to try the explanation of this phenomenon by observing the anatomical aspects until around the halfway point in this [19th] century.

In 1758, du Hamel (du Hamel du Monceau (Henri-Louis), *Physique des arbres* (Physical Structure of Trees), Paris, Guerin and Delatour, 1758, Vol I, page 129) found two causes for the falling of the leaves. He believes that there is, at the base of the petioles, a layer which always remains herbaceous and which is incapable of tolerating the cold weather during the winter. He also thought that the leaf stops growing as a result of its great perspiration while the stem continues to grow; this results in a tension which breaks the fibers connecting the leaf to the stem.

Later on, Mustel (Mustel, *Traite theorique et pratique de la vegetation*, Paris, Leboucher, 1781, Vol I, page 109) came up with the following rather astonishing theory. In autumn, the leaves are full of sap as a result of the lack of transpiration so that the sap moves up the stem since it can no longer find any room in the leaf itself; this results in a very strong pressure against the base of the leaf and as a result the leaf falls off.

According to Murray (Murray, Johann, *Opuscule* I, Goettingen, Dieterich, 1785, page 138), it is, on the contrary, the lack of sap which causes the leaves to die and which then causes them to fall off; he believes that the pressure exerted by the bud against the axilla of the leaf prevents the sap from reaching it.

In the opinion of Vrolick (Vrolick, Gerard, *Dissert. de defoliatione vegetabilium...*, Lugduni Batavorum, Long-Koop, 1796, 6 pages), the leaves complete their lifetime cycle at a given time. They fall because they die quite normally or because they die prematurely as a result of heat, cold, or diseases.

According to this author, the fall of the leaves is caused by the resorption of a portion between the dead leaf and the living tissue of the pulvinus, with the resorbed portion belonging to the latter.

In the beginning of this century [19th], Link (Link, Heinrich *Kritische Bemerkungen und Zusaetze zu Karl Sprengels' Werk: uber den Bau und die Natur der Gewaechse*, Halle, Kummel, 1812, page 51) thought that he could find the explanation of the fall of the leaves in the anatomic constitution of the base of the petiole. In his opinion, the tissue of the latter and the tissue of the stem are interrupted by a region in which the cells have a direction different from that of these two organs: he added that the leaf is separated in this region but he did not indicate how this separation takes place. Several years later, du Petit-Thouabs (du Petit-Thouars, Histoire d'un morceau de bois, Paris, 1815, page 136) picked up the theory of du Hamel according to which, as we saw earlier, the tissues linking the leaf to the stem are torn as a result of the growth in the diameter of the stem.

In 1821, Vaucher (Vaucher, Memoires de la Soc. de Phys. et d'Hist. nat. de Geneve, Vol I, 1821, page 120), thought that he could find the cause of the fall of the leaves, as did Link, in a special disposition of the tissues at the base of the petiole. According to him, the latter is separated from the stem by a parenchyma which maintains their continuity so long as it is full of sap; but the continuity ends as the parenchyma dries out and is altered. In addition, he thought that the fibro-vascular systems of the two organs were not perfectly continuous but were separated from each other by a parenchymatous suture.

About 2 years later, Schultz (Schultz, Karl, Die Natur der lebendigen Pflanze, Berlin, Reimer, 1823, Vol I, page 128), thinking along similar lines, believed that, on the level of the articulation of the petiole, the superposed elements of the wood and of the inner bark wall meet on the same plane, on whose level they then gradually are separated from each other, thus no longer permitting the circulation of liquids.

De Candolle (de Candolle (Aug. Pyr.), Organographie vegetale, Paris, 1827, Vol I, page 133) explained the fall of the leaves by the presence, at the base of the petiole, of a layer of cells which dry out and which are separated from the neighboring layer; the phloem-ligneous system is then torn off following this separation.

Treviranus (Treviranus, Christian, Physiologie der Gewaechse, Bonn, Mercus, 1835-1838, Vol I, page 435, Vol II, page 216), like some of his predecessors, thought that he could find a rather particular feature in the structure at the base of the petiole. In his opinion, the cell tissue here is always a little heterogeneous and this arrangement blocks the circulation of the sap as the vital activity of the leaf drops. The different cell masses are thus no longer kept together by the unity of their vital tendency and they separate from each other.

In 1859, Schacht (Schacht, Hermann, Lehrbuch der Anatomie und Physiologie der Gewaechse, Berlin, Muller, 1859, Vol II, page 136), guided by more complete anatomical knowledge, saw the cause of the fall of leaves in the delayed changed occurring at their base. According to this author, the death and, consequently, the fall of the leaf are caused by the rather delayed establishment of a cork across the base of the petiole; this cork stops the circulation of sap between the stem and the leaf.

In 1860, Mohl (Mohl, Hugo, von, "On the Anatomical Changes in the Leaf Joint which cause the Leaf to Fall," Bot. Zeit. 1860, pages 1 and 9) published a work on the falling of leaves which is considered as a classical treatise on this subject. He starts his report with a very well documented historical review of work done until 1860. (By the way, we were able to learn of the opinions of Mustel, Murray, Vrolick, Link, Schultz and Treviranus only after reading this historical review by Mohl.)

Mohl more specifically studied the case of Gymnocladus canadensis. He found that, on 4 October, there is a thick cork running across the node of the petiole; this cork establishes a clear separation between the petiole and the stem. The author notes that the cells of the pulvinus, located above this cork layer, are very clearly distinguished from those of the petiole by their reduced size; he further points out that a portion of this tissue with rather small cells, adjoining the cork, has a brown color, indicating the beginning of the death of the leaf; he used the term "rundzellige Schichte" [round-cell layer].

According to Mohl, the separation of the leaf occurs above this region, inside a stratum consisting of two layers of cells which are transversally partitioned; he calls this the "Trennungsschichte" [separating stratum]. This stratum is quite clearly distinguished from the rest of the pulvinus by all of the characteristics of a very strongly vegetative tissue. The author says that the separation of the organ occurs without resorption of tissues as the cells of this stratum are loosened and thus separates; but he does not give any indications as to how this separation takes place.

In the opinion of Mohl, the leaf bundles cross the cork and the stratum of round cells without undergoing any change.

Following the study of Gymnocladus canadensis, the author rapidly reviews the other species which he studied. In all cases he reports the presence of the separating stratum, partitioned like a cork, but existing here only for the purpose of separating the leaf and not serving for protection here. He also finds that the transversal cork of the base of the petiole does not exist in all cases and he indicates the species in which he has found this to be so and the species in which he did not find this.

In this work by Mohl, we do not get any indication as to what happens to the scar and to the leaf pulvini after the leaves fall. The author reported on this, as a matter of fact, in an earlier work (Mohl, Hugo, von, "On the Process of Cicatrization in Plants," Bot. Zeit. (Botanical Journal), 1849, No 36). In this work he points out that, during the first years following the fall of the leaf, the cicatrization cork exists in all pulvini and that it runs even across the phloem-ligneous bundles. According to him, the thalli of the vessels are transformed into cork after the dissolution of the vascular walls.

We would like to point out another report by Mohl (Mohl, Hugo, von, "On the Separation Process in Succulent Plant Organs," Bot. Zeit., Vol XVIII, 1860, page 273) which, so to speak, follows the preceding one.

Here the author, among other things, studied the artificial disarticulation of leaves and folioles on detached branches kept under conditions in which their desiccation occurs very slowly; he wanted to find out whether there is some relationship between this disarticulation and that of the leaves in autumn.

For this purpose, Mohl clipped the branches of various plants in a tin box; the air in this tin box was kept humid. He observed that a separating layer would form more or less belatedly at the base of the leaves and the folioles; this separating layer was similar to the separating layers found in autumn and acted in the same way; it differed, however, primarily by the complete absence or, shall we say, the rather small amount of starch in its cells. The author furthermore pointed out that, in disarticulations of this kind, there is never any formation of periderm, at the base of the organ, such as he had reported it earlier in the case of the autumn fall of many leaves.

In 1871, Mr. Wiesner (Wiesner, J., "Investigations on the Autumn Defoliation of Ligneous Plants," Sitz. d. K. Akad. d. Wissensch. zu Wien, 1871, pages 465 and 509), reviewed the study of the fall of leaves especially from the physiological viewpoint and devoted almost all of his work to the study of the action of transpiration on the fall of the leaves. We studied the question personally, primarily and almost exclusively from the anatomical viewpoint; we will therefore use only the anatomical portion of the results presented by this author.

Like Mohl, Mr. Wiesner confirms the existence of a separating layer in all cases; however, he does not give any indication as to its constitution. In his opinion, likewise, the leaf breaks off as a result of the loosening of the cells of (from) the separating layer, without any change in their walls. He explains this loosening in the light of the dissolution of the intercellular substance under the action of the organic acids; to support this statement, he mentions the fact that he observed that the yellowish leaves have a more acid reaction than the green leaves.

Mr. Wiesner does not agree with Mohl when the latter says that the leaf bundles are not modified on the level of the petiole node. In his opinion, these bundles undergo a reduction of volume, in autumn, down to the level where the separating layer will form and this helps the fall of the leaf by reducing its aspiratory strength.

During the following year, Ledeganck (Ledeganck, K., "Histochemical Research on the Autumn Fall of Leaves," Bull. de la Soc. roy. de Bot. de Belgique, Vol X, 1872, pages 133 and 167) took up this theory again and developed it even though Mohl had demolished the theory of Schacht by announcing that the cork might be absent before the fall of the leaf at the base of the petioles. He sees the predisposing cause for the fall of the leaves in the development of a peridermic layer across the base of the leaf and he sees its actual cause in the action of the cold weather which causes the two to become loosened by unequally retaining the empty and spongy tissue at the base of the petiole and the peridermic layer; the wind or any other mechanical cause then brings about the separation.

The author reports that he observed about 100 species but he confines himself to describing only the observations made on about a dozen of them.

Ledeganck distinguishes two types of suberification at the base of the petioles: suberification by layers, when the periderm forms an interrupted layer only upon the (to the) passage of the bundles; diffuse suberification, when the transformation occurs slowly as a result of the deposit of suberous matter in the cavity of some of the cells. As an example for the latter way of suberification, the author gives the case of Quercus robur; now, we can say, as of this moment, that the cells, which he describes as possessing a deposit of suberous matter in their interior, are sclerites. We will have occasion to come back to this later.

Mr. Mer (Mer, M.E., "Vegetative Phenomena Preceding or Accompanying the Decay and Fall of Leaves," Soc. Bot. de France, Vol XXIII. 1876, page 176) studied the phenomenon of the fall of leaves only from the physiological viewpoint. This author concentrated primarily on the disappearance of starch from the leaves prior to their fall and their change in coloring.

Brettfeld (Brettfeld, "On Cicatrization and the Fall of Leaves," Pringsheim's Jahrbucher, Vol XII, page 133) studied the fall of leaves in monocotyledons only; however, since our research does not cover this area, we will give the results of his work because of their importance. According to the author, the separating layer, in the monocotyledons, contrary to what happens in the case of the dicotyledons, forms at a time when the tissues are only very little differentiated; this also happens at a time when the base of the leaf is in full growth. During that time, the tissues of the pulvinus, located below the base, become sclerified and very often grow to three times their normal thickness. The author does not describe the mechanism of the separating layer.

The sclerified layer of the pulvinus may later on increase twofold by the addition of a periderm (monocotyledones arborescentes, Aroideae) or by the addition of a layer of fibrous reticulated cells (Orchidaceae).

According to Brettfeld, the fibro-vascular cords are not involved in the cicatrization of the wound and they are crushed by the periderm.

In a short note about 2 years earlier, Van Tieghem and Guignard (Van Tieghem, Ph., and Guignard, L., "Observations on the Mechanism of the Fall of Leaves," Bull. de la Soc. Bot. de France, Vol XXIX, 1882, page 312), gave new information on the mechanism involved in the fall of leaves. These authors did not study this phenomenon at the time of autumn defoliation; they studied it during the summer, in the month of July, causing leaves to fall from detached branches; these branches had been kept in an enclosed space saturated with humidity.

Van Tieghem and Guignard, like Mohl, studied the case of Gymnocladus canadensis not only from the viewpoint of the fall of the leaves but also from the viewpoint of the folioles.

As regards the latter, they found that there is only one separating layer forming at their base and that this layer developes through the partitioning (subdivision) of one cell layer, repeated two or three times. According to these authors, there is never any cicatrization below the wound, that is, neither before or after the fall of the foliole.

At the base of the leaves of the same species they found that, in addition to the separating layer, there develops -- at a rather early stage, around the middle of June -- a suberous layer which is increased on the inside by a periderm; this double armor involves the bundles here; (this suberous layer is the layer which Mohl called the "round-cell layer"; Mohl, by the way, was not aware of the cicatricial function of this layer).

As far as the function of the separating layer is concerned, these two authors advance an opinion that differs from that expressed by botanists earlier. According to them, there is a resorption of the middle layer in this stratum which divides it into two leaflets whose cells become roundish and grow toward each other until they meet; after that they exert pressure against each other and mechanically follow the leaf after the vessels, the sieve-like tubes, and the fibers have been broken.

Following this study of Gymnocladus canadensis, the authors did a summary of other cases in a few lines. They tell us that, before the fall of the leaf, there can develop only a single portion in the double armor existing in the case of Gymnocladus; in other words, this would be either the suberous strata or the periderm. Similarly, there may not be any cicatrization.

Mr. Staby (Staby, Ludwig, Ueber den Verschluss der Blattnarben nach Abfallen der Blaetter, Inaugural Dissertation, Berlin, 29 July 1885) studied only the cicatrization of the wound caused by the fall of the leaves. He points out the cicatrization of the vessels by means of gum from the wound and, in certain cases, by the thalli. In his opinion, the only cicatrization tissue here would be the periderm and he does not mention any of the other cicatricial strata pointed out by Van Tieghem and Guignard.

Mr. Staby gives us some indications on the focus of the appearance of the periderm in the leaf pulvinus; he then gives us some examples in which this periderm forms before and other examples in which it forms after the fall of the leaf.

The author found that the periderm, in all cases, runs across the entire pulvinus at the end of the 2nd year, except in genus Quercus where it appears only during the 3rd year.

For Mr. Staby, the phloem cords are not traversed by the periderm. In addition, this author, in contrast to the opinion expressed by Mohl, does not say that the thalli are transformed into cork after the dissolution of the vascular walls. He does not except the idea of the strangulation of these bundles, and as Brettfeld indicated. In his opinion, the vessels are broken and the periderm grows across them through the proliferation of the neighboring cells between their distant extremities.

The latest general research which, as far as we know, has been published on the fall of the leaves is the research by Mr. MÖlisch (MÖlisch, Dr., Hans, "Investigations on the Fall of Leaves," <u>Sitz. d. K. Akad. d. Wissench. zu Wien</u>, Vol XCIII, 1886, page 148).

This author devotes most of his work to physiology: the action of transpiration, of temperature, of humidity, and of light in the phenomenon of the fall of leaves. The anatomical part is very short but it nevertheless includes some very interesting results.

Like Mr. Wiesner, Mr. MÖlisch observed, in certain leaves, a contraction of the leaf bundles on the level of the surface of detachment but he notes that this exists at all times.

He finds that, at the moment the leaf falls, there may develop a periderm or some lignified layers. Depending on the particular case, these layers are either only the stratum with the round cells or they constitute only a zone of cells located above the separating stratum, or they constitute both of them together at the same time. The author goes into great detail on the Conifera which we did not touch.

With respect to the operation of the separating stratum, Mr. MÖlisch recalls the opinion expressed by Mr. Van Tieghem and Mr. Guignard on the resorption of a cell layer; he adds that he wanted to observe this phenommenon in the different species of dicotyledons but that he always arrived at a negative result. The author always found the cells of the separating stratum to be perfectly intact.

Mr. MÖlisch did not make any observations on the mechanism of separation; on the basis of his comparison with the ordinary mechanism of cell separation in vegetables, he maintains that the middle layer of cells in the separating stratum is dissolved; this dissolution occurs through the action of the gum ferment which had been discovered by Mr. Wiesner a short time before his research projects (Wiesner, J., "On Gum Ferment," <u>Sitz. d.</u>

K. Akad. d. Wissench. zu Wien, Vol 92, 1885, page 41). The author says, in effect, that he found this ferment to be present in a larger quantity in the cells of the separating stratum than in the rest of the pulvinus.

In addition to these general works on this topic which we are dealing with here, we might also mention the names of a few authors who incidentally touched one or the other part of our subjects here.

Mr. Strasburger (Strasburger, E., Manuel technique d'anatomie vegetale, French translation by J. Godfrin, Paris, Savy, 1886, page 168) studied the fall of leaves in the case of Aesculus Hippocastanum and found that there is, in this case, before the leaf falls, a periderm growing across the base of the petiole to the exclusion of the bundles. The author adds that the separation of the leaf occurs within a separating stratum situated above this periderm. According to him, the vessels of the leaf scars are compressed by the cells of the periderm which later on closes the wound completely.

Mr. Lignier (Lignier, O., "Research on the Comparative Anatomy of Calycanthaceae, Melastomaceae, and Myrtaceae," Arch. bot. du Nord de la France, Vol III, 1886-1887, page 128) devotes a few lines to the study of the fall of leaves in the case of Calycanthus occidentalis. The author finds that a suberous layer developes at the base of the petiole prior to defoliation; this suberous layer has numerous partitions; the latter develop in the cortical parenchyma and in all of the elements of the bundles. The author defines the position of the separating layer but he does not indicate how it functions.

Quite recently, in two communications addressed to the Academy of Sciences (Tison, A., "On the Fall of Leaves and the Cicatrization of the Wound," Comptes-rendus de l'Acad. des Sc., 19 June 1899; id., "On the Cicatrization of the Fascicular System and That of the Secretory Apparatus During the Fall of Leaves," Comptes-rendus de l'Acad. des Sc., 10 July 1899), I summarized the principal results of the research projects mentioned in this work.

Even more recently, Mr. Fouilloy (Fouilloy, Edm., "On the Fall of Leaves of Certain Monocotyledons, Revue generale de Botanique, Vol XI, 1899, page 306), studied the fall of leaves in several genera of monocotyledons with thick and deciduous leaves. Like Brettfeld, whom I mentioned earlier, this particular author says that the separating layer differs quite clearly by the smallness of its cells in the neighboring tissues and he points out that it is differentiated at a very early stage, long before the leaf falls. The wound is protected by the lignified layers below the zone of separation.

PART I

FALL OF LEAVES AND CICATRIZATION OF THE WOUND

This first part of my work will be devoted to a study of the anatomical phenomena which precede and follow the fall of the leaves, until the completion of the cicatrization.

Because of the wide variety of these phenomena in the various species, I thought that it might be best to select a few types and to study them in detail in the first chapter and then to summarize quickly all of the other cases which I examined, grouping them in other chapters, depending on their greater or lesser resemblance to the species considered to be typical.

Chapter I. Anatomical Study of the Fall of Leaves and the Cicatrization in a Few Selected Types

1st Type. Aristolochia Sipho L'Herit

The petiole of Aristolochia Sipho is almost cylindrical in its middle portion and has a swelling or a bulge at its base. It is inserted into the stem above this bulge, around an area abundantly covered with hair; the median line of this area is occupied by four buds which are increasingly developed as we go from the interior toward the exterior, in other words, as we go from the bottom to the top. The outermost three buds are located in a conical cavity in the bulge of the petiole; the first two buds are thus completely hidden while the third one is only partly hidden; this latter one, on the side of the stem, closes the entrance to the cavity of the petiole. The fourth bud, usually slightly detached from the other three, is in the open air.

At the base of the adult leaf -- before any changes leading to its fall -- the cells of the cortical parenchyma are all of the same shape and of the same differentiation as those of the petiole and the stem but they are not as large, their growth along the diameter being somewhat smaller; in addition, the intercellular channels here are either entirely absent or they are excessively reduced in size. The transition from this area to the cortical parenchyma of the stem and to that of the petiole is almost imperceptible.

The leaf bundles here are three in number. At the base of the petiole, these three bundles are reduced to roughly half with respect to volume (Figure 1) and with respect to the number of elements.

At this level only the vessels of the primary and secondary wood are lignified; the latter are elongated and have a very small diameter; the phloem is composed only of the sieve-like tubes, the mate cells, and the phloem parenchyma. In all cases I found a complete absence of ligneous fibers, phloem fibers, and lignified parenchyma. As for the sclerous phloem (ls, Figure 1), which, further up and further down, is partly composed of fibers and elongated cells, I might say that it disappears rather abruptly a little above the base of the petiole and then reappears a little below, in the pulvinus.

In its lower portion, the petiole thus reveals the largest possible reduction of the supporting tissue, thus offering a region of lesser resistance at that point. This arrangement is very good for the movement of the leaf but at the same time it is also the place where the leaf can break off.

The reduction of the phloem-ligneous leaf system at the base of the petiole, contrary to what Mr. Wiesner (loc. cit., page 105) believed and as Mr. Mölisch (loc. cit., page 178) stated, exists during the entire vegetative period of the leaf; it thus does not occur after the event, sometime before its fall and as preparation for this fall, as the first of these two authors thought. The bundles in this region, as in all of the other tissues of the petiole, simply turned out to grow much less than anywhere else and there is less lignification here.

The separation occurs primarily at the base of the petiole, a little above the insertion of the leaf. The first phenomenon preceding the defoliation is the increase in the density of the protoplasm in the parenchyma of the pulvinus. This region, moreover, is rich in chlorophyll and it is indicated on the outside by a green coloration which contrasts increasingly with that of the rest of the petiole, as the latter becomes more and more yellow; I will therefore call this region the "green region" hereafter. The cells with the dense protoplasm, which constituted, include only very little starch; on the other hand, there is much starch in the tissues in the region below the pulvinus.

While this protoplasm activity takes place at the base of the petiole, we can observe the beginning of the obstruction of the vessels in the bast-ligneous leaf system by the thalli. These latter penetrate in large numbers into all of the vessels of the primary wood and very rarely into those of the secondary wood. They are abundant primarily in the base of the petiole but they occur not only on this level; the vessels, in effect, are more or less completely obstructed by these cell proliferations, to a very great distance from the petiole, and, above, in the pulvinus, all the way to the point where the bundles re-enter the caulinary bast-ligneous system.

In the large spiral and spotted vessels, the thalli penetrate through many points at the same time; they become roundish in their interior and grow rapidly; through reciprocal pressure, they are very closely intertwined with each other. The walls, which have thus been formed, become level and their direction is highly variable; as a result all of the thalli together simulate a parenchyma inside the vessel. In those vessels with the smallest diameter, the thalli penetrate at more elongated points, advancing toward each other and intertwining their free ends, end-to-end; their separating walls in this case are perfectly transversal and simulate the partitions of the vessel. All of these thalli also push their walls very close to those of the vessels, fitting into all of their raised and depressed portions; finally, they often are partitioned off again in their interior.

Initially very thin, the walls of the thalli gradually become thicker and finally have the same thickness as those of the parenchymatous cells on which they depend. These thalli do not reveal any bordered pits, such as we have them in most of those that developed along the old vessels in the stems; these essentially are obstructing cells. Through their point of penetration, contact is maintained between them and the cells which formed them.

The development of the thalli, as well as the increase in the density of the protoplasm at the base of the petiole begins about 3 weeks before the fall of the leaf. When the thalli fill the vessels of the primary wood completely, they slow down the circulation of the liquids in these elements; as of that moment, the vitality of the leaf decreases rapidly.

There is no other change in the elements of the bundles before the fall of the leaf, except for the apperance of calluses in the sieve-like tubes in this region, as elsewhere in all of those throughout the rest of the plant.

The leaf becomes more and more yellow as its vitality decreases and the cells of the petiole die from its top down toward the base. During this time, a layer in the upper portion of the green region assumes increasingly individual characteristics in the sense that the protoplasm here becomes denser than anywhere else; this is the separating stratum which in this case is reduced to a single layer of cells.

This separating stratum developes precisely in the region of least resistance of the bundles, at the level of th ir contracted portion. It had a perfectly level surface, running quite noticeably perpendicular to the direction of the petiole which it traverses throughout its entire width (cs, Figure 1). Its internal border is situated a little above the axillary angle of the leaf.

While the separating stratum developes individual characteristics in the fashion just described, we find that the tissue of the petiole, above and opposite it, changes the nature of its walls which become lignified without increasing in thickness and which, from then on, very strongly fix the coloring substances of lignin (ammoniacal fuchsin, phloroglucin, etc.).

The region thus lignified includes one or more layers of cells; it reaches its maximum thickness on the inside of the petiole and it decreases as we approach its outside (rs). Very clearly outlined in its lower portion by the separating stratum and very definitely set off against the latter, it becomes smaller and smaller as we move upward. Sometimes the lignification also extends across the bundles, at the expense of their originally cellulose elements, including here the thalli; at other times, however, this development is very weak. Henceforward we will use the term "subcicatricial lignified stratum" in referring to this stratum.

This is the condition of the articulation (nodes) of the petiole a short time before the leaf falls.

The separating layer begins to function only a few days before the separation of the leaf as such. Sometimes we first of all have a few subdivisions throughout the entire region between the three entering bundles and a point halfway along them, but this only happens here. Then the cells of this layer grow primarily longitudinally; this growth involves a very small portion of their longitudinal walls, situated generally in their upper portion, in the vicinity of the lignified region of the petiole (cs, Figures 2 and 3). As the longitudinal growth is further accentuated, the cell wall becomes very thin in its region of growth and it finally appears to consist only of the primary membrane. The cellulose portion of the wall of the epidermal cells, which are a part of the separating layer here, also undergoes this elongation, after the break of the cuticle and the cuticular strata (m, Figure 3).

The longitudinal growth of the cells of the separating layer tends to remove the base of the petiole from the pulvinus. Only the leaf vessels resist this action and are not elongated. Their resistance and the movements of the leaf first of all cause a folding of the thinning walls of the separating stratum but the growth of the cells of this stratum and their turgescence, aided by those of the thalli at the same level, still growing, very quickly cause the ligneous vessels to break as a result of this traction (tension). The leaf is then held only by the delicate walls of the separating layer; thus its weight, which is tremendous when compared to the weak resistance of these walls, suffices to break the connection gradually and the leaf then falls.

The wind is another one of the most powerful agents in the fall of leaves; it can certainly cause the leaf to fall, all by itself, even before the resisting elements of the bundles have been broken completely by the action of the separating layer. Frost is also a very powerful agent in the fall of leaves, at least when the separating layer has arrived at a point in its development where its walls have become very thin. It seems probable that this latter factor takes effect by more or less rapidly inflating the turgescence water in the cells of the separating stratum and perhaps even by freezing the content of those cells which are near the surface of the petiole; in other words, this factor would thus promote the breaking of the last resisting elements. The leaf, now more or less completely isolated from the pulvinus, is heated as it is struck by the first rays of the sun; it becomes defrosted and then falls because of its own weight. This is why, in the last days of October, when the separating layers are fully active, the slightest frost will separate a large number of leaves.

Defoliation generally takes place, in the case of Aristolochia Sipho, during the second half of October. Normally, if the external agents do not abruptly cause the leaves to break off, it will usually be the oldest leaves, that is to say, those at the base of the growth, which will fall first.

Since the separating stratum is not very far from the insertion of the leaf, the leaf, when falling, leaves only a very small pulvinus on the stem. The fresh scar has a clear green color due to the chlorophyll which contains the immediately subjacent parenchyma. It has the shape of the insertion of the petiole, that is to say, the shape of a horseshoe (ci, Figure 4), where the two ends and the middle are considerably thicker while the two intercalated branches, on the other hand, are very narrow and almost straight. In the three thickened regions we have the three navels of the leaf bundles (cif, Figure 4). These do not have any raised or depressed portions since the bundles break off at the level of the separating stratum; nevertheless, they are quite clearly indicated by their coloration which is paler than that of the rest of the scar.

The space between the branches of the scar is occupied by the three lower buds which were protected by the petiole. These three buds are sometimes very clearly separated, at least at the top, and at other times very close to each other; in the latter case, the three of them together constitute a single conical protrusion. The fourth bud is found all by itself between the ends of the horseshoe and a little above. This entire group together, that is, the buds and the area between the branches of the scar, has a rather silvery and chatoyant (changeable color) appearance due to the long hairs covering it; on the stem, all of this constitutes a swelling or bulge which becomes increasingly marked as the latter grows oblique to its lower direction at the level of the insertion of the leaves.

Earlier we saw that the wound, produced by the leaf as it falls, was not protected in any way against external agents. At least, there is no defense of a histological nature, no defense in the way of lignification or suberification, since the tissues remain cellulosic and do not reveal any apparent changes. We did not find any defenses of a chemical nature, such as, for example, the presence of organic acids, tannin, etc. But the greater vitality of the cells of the pulvinus, which are completely filled with protoplasm perhaps constitutes a system of provisional defense until the subsequent changes which come rather quickly and which we are going to describe shortly. The resistance of a tissue to desiccation and invasion by inferior organisms is, as a matter of fact, related to the turgescence and to the vitality of this tissue.

At the surface of the scar we find the remnants of the thin walls that have been broken off the separating stratum. The primary vessels have already been filled (obstructed) by the thalli; but these thalli still have cellulosic walls, like the cells from which they are derived; the sieve-like tubes are obstructed by calluses.

The wound remains in this condition for a long time and cicatrization begins several days after the leaf has fallen. At that time we can observe a gradual change in the cell wall; this change occurs in the tissues of the leaf pulvinus and there is no further subdivision or partitioning; the cell walls are at that time impregnated with lignin and suberin. In addition, the cells are emptied and die off as this change in the walls progresses. In this manner we can observe the establishment of a ligno-suberous cicatricial layer below the surface of the wound.

(In true earlier notes I used the term "sclero-suberous" to indicate these tissues. Recent research and a more complete knowledge of the facts have caused me to drop this term and to use, instead, the term "ligno-suberous"; this term indicates more precisely the presence of lignin and suberin and, moreover, indicates the deposit of these substances independently of the nature of the tissues in which they are found. Hereafter, therefore, we will use the term "sclerous" to refer -- among the tissues which have lignified walls -- to those whose walls are, in addition, more or less thickened.)

This ligno-suberization does not appear in any particular place. Generally, however, it is found in the lower portion of the thin strip or layer (lamina) and, opposite the bundles, where it shows up first; very often, also, it appears in many places at the same time. As this transformation is further accentuated, the surface of the scar, initially clear-green, becomes a little brownish. A similar brown coloration visible around the pulvinus indicates the thickness of the ligno-suberous lamina and shows that it is larger opposite the three navels; its lower boundary is quite clearly indicated and is found almost at the level of the axillary angle (the line H, Figure 1, indicates this border).

Histological Study of the Ligno-suberous Cicatricial Stratum

The coloring substances common to lignin and suberin (iodine-containing reagents of cellulose (Mangin, L., "On the Iodine-containing Reagents of Cellulose," Bull. de la Soc. bot. de France, Vol 35, 1888, page 421), ammoniacal fuchsin, green of iodine, etc.) stain all of the walls of this stratum; here they reveal a very strong impregnation especially in its lower portion, gradually diminished toward the surface of the scar, however, without reaching it. Above the debris of the latter, we have, in effect, two or three layers of cells which remain cellulosic and which later on become flattened at the surface of the scar; hereafter we will refer to them by the name of "sacrificed parenchyma."

The special reagents of lignin (Wiesner reaction (Wiesner, J., "Note on Behavior of Phloroglucin and Some Related Substances to the

Lignified Cell Membranes," Sitz. d. K. Akad. d. Wissench. zu Wien, Vol 77, page 60), indole, and sulfuric acid (Niggl, "Indole -- a Reagent for Lignified Membranes," Flora, 1881, page 545), aniline sulfate, aniline hydrochloride, etc.) indicate the presence of this substance in the entire cicatrization lamina. Here it completely impregnates the thickness of the walls, except in the immediate vicinity of the cell cavities where the strata do not appear to fix these reagents in the same fashion; nevertheless, the indications thus furnished are not sufficiently clear in themselves. On the other hand, the special coloring substances of suberin (tincture of "alcanna" [alkane, alkannin], treatment by ammoniacal colors followed by washing in water acidulated by 1/10 sulfuric acid (Tison, A., "New Method of Coloration of Suberous Tissues," Assoc. franc. pour l'avancement des sciences, Boulogne Congress, 1899), etc.) vaguely indicate the presence of this substance in the strata of the walls which border on the cell cavities without, however, enabling us to determine the location precisely.

In order to determine the position of these two incrusting substances in the cell membranes of the cicatrization lamina with certainty, we had to use a new method which is much more precise than the earlier methods; we have always been able to use this new method with great success while the others turned out to be completely inadequate.

Our method consists in determining, first of all, on a control section, the double impregnation of the tissues by means of ammoniacal fuchsin or by means of iodine-treated reagents; then we treat the other sections by means of the solvents of lignin so as to retain only the suberin and so as to be able to study them afterward in order to determine the location of the latter (suberin).

The process of dissolution of lignin, which I found to be the easiest here, involves treatment with boiling Javel water for several minutes or, better still, with cold Javel water, stirring several days. The sections must be treated in this fashion, by one of these methods, until the ammoniacal fuchsin no longer stains all of the vessels; they are then very carefully washed because their walls are still more or less swelled (inflated) and have been rendered very brittle by this treatment, especially when we used boiling Javel water.

The reagents for lignin are then no longer fixed on any part of the section. On the other hand, iodine-containing phosphoric acid completely colored the walls of the vessels blue and, in the rest of the section, it also creates a blue color through almost the entire thickness of the cell membranes, particularly in the case of those which earlier did fix the coloring substances of lignin. There is only a very thin surface stratum which, after this treatment, appears more or less sinuous inside each cell and which is stained yellow, as before. It is also on this thin surface stratum -- and to the exclusion of the entire rest of the walls -- that ammoniacal fuchsin and the special coloring substances for suberin, which we pointed out rlier, are fixe

This suberous tum is very t s a matter of fact, it is a film. It differs ve arly from the kened strata which constitute the cell wall at th the leaf falls virtue of the fact that it is in discordance with ells at the leve the punctuations (bordered pits), into which i etrates and which covers all the way to the bottom (po, Figure).

It thus app s like a belated coveri stratum for the cell and not as the last thickening in the wall.

In summary, what we have said so far indicates that the cells of the pulvinus, which serve to make up the cicatrization lamina, lignify -- without thickening -- the cell walls which they have at the time the leaf falls (scl, Figure 5) and that they then cover them with a thin new layer which is immediately suberized (sub, Figure 5). The epidermal cells included in the thickness of the cicatrization lamina under o absolutely identical changes although they remain covered on the outside by he cuticle and the cuticular layers (ep, Figure 5).

The thickness of the thin internal suberous film is quite noticeably the same in all of the cells in the cicatricial lamina. The intensity of lignification, on the other hand, is quite variable. As in the case of the lignified region, which we pointed out above the separating stratum, this intensity is very great at the base of the cicatricial lamina and it decreases gradually as we go up so that it may very often be entirely absent in the cells in its upper portion which from that point onward are specialized only by virtue of the existence of the suberous film.

Because of the double impregnation of their cell membranes by lignin and suberin we called these cicatrization tissues "ligno-suberous strata or lamina," a term which is more precise than the term "suberous strata" which was used by Mr. Van Tieghem and Mr. Guignard (loc. cit., page 314) and the term "lignified strata" given by Mr. Mölisch (loc. cit., page 177).

The process of cicatrization in the leaf bundles is the same as in the cortical parenchyma; nevertheless, ligno-suberization reaches them only at the very last; it is, moreover, more intensive here and the lower limit of the modified tissue here defends a little lower, forming a slight curve toward the stem (I used dotted line H, in Figure 1, in indicating the lower limit of this cicatrization lamina). All of the bundle elements, except the vessels and the sieve-like tubes which I talked about earlier, thus lignify their walls (scl. gure 6) and are then covered by a suberous film (sub, Figure 6). The thalli, situated on the level of the cicatrization lamina, are modified like the parenchyma of the bundle of which they are nothing more than an appendage (dependents) (th, Figure 6).

After the fall of the leaves and before their ligno-suberization, these thalli often manage to dislocate the vessels in the region in which the cicatricial [scar] stratum forms; they do this by virtue of their growth and their reciprocal pressure. When the spacing of the broken portions of the vessels is not as great -- which happens more frequently -- these vessels continue in the same prolongation; in the opposite case they are more or less pushed back, a little bit in all directions, beyond their original axis.

The vessels of the secondary wood which, as we said earlier, usually do not have any thalli, are cicatrized, after defoliation, by the deposit of a substance which completely fills their cavity although this happens only at the level of the cicatrization layer (lig, Figure 6). This substance is also found in the cavity of the vessels that do have thalli when the vessels are not contiguous with each other; as for the thalli themselves, they never contain this substance. Later on we will study this blocking substance in detail as we go into the following type where it is found in great abundance.

In some of the vessels, the walls do not change at all. At the level of the cicatrization lamina, the sieve-like tubes have more or less lignified walls but they never have the suberous film inside (tcr, Figure 6) and they are almost more or less crushed by the neighboring cells. Neither in the case of Aristolochia Sipho nor in the other species studied later on did I ever discover the presence of thalli indicated by Mr. Van Tieghem and Mr. Guignard (loc. cit., page 312).

Within the cicatrization stratum we have elements other than the sieve-like tubes and the vessels in which the internal suberous film is also absent; these are the rare macled cells which are quite scattered. (Could not the absence of the suberous covering film, inside the vessels, the sieve-like tubes, and the crystal-bearing cells be due to the fact that these elements are dead at the moment of differentiation of the cicatricial stratum? The lignin which impregnates the wall of the sieve-like tubes and of the crystal-bearing cells would here appear to have been deposited by the diffusion of the one that produced the neighboring cells.) Like the wall of the sieve-like tubes, their wall is more or less lignified as is the thin envelope which surrounds the crystal and the few points connecting it to the wall (cr, Figure 5).

In general, the cicatrization which we have just indicated is the only one which one can observe during the first year (we count the years between two successive repetitions or recoveries of vegetation). The majority of the pulvini thus have nothing more than a ligno-suberous lamina to protect them through the winter.

Sometimes, however, some pulvini, generally those at the base of the growth, complete the preceding cicatrization with the establishment -- below the ligno-suberous lamina -- of a generating zone which, before the winter, produces just a few layers of cork which always have thin walls.

This generating zone is formed at the expense of the cells of the pulvinus which are in direct contact with the ligno-suberous lamina and by the subdivisions parallel to the lower limit of that lamina; these subdivisions or partitions begin in the internal region of the pulvinus and rapidly grow toward its outside.

Across the bundles, the generating zone is established at the expense of their living elements. The sieve-like tubes are never partitioned; they are first of all crushed by the cells of the generating zone; then they are broken due to the growth of the cork which grows continuously between their distant ends. The same is true of the secondary vessels although they rupture a little later and break without being crushed earlier.

In the vessels of the primary wood, on the level of the zone that generates the cork, the thalli are always numerous and very dense. Their fate is the same as that of the other parenchymatous cells on the same level; in other words, they grow longitudinally and they are partitioned transversally (thp, Figure 7). Under the double action of this growth of thalli in their interior and the cells bordering on the generating zone on their outside, the primary vessels are thus usually broken in several points that are very close to each other; their fragments, as well as their ornamentations, are more or less dispersed. The thalli then become closely intertwined with the neighboring generating cells and establish the continuity of the cicatricial cork, becoming involved in its composition. Sometimes the thalli, which are thus involved in the make up of the cork, are more or less flattened by the neighboring cells which grow faster than they do (c, Figure 7). It may also happen -- although this is quite rare -- that some thalli on that level do not participate in the formation of the cork and the continuity of the latter is then established, across the vessel containing them, in the same fashion as across the secondary vessels.

The cicatricial cork, like the lower limit of the ligno-suberous lamina which it follows, in traversing the bast-ligneous bundles, describes a more or less pronounced curve toward the stem (lic, Figure 8). We will come back to this special feature later on.

Although the crystal-bearing cells are located at the level where the zone that creates the cork is developed, they do not subdivide and they do not become involved in the proposition of this zone; this zone then passes below them.

Although it appears from the 1st year onward, the cork only becomes thicker during the second year; in the many cases in which it does not exist at that time, however, it begins to form always in the spring of the second year; its position is otherwise the same, below the first cicatrization lamina. The formation of its generating zone also begins in the axillary angle of the pulvinus and is propagated in the same fashion across the cortical parenchyma and the bundles.

In all cases, the cicatrization by means of this cork is completed at the end of the 2nd year (lic, Figure 8) and its thickness is then, on the average, 10-12 layers of cells. It ends against the surface of the leaf pulvinus, all around it, and sometimes slightly descends again downward; contrary to what we observed in the periderm of the stem (I always use the term "periderm" to designate particularly the cork of the stem, using the term "cork" as such for the secondary cicatricial suberous tissue) which appeared only later and at the expense of the subepidermal layers (Douliot, H., "Research on the Periderm," Ann. des Sc. nat. Bot., 7th series, Vol X, page 332), it is frequently in the epiderm itself that it developes in the vicinity surrounding the pulvinus.

Earlier I said that the cicatricial cork curves a little toward the stem while crossing the bundles (lic, Figure 8). Mr. Staby (loc. cit., page 19), who pointed out this deviation in a certain number of cases, attributes this to the presence of wound gum (this is the obstructing substance which I pointed out earlier) inside the vessels; by making the bundles resistant, this gum would appear to force the generating zone to go around the fascicular region in which it is located so as to take hold further down, at a level at which the gum no longer exists or at least at a level where it is no longer very resistant.

In the course of this work we will see that this deviation in the cicatricial cork layer occurs in most of the cases; but the explanation, given by Mr. Staby, although quite acceptable at first sight, did not appear satisfactory to me. As a matter of fact, in many species where the wound gum is almost absent or in those species, as in the present case, where it is found in a very small quantity, the cork similarly describes a curve downward. But there is more to this; there are other, opposite cases, where the gum does exist in the vessels up to a more or less great distance below the primary cicatrization stratum and where the cork grows no less directly across the bundles, without curving. The mistake made by Mr. Staby is due to the fact that he fails to take into consideration the ligno-suberization of the tissues of the pulvinus which he does not even mention; in his opinion, the cork is the only cicatricial tissue. As a matter of fact, in all of the cases in which I observed this inflection in the cicatricial cork toward the stem, across the leaf bundles, I always recognize on the one hand, that, as in the case of Aristolochia Sipho, the ligno-suberous differentiation here descended lower in the leaf scar than in the neighboring cortical parenchyma and, on the other hand, that the transformation of the cells of the parenchyma into ligno-suberous cells was here followed by their death and, furthermore, that it afterward rendered them incapable of constituting a generating zone. Now, this is why, in my opinion, the cicatricial cork in certain cases curves downward: not being able to grow across the ligno-suberous tissue, which is a dead tissue, it must go around the deviations in its lower surface.

In the case of Aristolochia Sipho it might also happen -- although of course very rarely and only opposite the three fascicular navels --

that the first layers formed by the cork generating zone under the primary cicatricial lamina are not suberized, as the following ones, but grow considerably along a longitudinal direction, in the fashion of the layer constituting the autumn separating stratum. As in the case of the latter, the delicate walls of these layers break, more or less regularly, however; this results in a partial exfoliation of the first cicatricial lamina. This phenomenon is quite obviously closely related to other more regular and better characterized phenomena which we will study in one of the following chapters and which I have given the name "revival of cicatrization" (Tison, A., "On the Fall of Leaves and the Cicatrization of the Wound," C. R. de l'Acad. des Sc., 19 June 1899).

2nd Type. Amorpha fruticosa L.

On its inside face and very near its point of insertion, between its two short and sharp stipules, the base of the leaf reveals a very large contraction above which it is swollen (P, Figure 9).

As in the case of Aristolochia Sipho, the cortical parenchyma -- at the base of the leaf -- is made up of cells that are a little smaller than the cells of the rest of the petiole and those of the cortical parenchyma in the stem. The circle formed by the leaf bundles becomes slightly flat above the insertion of the petiole, at the point where it is swollen, and is here constricted, on the right and on the left, forming three groups of incoming bundles, the middle one of which is larger than the other two. The total volume of these bundles is here much less reduced than in the preceding species; it roughly has the same size as in the rest of the organ. Nevertheless, here likewise the only lignified elements are the vessels; similarly, the external part of the bast, which is sclerous above and below this region (ls, Figure 9), becomes cellulosic here. At the level where the separating stratum will develop, the external region of the bast is thus soft; here we can still observe some fibers but they are rather rare here and they are cellulosic, like the rest of the tissue.

To avoid any future repetitions, we might say, as of this point, that the absence of the hard bast and the ligneous fibers turned out to be the general rule, at the base of the petioles, in all of the many cases which we studied. Similarly, at this level there are never any bast fibers in the secondary bast and the situation is almost always the same in the primary bast. In all cases, without exception, the only lignified elements which we find on the level of the separating strata of the leaves are the vessels.

The periderm of Amorpha fruticosa is, in the stem, situated a certain distance from the epiderm. It penetrates into the base of the pulvinus and ends here, remaining roughly at the same distance from the bast-ligneous bundles (pd, Figure 9); because of the growing thickness of the cortical parenchyma in this region, it is thus slightly removed from the surface of the pulvinus as it approaches its end.

As in the case of Aristolochia Sipho, we note that, sometime before the fall of the leaf, the region with the smallest cells in the pulvinus appears greener than the rest of the leaf and that it is characterized by a greater density of the protoplasm and, at the same time, by the relative abundance of chlorophyll. Nevertheless, as regards the distribution and frequency of starch, there is nothing special to be found in this region. In the case of Amorpha fruticosa, we do not have any thalli in the vessels before the leaf falls.

The separating stratum develops in the upper portion of the green region. It runs in a direction perpendicular to that of the incoming (reentering) bundles (cs, Figure 9). On the inside, it corresponds to the base of the moving swelling of the petiole; it cuts the bundles in the vicinity of the plant where they are reunited into three groups and it curves slightly toward the pulvinus as it crosses them.

During the development of the individual characteristics of the separating stratum, we get -- in the tissue near the petiole, above it -- a lignification similar to that which we reported in the case of Aristolochia Sipho. This results in the formation of a lignified subcicatricial stratum which is not at all thick (rs, Figures 10, 11, 12) and which is thinner on the outside of the petiole [thinner than the outside of the petiole].

Instead of being made up of a single layer of cells, as in the preceding species, the separating stratum of Amorpha fruticosa includes two or three superposed layers, within which there is no further subdivision (partitioning). In these cells, the protoplasm is very dense, even more dense than in the rest of the green layer.

If we examine the separating stratum at various times closer and closer to the fall of the leaves, we find, first of all, that the cell walls become slightly swollen (mu, Figure 10), gradually reducing the inside diameter [opening] of the cells and assuming more or less curvy sides. In the upper portion of the separating stratum (cs, Figure 11), the middle portion of the walls thus swollen is gradually dissolved and disappears so that all we have left here is a thin surface stratum on either side of it (ci, Figure 11); the cells on this level are also separated from each other and their protoplasm is enveloped only by the thin surface strata of the original wall. In the course of the dissolution of the walls, the cells, separated from each other by this method, remain irregularly attached; some of them remain attached to the pulvinus (b, Figure 12); these are by far the more numerous; others remain attached to the petiole (a, Figure 12). In some places, however, there may be a rather regular opposition of an uninterrupted layer of cells attached to the petiole and a layer that remained on the pulvinus. We may also have a cell in the separating stratum which is separated from its neighboring cells all around its circumference and which, consequently, has become entirely free-standing; this cell is not destroyed as a result of this and remains turgescent, like its neighbors.

After the separation, whose phases we have just indicated, the cells of the separating stratum are inflated and grow rapidly in a longitudinal direction toward their free ends. Between their thin walls, around their base of attachment, we can then see terminate, in a spongy point, the undissolved rest of the median region of the walls.

The longitudinal growth of the cells in the separating stratum, which border on both sides of the dehiscence crack, causes them to push against the opposite surface and to exert pressure on that surface; as a result, it tends to remove the petiole from its pulvinus. Under the influence of this separating force, the vessels and the sieve-like tubes of the vessels break. Since the leaf no longer has any connection with the pulvinus, it falls as a result of its own weight. As in the case of Aristolochia Sipho, defoliation is furthermore considerably promoted by the wind and the frost; we might even add that, in the majority of leaves, the fall is considerably accelerated by these two factors.

In growing across the bundles, the separating stratum is formed at the expense of the living elements of the bast and the wood. For this purpose, the few cellulose fibers and the elongated parenchyma of the primary bast also inflate their walls but, probably because of their great length which by far exceeds the thickness of the separating stratum, they are not detached and appear to dissolve completely.

I conducted some investigations on the histological changes which accompany the inflation (swelling) and partial dissolution of the membranes in the separating stratum. At the beginning of the swelling, the walls more energetically fix the acid coloring substances (Congo red, etc.) and they fix the basic coloring substances (naphthylene blue, safranin, etc.) less energetically than those of the parenchymatous tissues nearby. (This seems to indicate that the dissolution does not occur under the influence of the acid environment, as indicated by Mr. Wiesner, loc. cit., page 506.) This contrast in coloration is also further accentuated as the cell walls swell more and become more and more mucilaginous. At the moment the partial dissolution of the walls begins, the portions, which are going to be dissolved, only very weakly fix the basic coloring substances; it is above all in the middle region that this fixation persists longest; besides, ruthenium red, among these coloring substances, is the one which gives the most intensive coloration although it might still be very weak. At the moment of this dissolution, the acid coloring agents are still strongly staining the walls of the separating stratum although to a lesser degree than at the beginning of their inflation. Iodochloride of zinc and iodine-containing phosphoric acid produce almost no action at all here.

These various reactions tell us that the change in the walls consists in a mucilaginous transformation; looking at the classification of mucilages by Mr. Mangin ("On an Attempt at a Classification of Mucilages," Bull. de la Soc. bot. de France, Vol 41, page XL), we see that the mucilage in the separating stratum is mixed, that is to say, pecto-cellulosic, however, with predominance of the cellulosic substance. The weak coloration given it by ruthenium red is probably due to the fact that the derivatives of pectic compounds can be found here only in a very small quantity.

The thin surface strata of the wall, which are not dissolved and which continue to envelop the protoplasm after detachment, in my opinion did not seem to undergo any histological changes capable of being demonstrated with the help of coloring substances -- at least as far as one can tell from their thickness.

(In my historical summary I said that Mr. Mölisch reported the presence of gum ferment in a larger quantity in the cells of the separating strata than in the other cells of the pulvinus. In establishing this presence, the author used the Wiesner reaction. Here is the method involved: the sections are placed in a drop of 4% orcin solution under the cover glass; on the latter, we put concentrated hydrochloric acid; the preparation is then heated near the boiling point. Under these conditions, the content of the cells which enclose (contain) this ferment, as well as the walls of the mucilaginous cells, are inevitably stained, first, red and then violet; the lignified tissues are bound to be colored a dark red. After trying this reaction on the separating stratum in Amorpha druticosa, as well as on that of several other species, I was able to obtain a very nice dark red coloration of the lignified tissues, although I was not able to achieve the same result with the content of the cells of the separating stratum, nor with that of their mucilaginous walls.)

The detachment of the cells, inside the separating stratum, ordinarily begins in the external region of the petiole and gradually reaches its internal side. The average time for the fall of the leaves is in the second half of October. This fall generally occurs in the order of appearance of the leaves, that is to say, from the base to the top of the particular shoots.

The fresh leaf scar has a clear-green color; it has the shape of a triangle, quite rounded off at the points and slightly cord-shaped on the inside face (ci, Figure 13). At its surface we can observe either one single trilobed navel or three small navels in a triangular pattern, depending on the level at which the entering bundles were broken by the separating stratum; these navels appear slightly in intaglio. The leaf pulvinus protrudes very little; it is green in its upper portion and almost imperceptibly changes into the brown color of the stem as we go further down. Its green color is due to the presence of chlorophyll in the subepidermal tissues; this chlorophyll manages to conceal the brown color of the periderm of the stem less and less as the latter approaches the surface, at the base of the pulvinus. The leaf scar is topped by two buds; one of these buds is very close to the pulvinus and is very small; it is barely visible from the outside; the other one is located above and is much more developed, especially in the upper region of the shoots. The two short and sharp stipules of the leaf are attached to the right and left of the scar.

As in the case of Aristolochia, the wound has no protection at the time the leaf falls. Later on, the rounded cells of the separating stratum die and are flattened out on the surface of the wound. Then the wound, acing as an exciting surface on the tissues of the pulvinus, causes the formation of a ligno-suberous cicatrization lamina, below the wound; this happens after the leaf falls.

This lamina is differentiated entirely at the expense of the tissues of the pulvinus. It is about twice as thick toward the exterior; while its upper surface is almost parallel to the scar, its lower surface, which is almost level, start from the axillary angle of the pulvinus and decends very obliquely downward (ss, Figure 14).

The ligno-suberous change in the elements of the pulvinus generally starts around its circumference; it then progresses from the base of the lamina toward its upper portion. The elements of the bundles are the last parts to be affected by this modification. As this modification takes place, the color of the pulvinus changes from green to brown.

The ligno-suberization of the tissues, considered as a whole, is at a maximum in the lower portion of the lamina where it is, moreover, terminated rather abruptly. Its intensity diminishes rather gradually, on the other hand, as we go upward and, at a certain distance from the surface of the scar, all we have is the lignification. Above the region thus altered we have a rather thick stratum of sacrificed parenchyma (ce, Figure 14). In the ligno-suberous, the deposit of lignin, considered separately, also diminishes in intensity from the base toward the top; moreover, it is much larger in the internal cortical parenchyma of the pulvinus and in the cellulose elements of the bundles than in the external cortical parenchyma. The thickness of the suberous cover of the cells varies little throughout the entire thickness of the stratum.

The cells of the cicatrization lamina very often are filled, especially, at the base, with brown, gummy or resinous substances, similar to those we find very often in the cells of certain corks.

As in the case of Aristolochia Sipho, the sieve-like tubes and the vessels do not reveal a suberous film on their inside.

The sieve-like tubes are blocked by calluses; besides, at the level of the cicatrization lamina, they are almost all crushed by the neighboring cells (tcr, Figure 15). The fibers and the parenchyma with the elongated cells in the external region of the bast behave like the parenchymatous elements of the cicatrization lamina.

The petiole of Amorpha fruticosa has groups of articulated lactiferous organs in the bast of the bundles and in the vicinity of their trachea. These lactiferous organs are broken off at the level of the separating stratum and their content becomes solid in the air. Their walls, like those of the sieve-like tubes, are impregnated with lignin at the level of the cicatrization lamina; as in the case of the latter, they are not covered with an internal suberous film (1a, Figure 15).

The lower limit of the cicatrization in the bundles does not drop below that of the cortical parenchyma.

I indicated that there is no formation of thalli in the vessels before the leaf falls; I might now add that the thalli do not form after the leaf falls, either. The vessels are blocked only by the deposit, in their cavity of a substance called "wound gum"; this substance appears only after the leaf has fallen. This substance, which we observed earlier accompanying or replacing the thalli at the level of the cicatrization strata, in certain vessels of Aristolochia Sipho, develops in the case of Amorpha, all the way into the vessels of the bast-ligneous system of the stem. (In Figure 14, line lg represents the average lower limit of the tissue containing it.)

Its appearance in the vessels varies: sometimes it forms rounded masses toward the interior, along the vascular walls (V, Figure 16); at other times it completely obstructs their inside diameter (opening) (V_1); and then again it might only fill it up rather incompletely (V_2). On the other hand, it can be found either in the amorphous state (lga) or in the granular state (lgg); both of these forms, however, can be found in one and the same vessel (V). I think that these two states are the two ways in which the same substance can be differentiated; I believe that one of these forms is not a delayed modification of the other because the two states, amorphous and granular, exist already at the beginning of the appearance of this substance and because we still find these two forms in the old scars.

Like Mr. Frank ("On the Formation of Gum in Wood and its Physiological Significance," Berichte der deut. Bot. Gesellsch., Vol II, page 321) and Mr. Mölisch ("On the Thalli and Some Observations on the Healing of Scars in Plants," Sitz. d. K. Akad. d. Wissench. zu Wien, Vol 97, page 264), as well as Prael ("Comparative Investigations on Heart Wood Formations," Pringsheim's Jahrbücher, Vol 19, page 1), and Temme ("On Heart Wood, Its Formation and Its Physiological Significance," Theil's Landw. Jahrb., 1885, page 465), I was able to find that this substance was produced by the neighboring cells of the vessels, with the starch disappearing here gradually during its formation.

Colorless at the beginning, it very soon takes on a more or less yellow color on the level of the ligno-suberous lamina, like the vascular walls; its deposit is completed at the moment the ligno-suberization of the other elements of the bundles starts.

Mr. Frank and, above all, Mr. Temme pointed out that this kind of gum differed from the others in that it did not swell up in water, that it was insoluble in cold water, boiling water, ether, potassium, aqua regia, and cold nitric acid; that it behaves like the lignified walls toward the solution of fuchsin and the reagent of Wiesner. Moreover, Mr. Temme showed that boiling nitric acid would dissolve it. Mr. Mölisch announced also that this substance behaves toward aniline sulfate, metadiamibenzol, orcin, and thymol like the lignified membranes and he accepts the idea, therefore, that it contains vanillin.

I was able to reproduce most of these reactions and check on their accuracy. In addition, I found that this substance behaved in all points like the lignified membranes not only toward the reagents pertaining to vanillin but also toward all of the other reagents of lignin. The iodine-containing reagents, the ammoniacal coloring substances (fuchsin, methyl, green, gentian violet, acid green of Mangin, etc.), iodine green, and the colors of aniline stain this substance like the lignified membranes.

Sulfuric acid does not dissolve it but boiling nitric acid, cold Javel water stirred for several days, boiling Javel water stirred for several minutes, and hot potassium under pressure cause it to disappear entirely, just like the lignin in the lignified tissues.

Like Mr. Temme I was also able to find that the digestion of the sections, in a mixture of hydrochloric acid and potassium chlorate, within about one quarter of an hour removes the vanillin from the pseudo-gum as well as that of the lignified tissues; however, neither in the case of Amorpha fruticosa nor in the other plants which I studied did I ever observe the great solubility of the rest of this substance in alcohol, after the sections have undergone the previously mentioned digestion; according to the author, this solubility recalls the reaction of the resins. Similarly, I was never able to achieve the complete disappearance of this substance while checking on this digestion for half an hour and even more than that. The pseudo-gum, under these conditions, not only fails to disappear but does not become any more soluble in alcohol than after a digestion of a quarter of an hour. The same holds true after treatment with aqua regia which likewise removes the vanillin from the gum and the lignified tissues.

On the other hand, the reagents of vanillin (phloroglucin, indole, hydrochloric acid and aniline sulfate, etc.), after one or the other of these treatments, no longer stain this substance; however, the other reagents of lignin (ammoniacal colors, iodine green, colors of aniline, etc.) do stain it in the same fashion and roughly with the same intensity as before, just like the lignified membranes.

Mr. Mölisch (loc. cit., page 290), admits that this substance is a special gum in which vanillin is diffused as a result of its contact with the vessels. The author thus seems to think that it is a portion of the vanillin of the vascular walls which moves on into this substance. Now, it is easy to figure out that the intensity of coloration created by the coloring substances of vanillin in the walls of the vessels containing this pseudo-gum, is the same before and after its formation. Besides, the author tells that this gum is found -- below a wound in Saccharum officinarum -- in the sieve-like tubes and in the bast parenchyma; it was, however, not contained, in this case, in the neighboring lignified walls that were capable of giving it some vanillin.

On the basis of the various reactions mentioned earlier, I found that the substance, which blocks the vessels, only has the appearance of the ordinary gums. I was not able to find any chemical or staining reaction that would enable me clearly to distinguish the lignin which impregnates the lignified tissues. In my opinion this substance is not gum; instead, I think it is lignin that has been deposited in the vessels and that looks like gum. By the way, it is certainly not impossible for a substance, which is ordinarily diffused in the cell walls, to be able to exude and become deposited outside of them, in the cell cavities.

In summary, I think that the term "wound gum," which is commonly used to refer to this blocking substance down to this very day, is a rather unfortunately chosen term; it would appear to be inadequate not only because it has no relationship at all with gum, except for its appearance, but also because it does not always serve to cicatrize a wound. If, indeed, it does develop in the vessels of the wounded parts of the plants, either naturally (leaf scars), or artificially (punctures, branches cut or broken), then it may be deposited also and above all, as was demonstrated by the previously mentioned authors, in large quantities and concurrently with the thalli, in the other parts of the plants that are not injured, such as the heart of the wood. Hereafter I will therefore use the term "gummy lignin" in referring to this substance; this term is better because it precisely spells out its chemical nature and its physical appearance.

The production of gummy lignin is certainly the result of an excitation by the internal surface of the vessels with respect to the neighboring parenchyma, an excitation produced by the slow down and even the complete cessation of their conducting role. In Amorpha fruticosa, this excitation, instead of rendering the neighboring cells vegetative and causing them to form thalli, as in the majority of the vessels of the Aristolochia Sipho, instead gives them the role of the secretor and producer of a blocking substance.

Gummy lignin is sometimes also encountered on the level of the cicatrization lamina, in some of the sieve-like tubes, and in some of the intercellular channels.

The crystal-bearing cells are numerous in the leaf pulvinus of Amorpha. The crystals of oxalate of calcium, which they contain, are surrounded by a thin cellulose wall and partly enveloped in a considerably thicker portion of the cell wall which specializes at a very early stage by becoming lignified (es, Figure 17); they thus remind us of those of the leaf of Citrus vulgaria, as described by Witlin (Witlin, J., "On the Formation of Calcium Oxalate Pockets," Bot. Centralb., Vol 67, 1896, page 97).

On the level of the cicatrization lamina, the lignification invades the rest of the walls of the crystal-bearing cell as well as the envelope of the crystal; but there is no suberous film forming here, against it, around the cell cavity. On the contrary, I observed almost always that this cavity around the crystal and its envelope (lig, Figure 18) were filled with gummy lignin generally in the granular state.

The termination of the periderm of the stem inside the pulvinus is enveloped in the cicatrization lamina (pd, Figure 14) and the phellogen -- during its entire passage across the latter -- dies after becoming ligno-suberized, like the neighboring tissues.

In the sacrificed sub cicatricial parenchyma, the cells die rapidly; they are flattened more or less above the ligno-suberous lamina and the surface of the scar is thus slightly hollow around the bundles, causing them, from then on, to appear in relief. All of this sacrificed parenchyma is generally invaded by the myceliums of various mushrooms which almost completely fill the cavity of the cells. Despite the abundance of these mushrooms (fungi), I was never able to watch them penetrate into the cells of the ligno-suberous layer; this applies not only to Amorpha fruticosa but also to all of the other similar cases. This is the best proof that this ligno-suberous layer is sufficient to protect the plant until the cicatrization is absolutely complete.

During the first year, the cicatrization which I have just described, is the only one that occurs in the leaf pulvini of Armorpha fruticosa.

As the second year begins, we sometimes have a rather inactive growth (generating) zone developing against the base of the original cicatrization lamina (following line K, Figure 19). This zone produces only one or two layers of cork and does not extend across the bundles; very often it disappears even before growing across the entire pulvinus. After this zone, we have another much more active generating zone which appears at a lower level. It begins from the external base of the pulvinus and produces a cork which turns out to constitute an internal doubling of the caulinary periderm (lic, Figure 19) and which progressively extends upward, toward the axillary angle. On its way, this cork encounters the hard bast of the bundles and, since it cannot cut it, it, on the one hand, moves up along its outside face, gradually disappearing, and, on the other hand, goes around it laterally, so as to penetrate into the soft bast without changing direction. It then goes across the rest of the bundles, sometimes describing a very slight downward curve. In the axillary angle of the pulvinus it disappears at the base of the dormant bud or it continues with that of the shoot which constitutes this bud, growing along with it.

This second cork, which always develop and which we can consider as the true cicatricial cork, then grows across the pulvinus to a certain distance below the primary cicatrization stratum. The parenchymatous region of the pulvinus, included between the two, is then lignified sometime after the appearance of the scar cork, when the latter has already grown to a certain thickness.

The continuation of the cork across the bundles occurs as in the case of Aristolochia Sipho, except as regards the vessels which, not containing any thalli, are all broken by the longitudinal extension under the effort of the growth of the cork in thickness; the continuity of the cork is here established between their distant ends, such as we have it taking place across the secondary vessels in the previously mentioned species. The articulated milk-bearing organs, which are more or less crushed by the cells of the cork, similarly break at its level.

During the second year, one of the axillary buds of the fallen leaf begins to vegetate and provides a shoot; when this happens, the transversal growth of the base of this bud causes -- at a rather early stage and before the formation of the scar cork -- a longitudinal rupture in the tissues of the pulvinus. The crack thus produced involves only the cortical parenchyma; it runs almost along the plane of symmetry of the pulvinus, slightly to the side of the middle entering bundle; it then descends more or less far down along the stem; its two edges (lips) move further and further apart as the shoot grows. Usually this crack does not go beyond the customary level of differentiation of the scar cork; however, where this is the case, this cork grows around it, on the underside, in order to cicatrize this new wound.

3rd Type. Koelreuteria paniculata Lamk.

As far as the make-up of the base of the petiole of Koelreuteria paniculata is concerned, I might make the same general remarks as for the two earlier cases; the cortical parenchyma here has shorter cells than in the rest of the petiole; the ligneous fibers, the bast fibers and the hard bast are likewise absent here. As in the case of Amorpha fruticosa, the volume of the bundles here is scarcely reduced.

The periderm of the stem is very thick, especially at the base of the shoots, and continues under the epiderm of the pulvinus; it then terminates generally at the base of the petiole, a little above the level at which the separating stratum forms (pd, Figure 21).

The phenomena preceding the fall of the leaf are the same as in Aristolochia Sipho. The separating stratum develops in the upper portion of the green region, some distance from the axilla of the leaf (cs, Figure 21). Sometime before defoliation, thalli develop in the ligneous vessels at the base of the petiole: these thalli are numerous in the vessels of the primary wood and they are very rare in those of the secondary wood which is, by the way, not very well developed at that time. The only change we can observe in the sieve-like tubes involves the formation of calluses.

The one feature which distinguishes this type from the two earlier types is the way in which the separating stratum is made-up here; in this case, it is always of secondary origin. A zone of subdivision (partitioning) develops to this effect in the upper portion of the pulvinus and perpendicularly to the direction of the petiole; this zone is almost level except in the place where the bundles grow across it; here it rises slightly upward. This zone forms a lamina of constant thickness, essentially equal to the longitudinal diameter of the average cells of this region (about 60 mu); depending on the size, shape, and positions of the elements it encounters, the subdivision (cs, Figure 22) thus involves, either one or two cells or only a part of a cell; it always grows from the bottom to the top in each of them. The separating stratum is finally made-up of three or four layers of cells whose young partitions are essentially parallel to each other and to the general direction of the stratum; here the elements are primarily flat and they keep their thin walls.

Only the macled cells, their sieve-like tubes, and the vessels do not subdivide and the same is true of the cells of the caulinary periderm whenever it extends to that level. If a macled cell happens to be located in the way of the separating stratum, the latter goes around it, either above or below, and the subdivisions are produced in the immediately adjoining cells (cr, Figure 22).

The tissue of the petiole, in the vicinity and above the separating stratum reacts as in the two earlier types in response to the stimulation produced by the establishment of this stratum; following the partitioning of this latter layer, the walls are lignified (rs, Figures 22 and 23).

At the end of September, about 3 weeks before defoliation, the subdivisions that make-up the separating stratum begin; they appear first of all at the base of the lower leaves of the shoots.

Several days before the fall of the leaf, there is a noticeable longitudinal growth in the entire separating stratum; after that the dehiscence crack develops inside the latter, between its two upper layers. As in the case of Amorpha fruticosa, the separation is caused by a transformation of the cell walls into mixed mucilage and also by its partial dissolution. However, since these walls are not at all thick, especially in the case of the transversal walls which are young, there mucilaginous portion is rather small; the prior swelling of the membranes is therefore not at all accentuated here (cs, Figure 23).

The separation inside the separating stratum occurs in the following manner: a roughly equal number of cells remains on either side of the dehiscence surface; these cells are unattached on one portion of their circumference but they remain attached to the pulvinus and to the petiole along one of their sides. As in the case of Amorpha fruticosa, the longitudinal growth, in the opposite direction, of the two layers thus separated and their mutual pressure cause the mechanical detachment of the leaf by breaking the vessels and the sieve-like tubes, provided these have not already been broken off as a result of the longitudinal growth taking place in the entire separating stratum before this separation.

I pointed out earlier that, while the caulinary periderm rises just to the level of the separating stratum, the latter does not cut into it. Consequently, it does not undergo any histological change and it is then broken off like the vessels and the sieve-like tubes.

The leaves usually fall during the second half of October; their portion, which remains attached to the stem and which forms the pulvinus is rather considerable. The fresh scar is clear-green; it is almost cord-like [rope-shaped] and very long; its surface runs almost parallel to the axis of the stem (ci. Figure 20). Here a scar arc, slightly in relief, indicates the outline of the bast-ligneous leaf system.

In this third type we do not yet have any cicatrization of the wound at the moment the leaf falls, except, of course, for the fact that most of the vessels are blocked by the thalli with the cellulose walls. The tissues of the pulvinus are differentiated into a ligno-suberous lamina of the same nature as in the earlier types (ss, Figure 24) after defoliation. The ligno-suberization of this cicatrization lamina, whose lower boundary parallel to the surface of the scar is located exactly at the level of the axillary angle of the pulvinus begins to grow in its base region and, at the same time, in several places in the cortical parenchyma; it then progressively grows upward.

The distribution of lignin and suberin here is the same as in Amorpha fruticosa. However, in the area of the ligno-suberous stratum we very frequently have small portions which are more or less further apart and in which the cells keep their entirely cellulosic walls.

The crystal-bearing cells, which are inside this ligno-suberous lamina, do not have the thin suberous stratum which covers their neighboring cells on the inside.

The ligno-suberization of the bast-ligneous bundles comes later than that of the surrounding tissues. Here it invades all of the elements except the sieve-like tubes and the vessels in a process also recalling that of Aristolochia; however, this modification does not decend below the general level of the ligno-suberous lamina. In the ligneous vessels, the thalli become ligno-suberized like the cells at whose expense they are formed (th, Figure 25). These thalli develop, in the rest of the area, only in the vessels of the primary wood where they may be accompanied by a variable quantity of gummy intercalated lignin; it is this latter substance which is found only in the vessels of the secondary wood which it obstructs completely (lgg, lga, Figure 25); this substance is found sometimes in the amorphous and sometimes in the granular state.

As in the case of Amorpha, there remains -- between the ligno-suberous lamina and the surface of the scar -- a stratum whose cells have remained parenchymatous and which are more or less flattened out and which are afterward invaded by fungi; here, however, this sacrificed parenchyma is about 8-10 cell layers thick.

We encounter brown resinous substances, deposited in the cell-cavities, rather frequently in the pulvinus and primarily at the base of the ligno-suberous stratum.

As the differentiation of the ligno-suberous lamina progresses, the surface of the scar changes color and becomes clear-brown. This differentiation is terminated before winter and the stratum thus produced is the only defense of the plant against the wound caused by the fall of the leaf during the entire first year.

In the spring of the second year, the zone that generates the scar cork advances -- from the caulinary periderm and supporting itself on it on the level where the latter penetrates into the first cicatrization stratum -- below this first stratum, from the outside toward the bundles which it traverses in the same way as in Aristolochia Sipho; afterward, in the axillary angle of the pulvinus, it connects with the periderm of the new shoot formed by the bud or with the cork which develops below the bud when the latter fails to ripen (aborts). Its direction is a little more oblique to the axis of the pulvinus than that of the leaf scar.

The scar cork is thicker in the center of the pulvinus and primarily at the points where it cuts across the bundles (lic, Figure 26); it averages 10-15 layers at the end of the second year. After its development we very often have a new deposit of gummy lignon here, below that in the vessels.

As a result of the growing thickness of the important stratum of scar cork and also because of the obliqueness of its direction toward the axis of the pulvinus, the portion of the latter which is situated outside of it is pushed away toward the outside and is slightly buckled on the side so that the portion of the leaf bundles, which it encloses, is no longer located exactly in the prolongation of the remaining lower part of these bundles.

I did not observe anything like this in the earlier two cases. As a matter of fact, in Amorpha fruticosa the scar cork is not as thick so that, despite its great obliqueness to the direction of the bundles, the deviation which I have just pointed out is barely observable here; besides, the resistance of the hard bast helps here in keeping the two separated portions of bundles in the same prolongation. In the case of Aristolochia Sipho I pointed out a thick scar cork but the general direction here is perpendicular to that of the bundles so that their distant portions remain in the same prolongation.

4th Type. Paulownia imperialis Sieb.

Here I might make the same observations as in the case of Koelreuteria paniculata with respect to the constitution of the petiole on the level of the disarticulation of the leaf and the termination of the periderm of the stem along the pulvinus.

All of the phenomena which precede defoliation are more complex than in the earlier types. A longitudinal section of the base of the petiole, made several days before the leaf falls, shows in effect, a little above the insertion of the latter, a lamina of meristematic tissue in which the cells are subdivided (split) many times. This meristem lamina is very clearly delimited on the side of the petiole by the separating stratum which here occupies the upper portion and which is differentiated here, first of all, by its protoplasm which is denser than that of the rest of the meristematic stratum, and, second, by the presence of numerous grains of starch.

The partitions (rm, Figure 27) are less and less numerous in the upper part of the meristematic stratum where we have an average of 4-6 per cell; this holds true as we move toward its lower portion situated about half way between the separating stratum and the insertion of the petiole.

The new partitions mostly run parallel to the separating stratum, that is to say, transversally, but we can also find a large number with highly variable direction, either longitudinal or oblique (rm, Figure 27). As a general rule, the small or medium-sized cells split only transversally or obliquely. The large cells often split just once, that is, primarily longitudinally; then they split transversally or obliquely a certain number of times; or they subdivide transversally for a certain number of times and then we have one or several new cells splitting off obliquely or longitudinally. As a matter of fact, there is no regularity in the disposition of the new walls thus formed; the only thing we can say is that the transversal direction predominates.

In the parenchymatous elements of the bundles, on the level of this stratum, we can also observe several subdivisions which are rather small in number; we generally have one per cell.

The cell division described above begins to appear rather early throughout the entire thickness of the partitioned region. Starting at the end of August, this region -- in the petioles of the base of the shoots -- begins to be charged with a denser protoplasm and with starch; then it begins to subdivide rather quickly. The starch here disappears then altogether or partly as the cell division progresses. The same phenomena occur successively in the leaves as we move closer and closer to the top of the shoot.

Cell division is neither preceded nor followed by a growth in the diameter of the cells; in addition, the new cell walls are always thin.

In all cases, the meristematic lamina is entirely made up in the fashion I described earlier; this happens around the end of September, roughly one month before the average defoliation time [roughly before the halfway point during the defoliation period].

Numerous thalli appear in the vessels of the primary wood of the bundles around mid-October. These thalli always have very thin walls and are completely formed, throughout the entire base of the petiole, at the moment the leaf falls; after the leaf falls, they develop either very little or there is no new development at all.

At this time, likewise, we can observe a stratum of three or four layers of new cells occupying the upper part of the meristematic lamina; this stratum is specialized as a separating stratum by the apperance of grains of starch and through the increase in the density of its protoplasm. This stratum functions like that of Koelreuteria paniculata, that is to say, it increases first of all very slightly in thickness through the longitudinal growth of each of its cells; then this growth of the entire stratum is followed by a separation of its two upper layers. The walls of this stratum are not at all thick; their middle mucilaginous portion, which dissolves afterward, is also very thin.

The separation of the cells, inside the separating stratum, often begins in several places at once; more generally, however, it begins on the outside of the petiole.

In Paulownia I never observed any lignification in the tissues of the petiole above the separating stratum; however, we do find several subdivisions here similar to those in the meristematic stratum of the pulvinus.

The leaves usually fall early in November. The leaf scar is very wide and looks like a circle, slightly flattened toward the top. The bundle navels, arranged on an almost closed arc, are not readily visible. The leaf pulvinus protrudes, particularly toward the outside since the surface of the scar is slightly inclined toward the axis of the stem.

The phenomena preceding the fall of the leaf are more complex here than in the preceding species because there is a rather abundant subdivision of the tissues of the pulvinus, under the separating stratum; nevertheless, the wound usually does not reveal any trace of cicatrization at that time. I was able to discover small lignified spots only in a few samples; I was able to find them in the meristematic lamina, in the vicinity of the dehiscence surface, and along the circumference of the pulvinus.

After defoliation, cicatrization occurs, as in the preceding types, through the establishment of a ligno-suberous stratum which is quite similar to that found in Koelreuteria paniculata. Its upper boundary is not definite and is located in the vicinity of the base of the meristematic stratum whose cells ordinarily remain cellulosic and become more or less flattened at the surface of the scar. The lignification reaches this subdivided stratum only very rarely; in this case it is only indicated here rather weakly and it is never accompanied by the formation of a suberous film.

It is very interesting to note that, in the case of Paulownia imperialis, the establishment of the meristematic lamina does not seem to be very helpful in the cicatrization of the wound; contrary to what we will see later on in some similar cases, the histological changes that will cicatrize the wound occur not at the expense of these cells but at the expense of the cells of the subjacent tissue. This meristem lamina here rather appears to play the same role as the subcicatricial parenchymatous tissue of Koelreuteria, that is to say, it is comparable to the sacrificed parenchyma.

Before the complete differentiation of the ligno-suberous scar stratum, the cells of the pulvinus are often filled with brown resinous substances similar to those which we pointed out in the earlier types. This substance is rarely distributed uniformly throughout the entire pulvinus; it appears most often either only in the middle region of the cicatrization stratum or in two strips, one of which occupies the crust meristematic stratum while the other occupies the base of the scar lamina.

The cicatrization of the elements of the bundles occurs exactly as in Koelreuteria paniculata; the gummy lignon here develops, however, in a smaller quantity and the thalli here are more numerous.

The external cortical parenchyma of the pulvinus -- at the level of the primary cicatrization stratum -- reveals numerous more or less wide channels. These channels themselves are often blocked by a deposit of gummy lignin (lig, Figure 28), in a way similar to that described by Mr. Mölisch (Mölisch, Dr., Hans, op, cit., Sitz. d. K. Akad. d. Wissench. zu Wien, Vol 97, 1888, page 292) in a wound on the stem of Canna. Channels with a small or medium inside diameter (opening) are entirely blocked; the large channels are not completely blocked and the gummy lignin here is accumulated in small round masses located most often in the corners. The cicatrization, which we have just described, is the only one which occurs throughout the first year in all of the leaf pulvini. The scar cork appears in the spring of the second year. Most often, its generating zone grows below and against the 1st-year cicatrization strata; sometimes, however, it grows at a certain distance from these strata. In this latter case, the region of the pulvinus between the cork and the 1st-year cicatrization stratum remains cellulosic although it is impregnated with a brown substance that is rapidly soluble in Javelle water.

The cork generating zone appears first of all against the inside face of the pulvinus; it gradually grows around its circumference and then moves toward its center. It cuts the bundles by the same process as in Aristolochia Sipho but it crosses them directly, without curving toward the stem.

Along the circumference of the pulvinus, the scar cork extends at a right angle to the periderm of the stem. It is very thick at the end of the second year, especially on the level of the bundles where it has an average of 12-15 cell layers.

5th Type. Diospyros virginiana L.

In Diospyros virginiana, we find a different kind of complexity of defoliation phenomena in the sense that the cicatrization here begins to develop before the leaf falls.

A longitudinal section of the petiole, made several days before defoliation, shows us, in effect, a ligno-suberous cicatrization stratum which already grows across its base (ss, Figure 29) and which is established in the parenchyma of the pulvinus. The cells of this stratum have not undergone any subdivision before that (ss, Figure 31); this stratum is very clearly bordered on its upper portion by the plane of the separating stratum against which it terminates; the boundary between these two tissues is even better indicated whenever the cells of the second [tissue layer] are much smaller than those of the first.

Starting in the month of May, that is, at the time the leaf reaches its adult stage, the petiole, in effect, has a basilar articulation marked by a slight circular groove at whose level we find a specialized stratum running slightly oblique to the direction of the re-entering bundles. This stratum consists of three or four layers of cells which have been subdivided just once, primarily longitudinally, and which have then not undergone any intercalary growth (art, Figure 30); here the cells are therefore much smaller than in the petiole and in the future pulvinus so that they will quite definitely be separated from each other; here they are almost polygonal and they leave room between them only for some very small angular channels.

It is this stratum which, without any further subdivision, will be differentiated into a separating stratum in autumn. The position that will be occupied by the latter stratum is therefore clearly indicated already at the base of the adult leaf.

At the moment the leaf falls, the cicatrization lamina involves especially the cortical parenchyma in which its lower boundary is slightly convex toward the bottom (ss, Figure 29); however, the bast-ligneous bundles are already affected by ligno-suberization along their circumference and toward the upper portion of the lamina.

Contrary to what we have observed so far, the cicatrization stratum, from the histological viewpoint, is roughly homogeneous throughout its entire extent; the lignification here has the same intensity throughout and the thickness of the internal suberous film is the same in all of its elements.

As in Paulownia imperialis, which we studied in the preceding chapter, it is not differentiated from the subcicatricial lignified stratum.

When it does exist, the periderm of the stem ends a little below the separating stratum (pd, Figure 29).

The ligno-suberization of the cells of the pulvinus begins early in August in the pulvini of the leaves situated at the base of the shoots, a little later than in the others. The protoplasm here first of all becomes a little denser and the starch becomes more abundant. The impregnation of the walls with lignin and suberin comes next; it begins along the entire circumference of the pulvinus, against the separating stratum and in contact with the epiderm. From this point it advances at the same time toward the bundles and toward the base of the lamina; the starch disappears from the cells as this differentiation becomes more accentuated.

The formation of the ligno-suberous layer is generally terminated toward the end of September. The elements of the bundles are still intact at that time and the circulation is not obstructed in any way. Toward the end of that month, the few thalli appear in the big spiral vessels, since the base of the petiole does not undergo any other modification all the way to the end of October, which is the usual defoliation time. The ligno-suberous cicatrization begins to reach the elements along the circumference of the bundles, in the vicinity of the stratum with the small cells indicated earlier, sometime before the usual defoliation time; at the same time, this small-cell stratum develops into a separating stratum through the increase in the density of its protoplasm.

The functioning of this separating stratum differs just a little from the one we just described earlier. Before separation, each of its cells and, consequently, the entire stratum, grow longitudinally only about 1/5 of their original volume. Besides, although their cell walls fix the coloring substances of cellulose a little more energetically than the rest of the parenchyma, they do not appear to be mucilaginous; they are not swollen and they do not reveal any deformation due to softening. At the moment the leaf falls, we can only observe how these cells have become roundish and how the intercellular channels become wider; this happens particularly in the upper portion of the stratum, where the primary pectic membrane is dissolved not only in the corners but also in a large portion along the circumference of the cells which are thus isolated from each other into two rows (cs, Figure 31). Here or there, the dissolution may even occur along the entire circumference of a cell and this cell may thus be completely isolated from the others.

The separation inside the separating stratum generally occurs from the external region of the petiole toward its internal region. Contrary to what happens in the case of Paulownia imperialis, the cells of the two dehiscence surfaces grow very little longitudinally and in the opposite direction. The mechanical pressure which is exerted on the base of the petiole is therefore very small and it must be supported hitherly by the outside factors if the bundles are to be broken.

The leaf scar has the shape of a semicircle (ci, Figure 32) in whose center we can see a fascicular navel slightly in relief, naving the same shape as the scar. The leaf pulvinus is quite protruding here.

After the leaf falls and during the first year, the only change occurring in the leaf pulvini involves the completion of the cicatrization of the bundles. This happens in the same way as elsewhere but the process here is very incomplete: the gummy lignin here is almost entirely missing in the vessels and the same is true of the thalli; only some of their parenchymatous elements, especially at the base of the cicatrization lamina, are ligno-suberized; most of them remain cellulosic; after their death, they take on a dark brown color. This cicatricial modification in the bundles, although very minor, descend lower than that in the surrounding cortical parenchyma.

As in the types which we studied so far, the cicatrization here is completed during the second year with the establishment of a cork in immediate contact with the 1st-year scar stratum. The cork grows across the bundles in the same way as in Amorpha fruticosa and it curves toward the pulvinus. At the end of the second year it is rather thin and consists of only three or four layers of cells.

6th Type. Morus nigra L.

In Morus nigra the cicatrization is completed, before the leaf falls, by the ligno-suberization of a tissue of meristematic origin.

If we make a longitudinal section along the plane of symmetry of the petiole at that time, we will see a thick ligno-suberous lamina growing across the entire pulvinus and moving only around the bundles (ss, Figure 33). The general direction of this cicatrization stratum is almost perpendicular to that of the petiole but it has a slight concave area in its center. Its thickness increases slightly from the inside to the outside of the pulvinus and its lower boundary is situated a little above the place where the leaf is inserted into the stem.

All of the cells of the pulvinus which make-up this stratum are subdivided one or more times, at most, however, four times, depending on whether they are more or less elongated along the longitudinal direction. In this meristematic lamina we will once again find the same situation as in Paulownia imperialis as far the size of the new cells, the distribution, and the thickness of the new walls is concerned; however, the new walls or partitions here are more or less regularly oriented along the transversal direction (ss, Figure 34).

The crystal-bearing cells in this region never subdivide. (To avoid any subsequent repetitions, I would like to point out right now that this is always the case in the crystal-bearing cells, regardless of whether or not they are inside the meristematic tissue, the separating stratum, the cicatrization stratum, etc.) The same is true of the epidermal cells which are already very small here.

The ligno-suberous lamina is very clearly delimited in its upper part by the separating stratum on which it borders; it is also very clearly outlined along its base (ss, Figure 34). From the twin viewpoint of lignification and suberification, it is ordinarily very homogeneous throughout all of its parts. Sometimes, however, the suberization -- at the base of the lamina -- is limited not only by the thin internal covering stratum of the cells but also slightly impregnates the region adjoining their walls.

At the same time, the elements of the bundles are usually not affected by the ligno-suberization, not only when these bundles grow perpendicularly across the scar stratum but also when they circle it here almost horizontally. (The reunion of the leaf bundles, prior to their re-entry into the stem, as a matter of fact, takes place partly on the level of the ligno-suberous stratum and partly below it; it is thus not at all rare to see bundles growing across this stratum almost horizontally, over a more or less considerable length. The middle leaf bundle has a very curvy outline below the various cicatrization strata but this arrangement, which exists on the adult leaf, has nothing to do with the fall of the leaf (Figure 33). I found the same feature in this middle bundle in the case of Morus alba, Broussonetia papyrifera, Ficus carica, and Celtis occidentalis (Figure 60).)

Nevertheless, ligno-suberization may, even before defoliation, have reached those of these elements which are closest to the cortical parenchyma. Besides, all of the primary vessels are quite full of thalli from a short distance above the separating stratum all the way to a little below the ligno-suberous stratum.

In the case of Morus nigra, moreover, we have a lignification of the tissues of the petiole above the separating stratum (rs, Figures 33, 34, 37) but this lignification affects only one or two layers of cells.

The separating stratum is made up of three or four layers of new cells in the upper portion of the meristematic stratum; these cells have preserved their dense protoplasm and have not undergone any of the histological changes observed in the rest of this protoplasm. The protoplasm is a little thicker in its external region than in its internal region. The cells composing it are not necessarily the only ones that result from the subdivision of the primary layer of the pulvinus to which it owes its origin (as we can see, in effect, in Figures 34 and 37, cs); one original cell of this latter layer may, after subdivision, become at the same time involved in the constitution of the ligno-suberous lamina through its lower daughter cells, in that of the separating stratum through its middle daughter cells, and often even in that of the lignified, subcicatricial stratum through its upper daughter cells.

This is the situation at the base of the petiole a few days before defoliation.

The differentiation of the ligno-suberous lamina begins about one month before the leaf falls, around mid-September. The portion of the pulvinus which becomes involved in its composition proves to be abundantly provided with starch. The subdivisions appear here throughout the entire thickness of the strata at the same time but they are from the very beginning more active in its upper portion. Around mid-October, when all of the new partitions have been formed, the ligno-suberization begins to develop. It starts in the upper portion of the lamina and, at the same time, in the vicinity of the epiderm, against the bundles and in contact with numerous laticiferous organs which traverse this region; from these different points it rapidly covers the entire thickness of the meristematic stratum. At this moment, likewise, begins the proliferation of the thalli in the vessels.

The subcicatricial lignified stratum is differentiated a little later, at the beginning of the formation of the separating stratum and when the latter is already strongly turgescent. (This seems to prove that, in the case of Morus nigra, it is primarily this turgescence which acts as a stimulus on the neighboring tissues of the petiole, rather than the cell division that occurred earlier.)

The detachment of the leaves ordinarily occurs during the first days of November; this is a result of the functioning of the separating stratum which is exactly the same as in Koelreuteria paniculata. The doubling of the walls inside this stratum begins on the outside of the petiole and gradually progresses toward its inside.

The separating stratum is slightly concave in the center of the pulvinus; the surface of the fresh scar is therefore likewise concave. The fresh scar has a light-brown color due to the immediate contact of the ligno-suberous cicatrization stratum. Throughout its entire surface we can observe small points which look like a whitish dust and which are due to a little bit of dried latex coming from the broken laticiferous organs; we will come back to these laticiferous organs later on.

The cells of the separating stratum, which have remained attached to the pulvinus, die quite soon and are flattened against the surface of the scar.

The scar looks like an ellipse slightly flattened in its upper portion (ci, Figure 35). The pulvinus protrudes very much and extends laterally in the form of two little pouches which gradually disappear toward the middle of the outline of the stem.

After defoliation, the constitution of the ligno-suberous cicatrization lamina only undergoes the few changes described in this paragraph until winter comes. In the wood of the bundles, the thalli and the parenchymatous elements are ligno-suberized in their turn and the gummy lignin completes the cicatrization begun by the thalli. In the bast, consisting of sieve-like tubes especially on this level, we have a few parenchymatous elements which are likewise ligno-suberized but this cicatrization is quite incomplete and most of the tissue therefore continues to have cellulose walls.

During the second year, cicatrization is completed with the development of a cork below the ligno-suberous strata and in contact with them [at the point where they are in contact]. This cork appears in the external region of the pulvinus where it connects with the periderm of the stem. It is very thick at the end of the second year (lic, Figure 35); as a matter of fact, it is thicker than both of the annual strata of the caulinary periderm that develop each year. As in most of the preceding cases -- and for the same reason -- it cuts the bundles, curving more or less downward. It grows across the vessels in the same fashion as in Aristolochia Sipho, in other words, the thalli, located on the level of its generating zone, very often become involved in the composition of this latter zone.

In most of the pulvini, the cork generating zone also produces some phelloderm toward the interior (ph, Figure 36). The latter is composed of the parenchymatous cells arranged in radial files at angles which most often are quite rounded; (this phelloderm appears as I drew it (Figure 77) for Fraxinus Ornus); it is very thick in the center of the pulvinus and particularly across the bundles where it consists of 5-7 cell layers; its thickness diminishes from the center toward the surface, near which it ceases to exist. The development of this phelloderm increases the spacing between the portion of the bundles including the base of the pulvinus and that which is comprised in the first cicatrization lamina, although both of them continue as a prolongation of each other.

We noted earlier that the phelloderm, situated below the scar cork, is more or less developed, depending on whether the ligno-suberous cicatrization extends more or less deeply into the bundles during the first year, that is to say, depending on whether it forces the scar cork generating zone to bend more or less downward, toward the stem. Thus we see that -- while this cicatrization occurs at the same level as in the cortical parenchyma and while, consequently, the cork grows directly across the bundles -- there is no phelliderm forming below it [the cortical parenchyma].

When an axillary bud develops and gives rise to a shoot during the second year, the subjacent leaf scar splits rather early and quite regularly into two parts through a very deep longitudinal opening. The scar cork then grows below the wound produced by this new injury and plunges more deeply into the tissues of the pulvinus, thus forming a bay in which a thick phelloderm always develops.

Cicatrization of Laticiferous Organs

We know that Morus nigra has so-called branching milk-bearing organs which are particularly numerous in the cortical parenchyma. Their cicatrization is evidenced already by the fact that there is no flow of latex during the fall of the leaf.

Let us look at some longitudinal sections of the base of the petiole a few days before defoliation; these sections were so made that the milk-bearing organs could be observed over a rather long distance. Let us then successively treat them with carbon disulfide and Javel water in order to relieve the latter of their content. Each branch of the milk-bearing system thus cleaned then reveals quite clearly two partitions which close them off hermetically (cl_1, cl_2, Figure 37), one of them above the separating stratum, in the petiole, and the other below it, in the pulvinus. These two partitions are finger-shaped, with a convex area pointing toward the separating stratum; that is to say, they are turned toward each other. They are very thin in the region where they are attached to the wall of the laticiferous organ but they gradually increase in thickness until the top of their convex area.

In response to reagents, they behave like the walls of the laticiferous organs itself. The cellulose coloring substances are fixed on them and a little more energetically on the inside face of the concave area; the coloring agents of pectic substances are also fixed here but especially on the convex surface of the same region. When treated with Schweizer reagent, they become slightly thinner and the internal portion here becomes entirely dissolved; in the rest of the membrane, the coloring agents of pectic substances always indicate the presence of this latter substance.

From these observations we can say that these partitions are of the same kind as the parenchymatous tissue walls, with one difference, however: a thin region in their concave area is entirely cellulosic.

Of these two partitions, the one which developes below the separating stratum, grows into a point of laticiferous organs generally situated in the vicinity of the underside of the ligno-suberous stratum, either below or sometimes a little above (cl_2, Figure 37); very rarely it appears in the vicinity of the separating stratum; in these latter two cases, however, although situated in the middle of a ligno-suberous tissue, it remains pecto-cellulosic like the wall of the laticiferous organ which likewise does not change at the level of this tissue.

The second of these partitions -- the one which develops in the petiole, above the surface of leaf separation -- is, on the other hand, generally placed quite far from this surface (at a distance which is considerably greater than shown in Figure 37, cl_1, sometimes 7-8 times that distance). It never forms below the subcicatricial lignified stratum (rs, Figure 33) opposite which it appears very rarely.

In one of the many samples which I examined, one of the milk-bearing organs, by way of exception, revealed two partitions instead of one, above the separating stratum; the upper one only had a thin wall.

The occlusion of the laticiferous organs always causes the entire system to be hermetically closed on both sides of the dehiscence surface. If a laticiferous organ should indeed ramify either above or below this surface, then the occlusion may occur either before ramification through a single partition or after ramification through as many partitions as there are branches (cl, Figure 34).

What we have said so far in connection with the milk-bearing organs is the result of observations on sections whose latex had been removed in advance. I also studied these elements after having fixed their latex in order to be able to examine the relationships between it and the obstructing partitions.

The longitudinal sections in the base of the petiole show us then that the latex is directly in contact with the partitions and that it is found here on both faces (la, Figure 39). Generall, however, on their convex face, it ceases to be granular in their immediate vicinity and forms a very refringent mass, which is very distinct and which has a very variable shape (bl, Figure 39). The latter -- which is more or less of aluminous -- may, however, also be absent and, in this case, we observe a void between the granular latex and the convex surface of the partitions.

Between the finger-shaped partitions and below them, in the pulvinus, the latex completely fills the milk-bearing organs. Above these two regions, in the yellowish petiole, it is more or less strongly dried out and contracted.

This is the occlusion of the laticiferous organs at the time the leaf falls. Let us now see how this occlusion takes place.

If we cut the petiole a little above its space, about 1 cm from the latter, around the middle of September, and if we make this a transversal cut, by the way, we can see that the latex flows very actively from the two faces of the section. At the beginning of October -- in other words, when the subdivision is in full swing in the stratum which will constitute the ligno-suberous lamina -- this is still true for certain petioles; however, in others we can now detect only a very difficult flow on the portion which remains attached to the stem. A little later, the flow of latex stops completely on that side whereas it is always abundant at the base of the cut leaf and also at the base of any wound inflicted on the stem itself, in the vicinity of the pulvinus. At this very moment, therefore, early in October, the circulation of the latex is impeded in the base of the leaf.

If we examine the longitudinal sections of the petiole at that time, we no longer observe any of the finger-shaped partitions which we pointed out earlier; but we do observe the existence of masses of this refringent latex which we mentioned earlier (b1, Figure 38). In each milk-bearing organ we can see two of these, one above and the other below the separating stratum which, at that time, is already clearly indicated by its subdivisions and partitions. If we slightly press on the cover glass, we can see that the latex remained motionless between the two masses of one and the same laticiferous organ while it was able to move outside of them; these two masses thus act like a stopper. They are very difficult to crush and they reveal all of the reactions of latex, with one difference, however: they are almost insoluble in carbon disulfide and they are very difficult to dissolve in Javel water.

After the stoppage of the circulation of latex through the formation of these stoppers, we can observe the development of the finger-shaped partitions which constitute the final occlusion of the milk-bearing organs. I was not able to determine the way these partitions are formed with any degree of certainty; these partitions probably develop very rapidly. The youngest ones I was able to observe, around the middle of October, already were finger-shaped, just the way they are at the moment the leaf falls; however, their walls were still very thin. Even after proper cleaning with latex solvents, I did not note any nucleus in their vicinity; above and below it, however, the protoplasm was more condensed than in the rest of the laticiferous organs where it constituted only a few traces, here and there.

In almost cases, the partitions appeared immediately in contact with the refringent stoppers so that their convex side fits very closely against the latter (c1, Figure 39). As the partitions here become thicker (as far as I was able to see this thickening occurs especially on their concave side), the latex stoppers, on the contrary, appear to diminish on their side which is opposite to the partition; sometimes they then disappear completely; this is the place and the way in which a vacuum then develops in their place. All of this explains that, at the moment of defoliation and depending on whether the partitions are formed more or less belatedly, the occlusion of the laticiferous organs reveals the different states which I described above.

The fact that the finger-shaped partitions, during their formation and growth, are in intimate contact with the refringent masses of latex and that these masses disappear completely or partly as they become thicker, made me think, first of all, that they might be due to a transformation of these refringent masses. At no time, however, do the reactions of these masses in any way recall the reactions of the membranes which, as I said before, are entirely pecto-cellulosic; moreover, these masses are sometimes formed at a certain distance from the stoppers and they remain separated by a more or less long unchanged index (finger) of latex.

Summarizing all of the preceding observations, we have the following laticiferous organ cicatrization process in Morus nigra. First of all, at the base of the petiole, in each milk-bearing branch, we have a kind of concretion of the latex, forming two plugs, one above and the other below the separating stratum. This first modification certainly stops the movement of the latex in this region and permits the formation of the finger-shaped partitions which constitute the real closing as such. The formation of these partitions would, as a matter of fact, be very difficult in an element as unstable as latex. This is undoubtedly also the reason why these partitions appear almost always in contact with or at a small distance from the plugs; the latex is certainly much more stable in the vicinity of these arresting points. These partitions are probably not produced as the result of a division of the cell nucleus; instead they are probably due to the direct secretion of protoplasm which, as we have just demonstrated, is more condensed in the region of the milk-bearing organs, where they [the partitions] develop.

This means that the finger-shaped form of the two occlusion partitions of one and the same laticiferous organ is probably explained much more accurately by the pressure which the latex exerts on each of them, in the opposite direction. Perhaps the excitation, caused by the evolution of the separating stratum and the elongation of its cells toward the dehiscence surface, also helps in producing the convexity of the partitions in the milk-bearing organs.

The obstruction membranes always are finger-shaped but they do not always have the regular shape which we indicated earlier; sometimes, quite rarely, by the way, we find some that are not absolutely convex at their top but more or less flattened (2, Figure 40) and sometimes they are even partially folded back toward their concave area (1 and 3, Figure 40).

At the level of the separating stratum, the milk-bearing organs are finally broken as a result of the growing thickness of this layer, just as it happens in the case of the sieve-like tubes and the ligneous vessels (1a, Figure 37). At the level of the scar cork which forms a little further down during the second year, they are first of all, very much like the sieve-like tubes, constricted by the compression of the cells in the generating zone; then they are stretched and finally they are broken by the cork so that the latter, from here on, procedes between their extremities, without any break in continuity.

I might also point out that this is a case not above but below the finger-shaped partition, even though we may have a constriction and rupture due to the cork generating zone. In this case, I might add, these phenomena are not preceded, as we might expect, by the formation of a new convex partition on a lower level. In effect, it is the normal milk-bearing organ which is thus broken, and not its sacrificed portion.

7th Type. Aesculus Hippocastanum L.

As in the case of Diospyros virginiana and Morus nigra, we still have a cicatrization stratum in Aesculus Hippocastanum; this cicatrization stratum is leftover from the autumn defoliation time but the ligno-suberous lamina is here very much reduced and is already accompanied by a secondary cork which almost all by itself takes care of the cicatrization. A longitudinal section of the base of the leaf, a few days before it falls, shows us a cork lamina which grows across the entire cortical parenchyma (lic, Figure 41).

The direction of this cork lamina is a prolongation of that of the periderm of the stem (pd, Figure 41) and it is therefore very oblique to the direction of the leaf bundles. Its thickness is greater in the center of the cortical parenchyma where it consists of 8-10 cell layers (lic, Figure 42); the thickness diminishes abruptly at its point of contact with the periderm, especially in the external and lateral regions of the pulvinus. On the other hand, this cork ends around each of the bundles, curving slightly upward. Its cells are in all points similar to those of the periderm. Like these cells, they reveal a suberous framework which is not at all thick and a strong, hard thickening which involves only their internal middle portion. This thickening, moreover, is the same as we have it in the periderm of the stem although it does become thicker as it gradually forms part of the innermost cells.

Above and in direct contact with the cork, we have the ligno-suberous lamina which is formed at the expense of the cortical parenchyma. Opposite the region of juncture of this cork with the periderm of the stem, at the place where it is narrowest, it [the lamina] is thicker than elsewhere and compensates for the weakness of secondary suberous cicatrization. At that point, the cells, which are elongated very much longitudinally, have in advance been partitioned again three or four times. The ligno-suberous lamina -- which is therefore very thick above the narrowed portion of the scar cork -- abruptly loses its thickness toward the interior of the petioles; in the vicinity of the bast-ligneous bundles it consists only of two or sometimes only one layer of cells and it may be entirely missing in the entire middle and inside region of the cicatrization lamina (ss, Figure 41).

This is why I said earlier that the cicatrization stratum was almost entirely made up of cork in Aesculus Hippocastanum and before defoliation.

Between this cicatrization stratum and the separating stratum, we have a lamina of sacrificed parenchyma which does not undergo any change (ce, Figure 41). This parenchyma is thicker in the external region of the pulvinus where it averages three-four layers; it is reduced to a single layer in its innermost region.

The separating stratum consists of two or three layers of cells that have not been subdivided in advance; it is consequently of primary origin, as in the case of Amorpha fruticosa (cs, Figure 42). As in several of the preceding types, we have in the petiole, above it, a reaction on the part of the neighboring tissues and this is expressed by the lignification of their walls (rs, Figures 41 and 42).

Earlier I pointed out that the scar cork does not grow across the leaf bundles around the time of defoliation. However, these leaf bundles are partly cicatrized by the ligno-suberization of those of their cellulose elements which are closest to the cortical parenchyma and which are located at the level of the cicatrization lamina. Moreover, the vessels, especially those of the primary wood, are abundantly filled with thalli throughout the entire base of the petiole and to a point very near their re-entry into the caulinary system.

This is the situation of the base of the leaf a few days before the leaf falls.

The cicatrization lamina (cork and ligno-suberous tissue) is formed very early.

It appears at the end of June in those leaves which are at the base of the shoots and toward the end of July it is already partly formed in all leaves.

It ordinarily begins to appear in the cortical parenchyma, halfway between the bundles and the epiderm. Here it forms, first of all, several areas in the dorsal region of the petiole; then these areas are connected to each other and the lamina thus advances in the form of a circle arc, around the bundles, soon meeting again in the internal cortical parenchyma; at the same time it moves, on the one hand, toward the bundles and, on the other hand, toward the surface of the petiole.

At the beginning of the differentiation of the cortical areas, the thin ligno-suberous region of the upper part is differentiated here first and afterward below and against it; this leads to the appearance of subdivisions in the generating zone which will furnish the cork toward the outside. The areas then become gradually larger and ligno-suberization always precedes the appearance of the generating zone below them.

In all of the pulvini, the cork lamina is completely formed toward the middle of August. At that moment it almost has its final thickness in the vicinity of the cortical parenchyma. It already touches the bundles but it terminates, around the circumference of the pulvinus, at a certain distance from the periderm of the latter, with which it does not yet come into contact. At that time there is no indication whatever of the separating stratum.

Toward the end of August the cicatrization lamina reaches its ultimate thickness but it always leaves the bundles intact and it does not yet make contact with the periderm of the stem. The situation remains the same up to the end of September. Only then does the scar cork generating zone continue to advance toward the surface of the petiole, preceded by the subdivision and the ligno-suberization of the external cortical parenchyma; now only then does it unite with that of the periderm of the stem along the entire circumference of the petiole. It is because of this belated contact that the cork is always less thick than anywhere else, along the circumference of the pulvinus; in the end, however, the greater thickness of the ligno-suberous tissue in this region here gives the entire cicatrization lamina a greater thickness than anywhere else.

While the scar cork is thus completed through its connection with the periderm of the stem, the cell stratum which will be separated is filled with starch; at the same time the density of its protoplasm increases. On the other hand, the subcicatricial lignified strata is differentiated above it in the petiole as of the moment this stratum developes its individual characteristics. It is around this time that the thalli proliferate in the vessels and that the ligno-suberization gradually reaches the elements of the bundles in the pulvinus. In the rest of the leaf, the cells die from its top to its base, all the way to the separating stratum, and defoliation takes place.

The mechanism of the fall is identical to the one we had in Amorpha fruticosa; however, the walls of the cells making up the separating stratum are not at all thick; their middle region is transformed into mucilage; it inflates and dissolves as it is very weak. On the other hand, the growing thickness of the entire stratum is more considerable before the separation.

The leaves fall around the beginning of November and it is usually the oldest leaves which fall first. The fresh scar has a bright gray color; it is shield-shaped and on its surface, arranged in an arc, has five-seven fascicular navels slightly in relief and decreasing in size from the center of this arc toward the extremities.

Since the separating stratum is almost a direct continuation of the surface of the stem, we do not have a pulvinus as such here.

The 1st-year cicatrization of the bundles occurs in all cases, after the leaf falls, through the ligno-suberization of all of their parenchymatous elements at the level of the cicatrization lamina; this modification extends more or less deeply, depending on whether it occurs sooner or later. The gummy lignin is rare in the vessels; as we saw earlier, these vessels are already almost completely plugged by the thalli before the leaf falls.

In general, the ligno-suberization of the elements of the bundles is the only cicatrization which occurs here at the end of the first year. Sometimes, however, before winter comes and at the base of the shoots, primarily, this cicatrization is completed through the continuation of the cork lamina, across the bundles below their ligno-suberized portion.

In this latter case we get a generating zone growing across these bundles; this zone is based on or supported by that of the cicatricial scar at the point of curvature which it describes as it moves up along the bast-ligneous cords; the new subdivision is established across all of the elements except the sieve-like tubes and the vessels. This transfascicular generating zone most often forms a slight curve toward the stem; this curve is more or less pronounced depending on whether the ligno-suberization of the elements of the bundles decends more or less downward, below the level which the scar cork occupies in the cortical parenchyma. As in the case of Aristolochia, the thalli of the vessels are most often involved in the composition of this cork (thp, Figure 43).

When the generating zone thus grows across the bundles before winter it never produces more than two or three layers of cork whose elements always have thin walls and which do not have the hard thickenings of the cells of the extra-fascicular cork. Often, also, it manages to cross only a portion of the bundles.

During the second year, the transfascicular cork generating zone furnishes a new stratum of cells, the first of whose layers, like those during the preceding year, have thin and suberous walls, whereas the later ones have more of the hard thickenings of the cells of the caulinary periderm. When the cork does not grow across the bundles or when it grows across them rather imperfectly after the first year, it does so during the second year but the curve, which it then describes across these bundles, is always more accentuated.

In the bast of the fibers of Aesculus, we have a small number of articulated laticiferous organs. At the base of the petiole, these milk-bearing organs have cells that are shorter than anywhere else. As the ligno-suberization of the bundles developes gradually, after the leaf falls or sometimes even before it falls, these milk-bearing organs are partitioned transversally once or twice at the level of the cicatrization lamina and they are ligno-suberized like the parenchyma. During the formation of the cork across the bundles, these milk-bearing organs may sometimes be crushed but most often they subdivide at the level of the generating zone and they participate in its composition. (Figure 78, which I do to illustrate the laticiferous organs of Acer campestre, also shows what goes on in the case of Aesculus.)

8th Type. Forsythia suspensa Vahl.

In Forsythia suspensa we find a cicatrization which is even more complex than in Aesculus; this cicatrization is found at the moment the leaf falls.

Here, in effect, we note a double cicatrization lamina below the separating stratum; this cicatrization lamina is quite well characterized; in other words, we have here a complete ligno-suberous lamina which is doubled, on the side of the pulvinus, by a scar cork (ss and lic., Figure 44).

The general direction of this double cicatrization lamina is slightly oblique to that of the re-entering bundles; its lower limit is almost level in the external cortical parenchyma and it curves slightly toward the stem in the internal cortical parenchyma.

In the entire external and lateral region of the pulvinus, the cork is connected to the periderm of the stem, curving downward. In its internal region, it is connected similarly with the superficial periderm although this time it curves strongly upward (lic, Figure 44).

The double cicatrization stratum is interrupted by the foliar bast-ligneous system in the same way as in Aesculus. Sometimes, however, the ligno-suberization already reaches a portion of the bundles before the leaf falls; but the cork lamina never touches them before this period.

The ligno-suberous portion of the cicatrization strata is entirely formed of unpartitioned primary tissue (ss, Figure 45). Here the lignification is very homogeneous throughout its entire thickness and the internal suberous film of the cells here is a little thicker than in the preceding case.

The separating stratum is found in direct contact with the ligno-suberous tissue; like the latter, it is not of meristematic origin; on the average it consists of only two or three cell layers (cs, Figure 45). Slightly concave in the cortical parenchyma around the bundles, it rises slightly toward the petiole as it crosses these bundles.

As in the case of Diospyros virginiana and Paulownia imperialis, there is no trace of lignification above the separating stratum at the base of the petiole.

No thallus is produced in the vessels of the leaf scar before the leaf falls.

The cicatrization stratum begins to differentiate at the beginning of September. The ligno-suberous portion appears first. The histological modification of the cells in this portion, followed by the disappearance of their content, begins almost at the same time, against the external and lateral surface of the pulvinus and, in the internal cortical parenchyma, against the bundles. From these two regions it advances at the same time toward the bundles and the inner side of the pulvinus. Soon the ligno-suberous lamina is completely differentiated throughout the entire extent of the petiole. Only then does the secondary cork generating zone develop below and against it. Thus the ligno-suberous portion of the scar lamina is formed completely before its secondary suberous portion. The latter is detached from the periderm in the external region of the pulvinus; it moves toward the bundles, goes around them without touching them, and then continues, on the other side, all the way to the internal periderm. It includes 4-6 layers of cells before defoliation; its generating zone ceases to function at that time; its cells are flat, like those of the caulinary periderm and, as in the latter, it may be accompanied by one or two parenchymatous phellodermic layers.

The leaves are generally detached during the second half of October. The cells of the separating stratum are characterized at that time in the same fashion as in the preceding types. As in the case of Diospyros virginiana, the cells of this stratum are separated without any prior swelling and they are detached by the simple dissolution of the intermediate [dividing] pectic membrane. As in the other cases which I have just mentioned, there is still almost no growth on the part of the two separated layers in the opposite direction.

At the moment of defoliation, the wound left behind by the falling leaf is already completely cicatrized by a double primary ligno-suberous and secondary suberous lamina, except on the level of the bundles. The form of the leave scar (ci, Figure 46) is triangular and the points are quite rounded. This scar is topped by two or three big buds arranged in a radial line. A fascicular node in relief then appears in its center. The pulvinus protrudes very much and has three small swellings (pads) which shoot off at angles from the scar and descend up to a certain distance below it, along the internode.

After the leaf falls, the only changes that occur on the level of the scar strata are found inside the bundles. The cork, it is true, never crosses the latter during the first year but the ligno-suberization reaches their parenchymatous elements to a very great distance below the double cicatrization stratum. No thalli develop in the vessels but the latter are entirely plugged up by the gummy lignon. The latter develops only at the level of the cicatrization strata.

During the second year the scar cork grows across the bundles (lic, Figure 47), forming a very accentuated curve toward the stem. Its thickness, at the end of the second year, is considerable in this region of the curve, even more considerable than both of the annual two strata of the rest of the scar cork. The general direction of the growth of this cork is so arranged that the portions removed from the bundles [the distant portions of the bundles] are in the same prolongation.

Sometimes the periderm of the stem transforms its last layer into sclerites, toward the end of the second year; in this case, that [the layer] of the scar cork is always modified in the same fashion.

When a bud develops above a scar, the latter sometimes is not altered; more often, however, the growth of the base of the bud forces the scar to split. The rupture occurs very regularly along two small lateral cracks on either side of the navel, between the three small pouches of the pulvinus. The edges of these cracks are never far apart; however, while the new wound developes below the cicatrization strata of the first year, the scar cork grows below the exposed surfaces.

9th Type. Alnus glutinosa Gaertn.

Alnum glutinosa is an example of the greater complexity of differentiation of the scar tissues of the pulvinus at the moment the leaf falls.

Longitudinal sections in the base of the petiole made several days before defoliation revealed the presence of a double cicatrization lamina as in the case of Forsythia suspensa (ss and lic, Figure 48); however, this double lamina differs essentially from that in the former species in that its ligno-suberous portion is of meristematic origin.

The partitions [subdivisions] (ss, Figure 49) are very numerous in this part of the scar stratum and they are very similar to those which we mentioned in connection with Paulownia imperialis and Morus nigra; however, they are here less abundant toward the top and they become more and more abundant toward the bottom. Besides, as they increase in frequency toward the lower region of the cicatrization lamina, they also turn up more regularly in a transversal fashion, especially in the elongated cells of the external region of the cortical parenchyma; thus we have a rather imperceptible transition from the upper portion, in which the partitions are irregular, to the lower cork, where all of the partitions are transversal (lic, Figure 49). Along the entire external circumference of the pulvinus, the lamina of scar cork connects with the periderm of the stem below its termination, forming a very acute angle with it (lic, Figure 48), so that, in this region, the upper limit of the double cicatrization lamina is almost perpendicular to the direction of the petiole; this double lamina thus forms a wedge along the dorsal side of the pulvinus.

The thickness of each of the two cicatrization strata diminishes as we go from the outside toward the inside. The diminution of the cork very often reduces the latter, in the vicinity of the inside corner of the petiole and the stem, to a single layer of cells; sometimes it even causes it to disappear a short distance from that region (lic, Figure 48).

Between the separating stratum, composed of two or three layers of cells, and the cicatrization lamina, we have a stratum of sacrificed parenchyma which also reveals several meristematic re-subdivisions and which, consisting of two or three layers in the external region of the petiole, diminishes in thickness as it approaches the leaf bundles; in the end, it is completely absent in the internal cortical parenchyma where the separating stratum is in direct contact with the cicatrization lamina (cs, Figure 48).

The separating stratum itself loses thickness from the outside toward the inside of the pulvinus. In this latter region, it is reduced to two or even one single layer of cells.

The subdivisions which we mentioned in connection with the scar strata and in the sacrificed tissue do not meet, except at these two levels; we can still detect some of them in the separating stratum and even in the subcicatricial lignified region which, in the species, is not at all thick and very little lignified.

Throughout the entire base of the petiole and before the leaf falls, we have many thalli inside the vessels, especially in those of the primary wood. Certain secondary vessels may already have some gummy lignin inside them at the level of the cicatrization strata and even higher up in the petiole. Finally, almost always, a large portion of the bast-ligneous bundles has already been invaded by the ligno-suberization but they are never touched by the scar cork before defoliation.

As in the case of Forsythia suspensa, the double cicatrization lamina forms long before the leaf falls. The subdivisions in the portion of the pulvinus which turns into the ligno-suberous part appear, around the middle of August, almost at the same time throughout the entire width of the pulvinus and especially at the base of the lamina. As in the case of Morus nigra and Paulownia imperialis, the division of the cells of this stratum is neither preceded nor followed by any intercalary growth.

Toward the end of August, the ligno-suberization of the elements appears in the outside region of the pulvinus; it then spreads rapidly across the entire organ, avoiding only the bundles. Contrary to what happens in the case of Forsythia suspensa, the secondary suberous portion of the double cicatrization lamina does not wait for the completion of the ligno-suberous portion before it starts forming; its generating zone, in effect, is developed below the ligno-suberous portion as ligno-suberization progresses here. Starting at the end of September, the scar stratum is entirely formed so that it is there for us to see at the moment the leaf falls, although at that moment it still leaves the bundles intact.

Generally defoliation does not occur until the end of October. Sometime before that period, the thalli proliferate in the vessels while ligno-suberization invades the parenchymatous elements of the bundles.

As we pointed out earlier, the separating stratum is partly of meristematic origin. The separation occurs inside, as in the case of Amorpha fruticosa; however, in the innermost portion of the pulvinus, where it is often made up only of a single cell layer, we do have a rupture in the longitudinal walls while the leaf is separated; this rupture is of the kind we mentioned in the case of Aristolochia Sipho.

The macled cells with calcium oxalate are numerous, at the base of the petiole, in the parenchyma where the cicatrization stratum develops These cells which, at the moment of differentiation of the scar tissues, still contain traces of protoplasm, however, do not subdivide, like their neighbors; instead they are ligno-suberized, like their neighbors. Each of them, in effect, then has lignified walls and, on its inside, it has a thin suberous film which covers not only the inside surface of the cell wall but also the thin enveloping membrane of the macle and the points which connect this membrane to the walls of the crystal-bearing cell (ev, Figure 50).

After the leaf falls, the leaf scar reveals three fascicular navels in relief. The ligno-suberization of the parenchymatous elements of the bundles, which began even before defoliation, is completed after the latter and extends well below the cicatrization strata (the dotted line H, Figure 48, indicates the limit of this differentiation). The gummy lignin continues to be deposited in the vessels where there are no thalli; but the cicatrization of the vascular apparatus occurs primarily through these thalli.

The scar cork lamina in the meantime has stopped growing thicker even before the leaf falls; in addition, it never grows across the bundles during the first year.

The changes occurring in the leaf pulvini during the second year are the same as in the case of Forsythia, with one difference, however: the cork here is not as thick across the bast-ligneous tissues and, since the general direction of this cork is oblique to that of the bundles, their portion on the inside of the ligno-suberous lamina does not constitute a prolongation of their lower portion, as in the case of Koelreuteria.

10th Type. Spiraea opulifolia L.

The feature that characterizes the type Spiraea opulifolia, most of all is a special disposition of the cicatrization tissue whose cause resides in the fact that the periderm is developed here very deep inside the stem and the leaf pulvinus, in contact with the bast.

If we examine longitudinal and transversal sections of the base of the petiole, at a time when the periderm of the stem is already well developed, that is to say, toward the end of the summer and, consequently, quite sometime before the leaf falls, we notice the following arrangement. Instead of being superficial, as in the earlier cases, and instead of constituting, at the base of the petiole, a single wide opening through which the majority of the tissues, coming out of the leaf, must pass, the caulinary periderm is very deeply located behind the bast and has three very small openings through which pass only the three leaf bundles. The sides of these openings extend upward, against the surface of the bundles, forming around each of them a peridermic sleeve of a certain length (mp, Figures 51 and 52). (We might note that this periderm, which is so deep in the stem, disappears in the the base of the axillary bud, becoming superficial at this point, as shown in B, Figure 51.)

Except for this arrangement of the periderm at the base of the petiole -- an arrangement which, as we shall see later on, modifies the ultimate state of cicatrization, the phenomena which come before the fall of the leaves are pretty closely related to those which we pointed out in the Paulownia imperialis type.

The separating stratum developes a little above the termination of the circumfascicular peridermic sleeves (cs, Figure 51) and its surface is irregular. As a matter of fact, this surface is quite noticeably transversal in the internal cortical parenchyma where as it crosses the external cortical parenchyma obliquely from top to bottom.

The meristematic action is very energetic in the separating stratum; here we may have as many as eight subdivisions and sometimes even more (cs, Figure 53). Below it, in the pulvinus, we also have a cell division but it is less intensive and the thickness of the tissue which it involves is quite small. Above it, in the base of the petiole, contrary to what we saw in the case of Paulownia, the meristematic action can be observed also (rs, Figure 53) up to a distance that is much more considerable than below and whose intensity diminishes as we go from the separating stratum upward. In the end and before the leaf falls, this thick subdivided portion of the petiole, above the dehiscence surface, undergoes lignification comparable to the one we just pointed out in some of the earlier types although the thickness is always smaller. The cicatrization of the wound, which takes place after the leaf falls, is very incomplete. As a matter of fact, there is no ligno-suberization of the cortical parenchyma in the pulvinus; this process can otherwise be observed at almost all of the outside levels of the periderm. It is the remnants of the thick separating stratum as well as the subjacent tissue of meristematic origin which, becoming more or less flattened out at the surface of the pulvinus, constitute the only protection for the wound here.

During the first year, the fascicular system is protected on the outside by the peridermic sleeves (muffs); during that year, this system is more or less subjected to the action of outside factors along its rupture surface because we get a very weak ligno-suberization of the elements and a deposit of gummy lignin in the vessels only very rarely; these two types of modifications occur elsewhere, not in the immediate vicinity of the wound, but at the base of the sleeves.

During the second year, the scar cork is differentiated only across the bundles; it developes below their more or less ligno-suberized zone (lic, Figure 54), and its generating zone connects with that of the periderm of the stem. Starting at that moment, the generating zone for the perifascicular sleeves ceases to function.

(Although they do not directly involve the cicatrization of the pulvinus, I believe that I ought to point out the following facts: while the axillary bud aborts and dies, there developes, below it a periderm which, on the one hand, connects with the scar cork of the leaf bundles and, on the other hand, with the periderm of the upper internode of the stem. In the opposite case, the bud either remains dormant or it furnishes a shoot; we can then observe the development of a deep periderm behind the superficial periderm of the bud. It is therefore this deep periderm which then connects with the scar cork of the leaf bundles; Po, Figure 54.)

This type is thus distinguished from the preceding ones primarily by the fact that -- below the wound -- there is no scar cork being differentiated across the cortical parenchyma. The plant, in effect, uses in the leaf pulvinus the same method of protection as in the stem because, as in the latter organ, it sacrifices the entire cortical parenchyma and protects only the central cylinder through the periderm or, at least, the bundles which are its extension. This is why only the latter are effectively cicatrized during the 2nd year.

11th Type. Hamamelis virginiana L.

In all of the preceding types we were concerned only with the means of cicatrization which develop in relation to the wound itself, resulting from the fall of the leaf. The type Hamamelis virginiana is characterized by the formation of a new surface of dehiscence behind the first; this phenomenon I called the "revival of cicatrization" (Tison, A., "On the Fall of Leaves and the Cicatrization of the Wound," C. R. de l'Acad. d. Sc., 19 June 1899). I will also show that it is a good idea to tie the case of the marcescent leaves in with this type.

In anything that does not pertain to the revival of cicatrization, Hamamelis virginiana can be very easily related to the type Koelreuteria, with the following modifications.

The separating stratum is derived from a single layer which is subdivided on the average two or three times in the dorsal region of the petiole and only once in its internal region. It is consequently made up of three or four layers of new cells in the first and of only two layers in the second. It is rare for the periderm of the stem to grow up along the pulvinus, to the detachment surface; the epiderm almost always subdivides like the cortical parenchyma, at the level of the separating stratum. These subdivisions, which are mostly one in number or very rarely two, involve only a single or only two rows of epidermal cells, depending on whether they are larger or smaller.

As in the case of Koelreuteria, we get a lignification of the tissues of the petiole above the separating stratum but it is not at all accentuated (rs, Figure 55).

During the first year, the cicatrization of the tissues of the pulvinus completely recalls that of Koelreuteria; it forms a lamina which is similarly ligno-suberous at the base and which is only ligneous near its upper face. I might mention that I was twice able to observe a thallus, passing from one vessel to the other, in the bundles (th, Figure 56).

The changes which occur in the leaf pulvini, during the second year, are much more complex than those we observed so far and these are the changes which characterize this particular type.

Revival of Cicatrization

Toward the end of February, in the case of some of the leaf pulvini, and in the month of March, for most of them, we get a series of modifications below the cicatrization lamina from the first year (ligno-suberous stratum); these changes lead to the establishment of a new separating stratum. This stratum is similar to the one which, during the preceding year, caused the leaf to fall in autumn; but it differs from it in that it is not preceded by a meristematic subdivision and that it therefore resembles the autumn separating stratum of the type Amorpha fruticosa.

The new dehiscence surface runs parallel to the surface of the scar and is located a little above the axillary corner of the pulvinus. It develops, not in contact with the ligno-suberous lamina, but a little below, leaving a thin lamina of parenchyma between it and the latter. Consisting of three or four layers of cells in the dorsal region of the pulvinus, the new separating stratum gradually loses thickness toward the interior and usually even ceases to exist a short distance from its axillary side.

Inside this stratum, the separation of cells occurs in the same way as inside the autumn separating stratum of the type Amorpha. The different phases of the phenomenon here are even easier to observe because they occur very slowly, contrary to what happens when the leaves fall.

The new separating stratum begins to differentiate in the vicinity of the bast of the bast-ligneous leaf system. It extends from this point across the bundles at the expense of their parenchymatous elements and across the rest of the pulvinus; the separation then occurs on the inside, following the same progression. In the epidermal cells we can observe the same changes at the expense of the cellulose portions of their wall, after the rupture of the cuticle.

As we observed earlier, all of these changes occur slowly. The longitudinal growth of the separated cells of the separating stratum ordinarily occurs only toward the end of March. It causes the progressive removal of the original cicatrization lamina from the rest of the pulvinus by breaking the vessels and the sieve-like tubes, however, this lamina is still retained by the thin internal region which has not been traversed by the separating stratum and it therefore does not become detached. At this time we can therefore (Figure 57) observe certain kinds of small valves which are raised in the manner of a lid above the leaf pulvini and which are retained only by their internal portion. A slight pressure should immediately cause them to fall.

Ordinarily, this occurs gradually under the influence of external factors (shocks, changes in temperature, desiccation, etc.). The fact is that the structure of these valves is not homogeneous; they are cellulosic in their upper portion and they are ligno-suberous at their base; besides, the desiccation, acting unequally on each of their tissues, causes them to curve slightly upward and more or less widens their detachment crack. In all cases, starting in April, they are all more or less removed from their pulvinus to which they adhere only weakly on their inside. There are still quite a few of them in May and some of them last even longer.

As soon as the valve rises, the cells of the separating stratum, which have remained on the surface of the rest of the pulvinus, are flattened on it.

The formation and detachment of the valve lead to the disappearance of the first scar stratum and the exposure of the tissues of the leaf pulvinus at a level closer to its insertion. This new wound is gradually cicatrized as it developes, first of all, through the differentiation of a ligno-suberous stratum composed of two or three layers near the new surface, and, then, above it, through the establishment of a cork which will form the final cicatrization. This cork grows across the bundles and is about seven to ten cell layers thick at the end of the second year.

Marcescent Leaves

Everything we have just said about Hamamelis virginiana applies to those leaves that fall in autumn and their pulvini; in this same species, however, there are many leaves, which are called "marcescent" [withering], which remain attached to the tree after they die and until the beginning of the next year. (The marcescent leaves are generally those that are formed last, that is to say, those that are inserted on the short and late-growing shoots and that have not completed their vital cycle at the moment of the first frost which kills them.) We are now going to study the anatomical features related to this marcescence.

At the time the deciduous leaves fall, the base of those that are marcescent does not reveal the subdivisions or partitions from which the autumn separating stratum usually results. Here, however, we can sometimes observe -- in the cortical parenchyma and on the same level -- small areas of mucilaginous cells inside of which we may have a partial separation (cs_1, Figure 58).

Sooner or later, as the bad-weather season saps the vitality of these leaves, we get thalli in the vessels of their bast-ligneous system, as in those of the deciduous leaves.

Later on, after these leaves have fallen, a primary cicatrization lamina is differentiated at the base of the marcescent leaves as the leaves die; this primary lamina is similar to the one we described in the pulvinus of the fallen leaves; that is to say, it is ligno-suberous only at the base and it is ligneous only in its upper portion (ss, Figure 58). However, it is not as thick and it becomes thinner, the later the leaf dies.

The marcescent leaf and its pulvinus remain in this condition until the spring of the next year. The leaf becomes increasingly dried out and its petiole becomes stained (in the sections, this stained portion of the petiole resumes its normal volume in contact with water) up to the level of the cicatrization stratum whose nature, partly ligneous, prevents any deformation.

Then, at the beginning of the second year, at the time when the new separating stratum is developed in the pulvini of the deciduous leaves, causing the revival of cicatrization, there is a similar stratum forming at the same level (cs_2, Figure 58). This separating stratum, in the same section, includes the cicatrization lamina and the dead leaf. The fall of this leaf occurs much more regularly and much sooner than the revival of cicatrization in the pulvini of the deciduous leaves; this period usually comes in the beginning of April. The mechanism of the separating stratum is, in effect, aided by the action of the weight of the leaf and especially by the action of the wind.

Behind the surface exposed by this fall we now get the development of cicatrization strata similar to those which form in the pulvini of the deciduous leaves after the revival of cicatrization.

This means that, from the viewpoint of anatomical changes occurring in the leaf pulvinus, the marcescent leaves of Hamamelis virginiana really differ from the deciduous leaves of the same species only by the absence or incomplete development of the autumn separating stratum.

Summary of Selected Types

In all types, except Aristolochia Sipho, the separating stratum almost always consists of several cell layers and the detachment occurs through the dissolution of the middle strata of the walls in its upper region. In the case of Aristolochia Sipho, it consists of a single layer whose cells are elongated and break afterward; we might also point out that the same form of dehiscence is again encountered in the internal region of the pulvinus of Alnus glutinosa, where the separating stratum often is composed only of a single layer.

In most of the types we can observe the differentiation of a subcicatricial lignified stratum above and against the dehiscence surface, at the base of the portion of the leaf that is going to fall.

Here are the changes which occur in the tissues, below the separating stratum: (1) sometimes we have a subdivision of a part of the tissues in all directions; (2) the formation of a ligno-suberous lamina at the expense of the primary tissues which have or have not undergone prior subdivision; (3) the formation of a secondary subjacent cork. When the second and third of these changes occur before the leaf falls, they almost always involve only the non-bast-ligneous tissues and they always, to a great extent, move around the latter. These are invaded only later on by ligno-suberization and then they are traversed by the cork.

Between the ligno-suberous lamina and the separating stratum we may have several layers of sacrificed parenchyma which has remained cellulosic.

The secondary cork lamina always, in the end, connects up with the periderm of the stem and thus completely blocks the opening across which the tissues of the leaf would move out. It exists in all types and turns out to be a component of final cicatrization.

In the three first types (Aristolochia Sipho, Amorpha fruticosa, and Koelreuteria paniculata), there is no modification of the tissue below the separating stratum, before defoliation, and there is only a rather thin lignification of the tissues above it. After the leaf falls, a ligno-suberous lamina is differentiated in the pulvinus, starting from the first year; this is doubled by a cork during the second year. The three types differ from each other because of their separating stratum; the separating stratum of the first type is made up of a single layer; that of the second type consists of several primary, non-subdivided layers; that of the third is of meristematic origin. The fourth type (Paulownia imperialis) resembles the third except for the fact that the meristematic action takes effect not only in the separating stratum but also in the subjacent parenchyma of the pulvinus.

In the following five types, the cicatrization is always more or less completed before defoliation: by a ligno-suberous lamina of primary origin in Diospyros virginiana; by a similar stratum of meristematic origin, that is to say, formed at the expense of the primary tissue which has earlier been subdivided in all directions, in the case of Morus nigra; particularly by a cork of secondary origin in the case of Aesculus Hippocastanum: by a ligno-suberous stratum of primary origin, reinforced [doubled] by a cork layer in Forsythia suspensa; finally, by a meristematic ligno-suberous stratum, doubled by a cork layer, in Alnus glutinosa, which is the most complex type.

The feature that characterizes the type Spiraea opulifolia, is -- as a result of the deep location of the periderm in the stem and in the pulvinus -- the scar cork which develops only across the bast-ligneous bundles.

As for the type Hamamelis virginiana, I might say that I included it particularly for two reasons: (1) because it shows, during the second year, the coppice shoot [rejection] of the first scar strata by a procedure which I described with the term "revival of cicatrization"; (2) because it has "marcescent leaves." The persistence of the latter, during the winter, results from the incomplete development or the complete absence of the ordinary separating stratum; they fall during the spring of the second year as a result of the revival of cicatrization.

Chapter II. Species Related to Type Amorpha fruticosa

(I want to study the species related to this second type at this point because I was unable to find the features, which characterize the separating stratum of Aristolochia Sipho, in any other plant; in other words, this is the only place where I was able to find this stratum made up of a single layer over its entire extent and this is the only place where the leaf is dehisced as a result of the rupture of the walls in all of the cells of this layer. The ligneous plants, which reveal a similar way of leaf detachment, are probably rare. Besides, I showed earlier that similar events can occur partly also in Alnus glutinosa; I will also demonstrate these events in Rhus Cotinus. We will see, furthermore, as we continue with our work here, that we also have separations of marcescent leaves and revivals of cicatrization due to similar processes.)

We recall that, in this type, the separating stratum is of primary origin and that it consists of two or three layers between which the separation takes place after the dissolution of the middle intercellular strata. There is no trace of cicatrization in the pulvinus at the time of defoliation. Later on, at the end of the first year, a primary ligno-suberous stratum is formed; after that a secondary subjacent cork is formed during the second year.

Here is a list of species related to this type: Benzoin odoriferum, Planera Richardi, Hippophae rhamnoides, Coronilla Emerus, Crataegus monogyna, Pyrus communis, Mespilus germanica, Castanea vulgaris.

Benzoin odoriferum Nees d'Es.

Benzoin odoriferum differs from Amorpha in that the cicatrization of the vessels here is accomplished almost entirely by the thalli which are developed before the leaf falls; this reminds us of the case of Aristolochia Sipho whose walls, however, are thicker than those of their generating cells. Below the ligno-suberous lamina and even before the leaves fall, these thalli not only become thicker but they are also heavily lignified; they reveal numerous bordered pits corresponding to the ornamentations of the vessels which contain them. The same is true of their generating cells.

The primary scar stratum is not as homogeneous as in the case of Amorpha; it is lignified only in its upper half and it is ligno-suberous only in the other part; besides, this ligno-suberization here does not occur in all cells; some of them, here and there, are only lignified.

The secondary cork is developed here in contact with the preceding tissue and it grows across the bundles by the same process as in Aristolochia Sipho. It is very thick and, as in the periderm of the stem with which it connects, the cells of its layer which is closest to the generating zone have a very accentuated suberous thickening in their outside wall. The phelloderm corresponding to this cork is not as thick as that of the stem.

The cortical parenchyma of the pulvinus includes many secreting cells. As in the rest of the plant, they are doubled on the inside at the moment of defoliation by a thin suberous stratum; but they do not undergo any other modification at the level of the scar strata.

Hippophae rhamnoides L.

The petiole of this species has an articulation at its base which is marked by a circular groove which is more accentuated on its outside surface (Figure 59).

In a longitudinal section, the tissues of this articulation reveal a region of very small cells, as in the case of Diospyros virginiana; however, we have a gradual and sometimes rather rapid transition from this region to the tissues of the petiole and to those of the pulvinus. On the other hand, the constriction of the petiole is barely noticeable on the leaf bundles. The periderm of the stem, which is very thick, disappears abruptly at the level of this articulation (joint).

The separating stratum (cs, Figure 59) is formed at the expense of the small cells in this latter stratum [periderm]; the separating stratum here is located, however, a little above the bottom of the groove. In this particular case the separating stratum here reveals a surface which is slightly concave toward the pulvinus in the cortical parenchyma and concave [sic] toward the petiole in the passage of the bundles. Otherwise its constitution and its function are the same as in Amorpha fruticosa.

The lignification of the tissues of the petiole, above and against the separating stratum, is very pronounced. It involves usually four to six rows of cells and it may climb even higher along the bundles without crossing them (rs, Figure 59).

The ligno-suberous stratum extends to a point at which it is in immediate contact with the debris of the separating stratum and, on the other hand, descends lower, inside the bundles, than in the cortical parenchyma.

The cavity of the vessels is also blocked here by gummy lignin, although this happens here only at the level of the cicatrization stratum. The deposit of this substance begins in the near-by vessels of the trachea and before the leaf falls.

Crataegus monogyna Jacq.

The petiole of this species, like the one of Hippophae, reveals a joint at its base; here the bundles are reduced to roughly one third of their volume. The separating stratum likewise is developed here a little above the bottom of the groove; but it is concave toward the pulvinus, at the level of the bundles, and concave toward the petiole, in the cortical parenchyma. Some of its cells sometimes reveal a transversal partition but this is very rare and almost the entire stratum is made up like the one of the Amorpha type which is of primary origin.

Except for these few modifications and the lesser thickness of the lignified subcicatricial stratum, everything else is as in the case of Hippophae.

Castanea vulgaris Lam.

The general characteristics here are the same as those of Amorpha but the vessels are obstructed by thalli even before the leaf falls. The gummy lignin, which appears after the leaf falls, may also be encountered again all the way into the bast-ligneous system of the stem, although only in the secondary vessels.

The scar cork, which developes during the second year below and against the ligno-suberous stratum, grows across the bundles in the same way as in Aristolochia Sipho.

The crystal-bearing cells are abundant at the base of the leave; at the level of the cicatrization strata, some of them lignify only their walls but most of them undergo ligno-suberous differentiation, like the other cells of the parenchyma; the internal suberous film here reveals the arrangement which I described and illustrated for Alnus glutinosa (sub, Figure 50).

Coronilla Emerus L.

The petiole of Coronilla Emerus reveals a joint like that of Hippophae rhamnoides. The separating stratum developes likewise at the expense of the cells in this joint but on the level of its most contracted portion. Similarly, the ligno-suberous stratum, which is not at all thick, is in direct contact with the separating stratum.

The scar cork begins in the vicinity of the bundles and it grows across all of the tissues from that point on. Besides, since there is no more periderm on the stem during the second year, this cork gradually disappears below the epiderm of the pulvinus, curving slightly downward.

Planera Richardi Michx

The base of the leaf of this plant also has an articulation a little above its insertion; at the level of this joint the bundles loose only very little of their volume.

The variations of the normal type, in the base of the petiole, are the same as in Hippophae.

The crystal-bearing cells, which are very numerous in the cortical parenchyma of the stem and of the petiole, are almost entirely absent at the level of the articulation of the latter; those which are inside the cicatrization stratum only lignify their walls.

Pyrus communis L.

Pyrus communis is quite closely related to the last two species.

It is distinguished from all of the other preceding individuals, which I related to the Amorpha type, by the fact that the scar cork very often appears below the ligno-suberous stratum, in the pulvini of the base of the shoots, already during the first year, after the leaf has fallen; it then connects with the periderm of the pulvinus along its entire circumference and sometimes crosses the bundles themselves before the winter; this happens in the same way as in Amorpha. Its thickness varies between one and three layers of cells which always have thin walls and which, by vitue of this fact, differ from the cells of the periderm of the stem which have strong suberous thickenings on their outside walls. During the second year its generating zone begins to function once again and continues to thicken it. In the pulvini at the top of the shoots this tissue developes only during the second year. This second-year cork always reveals the suberous thickening that characterizes the periderm of the stem.

Mespilus germanica L.

This species differs very little from Amorpha fruticosa; however, as in the case of the preceding Pyrus, a thin cork often developes here before the first winter; this cork has very thin walls and is found below and against the ligno-suberous stratum; but this is the case only in the pulvini at the base of the shoots. Likewise, a final cork developes here only during the second year; this final cork would be histologically similar to the periderm of the stem, that is to say, it would have a suberous thickening on the outside half of its cell walls and a hard thickening with pits on the other half. The suberous thickening here also increases in size in the vicinity of the generating zone whereas the hard thickening continues to lose thickness.

In transversal section, the longitudinal walls of this cork often look very sinuous, somewhat recalling the cork in many epiderms of leaves seen from the front.

Evonymus europaeus L.

This plant is not entirely comparable to the Amorpha type; it is in some ways related to the Diospyros type, in the sense that the cicatrization of the wound sometimes begins before the leaf falls. But the ligno-suberization of the elements of the pulvinus -- when it does exist at the moment of defoliation -- involves only a few layers adjacent to the separating stratum and especially in the external region of the cortical parenchyma;

most often, it exists only in this region. After the fall of the leaf, the ligno-suberization extends from the separating stratum toward the base of the pulvinus and achieves great thickness. The scar cork appears only during the second year.

In this species, the subcicatricial lignified stratum is not at all thick and very little lignified.

Chapter III. Species Related to the Type Koelreuteria paniculata

We might remember at this point that the type Koelreuteria differs from the type Amorpha by the presence of cell subdivisions in those layers which will constitute the separating stratum and that the separation -- which occurs inside it between the two upper layers -- is preceded by the longitudinal growth of all of the cells in this stratum and, consequently, by its thickening. Besides, the cicatrization of the wound through lignification and suberization takes place only after the leaf has fallen, as in the case of Amorpha.

Among the plants revealing changes similar to those of Koelreuteria paniculata, I might mention the following: Paliurus aculeatus, Celtis occidentalis, Staphylea trifoliata, St. pinnata, Carpinus Betulus, Quercus hispanica, Q. pedunculata, Sorbus Aria, S. hybrida, S. aucuparia, Cotoneaster melanocarpa.

However, I will only describe the first two species here and we will relate the study of the others to the Hamamelis virginiana type to which they are also related either because of the existence of the revival of cicatrization or because of the presence of marcescent leaves, or because of both of these factors.

Celtis occidentalis L.

The petiole of this species has a swelling, at its base, located on its inside (P, Figure 60), like that of Amorpha fruticosa.

Against the hard bast of the stem and of the petiole and outside of it we have an almost entirely crystal-bearing tissue which is particularly well developed in the stem and the pulvinus. In the stem this tissue has very thick walls which are heavily lignified and which reveal numerous pits. The enveloping membranes of the crystals and the rare bridges which connect them to the wall of the crystal-bearing cells are likewise very thick, lignified, and spotted so that the cell cavities in this tissue are extremely reduced in size and so that the crystals here clogged [stuck] in a lignified mass. Similar lignifications occur here and there in the petiole but they involve only a few cells. Finally -- and this is the most important point I want to bring out -- the lignification of this tissue always -- like that of the hard bast -- stops at the level where the separating stratum and the cicatrization lamina form (crs, Figure 60). In this region, the various walls of this tissue are, of course, always very thick but they are completely cellulosic.

In Celtis occidentalis the preparation for the fall of the leaf does not produce any lignification in the base of the petiole above the separating stratum. In the pulvinus, the numerous crystal-bearing cells, which are inside the ligno-suberous stratum, do not reveal an internal suberous film.

In many of the pulvini, the scar cork is accompanied by a phelloderm which is particularly well developed at the level of rupture of the bundles and in the internal portion of the pulvinus where its thickness may amount to five or six layers of cells. Almost all of these cells become crystal-bearing and sclerous (ph, Figure 61), especially in the thickest regions.

Paliurus aculeatus Lamk.

Here are the special features of P. aculeatus, compared to Koelreuteria paniculata:

As in the case of Spiraea opulifolia, there is a very pronounced lignification of the elements of the petiole (rs, Figure 62) above the separating stratum; this lignification involves an average thickness of 10-15 layers of cells.

The petiole and the pulvinus reveal large elements which look like secreting cells to me (E, Figure 62) and which are sometimes found on the level of the separating stratum. The latter then surrounds them below and establishes its subdivisions and partitions in the elements which border on them (cs, Figure 62). It then happens on occasion that the portion of the separating stratum thus formed proliferates slightly within the big secreting cell, pushing its wall before it; however, at the time of defoliation, this doubling process does not occur although the mucilaginous transformation of the walls occurs below the gland, as elsewhere; the continuity of the surface of dehiscence then developes opposite this region as a result of a rupture of the lateral walls of the secreting cell.

In the pulvinus, the changes which follow the fall of the leaf are the same as those in Koelreuteria paniculata; here the vessels, however, are entirely cicatrized by the gummy lignin.

Chapter IV. Species Related to the Type Paulownia imperialis

We recall that this type, like the preceding type, is characterized by the presence of subdivisions and the absence of cicatrization in the base of the leaf at the moment the leaf falls. It differs by virtue of the fact that the meristematic action involves not only the separating stratum but also a more or less considerable thickness of the pulvinus below this stratum.

Here are the species that are related to that type: Tilia europaea, Corylus Avellana, Broussonetia papyrifera, Periploca graeca, Ficus Carica, Evonymus latifolius.

Tilia europaea L.

The subdivisions of the meristematic region are much less numerous than in Paulownia. We have only one or two per cell in the separating stratum and most often we only have one in the parenchyma situated below it. The portion of the pulvinus which is involved in these subdivisions is mostly made up of very numerous macled cells which themselves do not subdivide.

Tilia europaea also differs especially from Paulownia by the fact that there is a lignified region, almost as thick as that of Spiraea opulifolia, at the base of the petiole, above the separating stratum.

Among the numerous macled cells which are inside the ligno-suberous stratum, a small number becomes lignified while the majority becomes ligno-suberized like the other cells of the parenchyma; the internal suberous film here reveals an arrangement similar to that we illustrated for Alnus glutinosa (sub, Figure 50).

The periderm does not yet exist here during the second year along the periphery of the stem and pulvinus of T. europaea; likewise, the scar cork which forms at that time, immediately below the ligno-suberous stratum, extends all the way to the epiderm; in the dorsal and lateral part of the pulvinus it curves slightly downward due to the subdivision of the epiderm itself. Later on, the periderm of the stem, which will form in the subepidermal layer (*), will connect with it. At the end of the second year, the scar cork is characterized by great thickness.

(*) This subepidermal location of the periderm of the stem was mentioned by Sanio (according to Douliot, "Research on the Periderm," Ann. d. Sc. nat. Bot., 7th series, Vol X, 1889, page 335). I was able to reassure myself that although, in the majority of cases, this periderm is indeed subepidermal, it may, here and there, be derived from the epiderm itself and consequently occupy the same position as the edges of the scar cork.

Secretory Sacs

The secretory sacs are numerous in the cortical parenchyma of the plant, especially in the petiole; they are very rare in the portion of the pulvinus where all of the transformations, which I have just listed, occur. When mechanisms of this kind are found inside the ligno-suberous stratum, they undergo no change other than the ligno-suberization of their epithelial cells. The separating strata are interrupted at their level whereas the scar cork surrounds them below.

Corylus Avellana L.

In this species, as in Tilia europaea, the subdivision is not at all intensive in the parenchyma situated below the separating stratum. Here the epiderm subdivides neither at the level of the latter nor further down.

The lignified region of the petiole, above the dehiscence surface, is very thick especially in the internal region of the organ.

After the leaf falls, there forms a ligno-suberous stratum, as in the typed species; but this stratum is differentiated not only at the expense of the primary tissues of the pulvinus which are placed below the meristematic stratum; it is also differentiated by virtue of the fact that it takes over [borrows] the latter almost entirely. The region closest to the surface of the wound remains cellulosic.

The cicatrization of the vessels occurs especially due to the gummy lignin and this substance often appears even before the leaf falls in a point above the separating stratum, at the level of the lignified and thick region of the petiole.

The crystal-bearing cells become lignified when they are located on the level of the ligno-suberous stratum.

Broussonetia papyrifera Willd.

In Broussonetia papyrifera, the meristematic action is very forceful at the base of the leaf whose tissues, as far as the arrangement of the new partitions is concerned, reveal the aspect of those of Morus nigra [ss, Figure 34); in Broussonetia, however, as in the type Paulownia imperialis, to which we are quite close now, this meristematic region is not yet cellulosic at the moment the leaf falls. On the other hand, we have here a subcicatricial lignified stratum which is not at all thick.

Ligno-suberization occurs after the fall, not at the expense of the primary tissue of the pulvinus below its subdivided region as in the case of Paulownia but entirely at the expense of the latter, without any overlap on the subjacent primary tissue.

As in the case of Morus nigra, the secondary scar cork is often accompanied by a very thick parenchymatous phelloderm.

The occlusion of the branching milk-bearing organs of this plant occurs in exactly the same fashion as in Morus nigra. I would like to refer the reader to the detailed study of this species presented earlier.

Periploca graeca L.

In this plant, the subdivisions are particularly numerous in the separating stratum where they are more or less regularly oriented transversally. Above this stratum we have a more or less thin subcicatricial lignified region.

As in the case of Broussonetia papyrifera, the ligno-suberous cicatrization lamina is differentiated only at the expense of the meristematic region of the pulvinus.

The branching milk-bearing organs of this species are blocked in the same fashion as those of Morus nigra although the finger-shaped partitions here are much less convex. In addition, their obstruction often remains in the first stage of that of Morus nigra, that is to say, only the two modified plugs of latex are found on either side of the separating stratum and there is no partition developing in the area where they are in contact.

Ficus Carica L.

The anatomical changes which occur in the base of this species are the same as in Broussonetia papyrifera. Very often, ligno-suberization appears, before defoliation, below and against the separating stratum in the small flat areas situated in the vicinity of the milk-bearing organs. This ligno-suberization reaches the rest of the meristematic stratum only after the leaf has fallen.

The cicatrization of the milk-bearing organs occurs in the same fashion as in Morus nigra.

Evonymus latifolius Scop.

In this species the meristematic region is not at all thick below the separating stratum; ordinarily it involves only three or four cell layers. Besides, E. latifolius is very much like the type Morus nigra in the sense that, although the ligno-suberous cicatrization is not, as in the former, complete at the moment the leaf falls, it has at least begun in the outside region of the pulvinus. This cicatrization, at that time, only involves the very small meristematic portion adjoining the separating stratum. The first-year cicatrization is completed after defoliation through the extension of the ligno-suberization toward the bottom in the primary tissue of the pulvinus.

The many macled cells, which exist at the level of this cicatrization lamina, are ligno-suberized like the elements of the adjoining parenchyma.

Chapter V. Species Related to the Type Diospyros virginiana

We will recall that this type differs from the earlier types by the presence -- below the separating stratum -- of a ligno-suberous lamina which is already characterized at the moment the leaf falls. This lamina is entirely formed at the expense of the primary tissue of the pulvinus without any prior subdivision.

Here are the species related to this type: Syringa Josikoea, S. persica, Xanthoxylon fraxineum, Ampelopsis hederacea, Negundo fraxinifolium, Rhus Cotinus, Rhus Coriaria.

Syringa Josikoea Jacq.

The petiole of this species, like the one of Diospyros, has an articulation marked by a stratum of very small cells very clearly outlining the upper extremity of the pulvinus.

The formation of the cicatrization lamina starts in the same regions as that of Diospyros and it progresses similarly although it appears a little later toward the end of August.

Syringa persica L.

S. persica differs from the preceding species only by virtue of the fact that the ligno-suberous differentiation in the pulvinus does not come as early [precociously]. This differentiation only appears toward the middle of September here.

Xanthoxylon fraxineum Willd.

This species and the following ones, which I tied in with the Diospyros type because of the state of cicatrization at the moment of defoliation, however, do not reveal any articulation at the base of their petiole, such as we would find it in the case of the former. Besides, the separation of the cells, during the fall of the leaf, is here preceded by the formation of a mucilage, as in the case of Amorpha fruticosa.

In Xanthoxylon, the petiole, above its point of insertion, reveals a swelling at whose base the separating stratum is established.

The surface of the latter (cs, Figure 63) forms a circular concavity in the cortical parenchyma while it rises all around the bundles. Its tissue is made up of one or two layers of cells of the pulvinus which do not differ from their neighbors in size but which often are split once or twice in advance.

The upper limit of the ligno-suberous lamina (ss, Figure 63) is quite noticeably parallel to the separating stratum, that is to say, it likewise forms a circular concavity around the bundles. Its lower surface is noticeably more concave because the thickness of its tissues is at a maximum halfway between the bundles and the outline of the pulvinus. This stratum is not as homogeneous as that of Diospyros virginiana and we only have lignification therefore in a thin region of its upper part. Furthermore, there are several layers of sacrificed parenchyma which separate it from the separating stratum and the latter is topped by a subcicatrical lignified stratum (rs, Figure 63) consisting of three or four cell layers.

In the case of this Xanthoxylon, ligno-suberization appears toward the end of August in the region of the cortical parenchyma that is halfway between the bundles and the edge of the pulvinus, that is to say, in the region where the scar stratum will reach its maximum thickness. Later on, a short time before defoliation, the separating stratum developes and this is followed by the lignification of the tissues above it.

The vessels are blocked especially by thalli developed before the leaf falls.

The scar cork, which grows across the entire pulvinus during the second year, begins to appear opposite the thickest region of the ligno-suberous lamina. It grows across the bundles quite directly by the same process as in Aristolochia Sipho. It is similar to the periderm of the stem, that is to say, like the latter, it reveals a strong lignified thickening on the outside walls of its cells; this thickening consists of neatly stratified cells which almost entirely block the cell cavity.

Ampelopsis hederacea Michx

As in the case of Diospyros virginiana, Ampelopsis does not have a lignified region above the separating stratum. The two or three layers which make up the latter are composed of cells that are not subdivided in advance.

The ligno-suberous stratum has essentially the same thickness everywhere. Here ligno-suberization begins much later than in the type, that is, around the end of September, but it starts also along the outside circumference of the pulvinus.

Most of the vessels here are obstructed by thalli developed before the leaf falls in the entire base of the petiole.

The crystal-bearing cells and the cells with the raphides, which are very numerous in this same region, get lignified walls when they are included in the ligno-suberous stratum.

Rhus Cotinus L.

The ligno-suberous lamina of this species differs very little from that of Diospyros; however, it is a little thicker in the external region of the pulvinus (ss, Figure 64) and, in addition, we sometimes note a few subdivisions here, all of which are found at its base. Finally, as in the case of Morus nigra, the suberization of this same region not only causes the formation of the cell film but also leads to the impregnation of a part of the rest of the walls.

The separating stratum (cs, Figure 64), like that of Alnus glutinosa, is very clearly outlined between the lignified region of the petiole and the ligno-suberous stratum of the pulvinus; it is likewise made up of two or three layers in the external region of the pulvinus and it has only one layer in its internal region. In this latter portion, dehiscence occurs due to rupture of the walls in the same fashion as in Aristolochia Sipho.

The primary cicatrization lamina forms around the beginning of September. The ligno-suberization of the elements of the parenchyma, which are forming here, begins against the bundles and grows from there toward the edges of the pulvinus. This differentiation, furthermore, progresses from the base of the lamina toward its top and, a short time before the leaf falls, reaches almost all of the bundles.

Among the many macled cells which are located in the petiole, those that are included in the primary cicatrization stratum get lignified walls.

Cicatrization of Secretory Canals

In Rhus Cotinus we have wide secretory canals inside the bast of the bundles (ca, Figure 64). There are three of this canals near the base of the leaf; one of them is located in each of the three groups of re-entering bundles. Before defoliation and at the time when ligno-suberization of the scar lamina begins to appear, the epithelial cells in each one of them lose their secretory function and become vegetative. They then grow toward the access of the canal whose inside diameter (opening) they soon block completely (th, Figure 65); however, their growth is unequal and some of them penetrate only to the center; the obstruction is then completed by the enlargement of their extremities. Many of these epithelial cells split in advance once or twice, parallel to the surface of the canal, before growing; but in that case the innermost daughter cell is the only one to show any considerable development (b, Figure 65).

(This tissue, which blocks the secretory canals, at the base of the petiole, is similar to the one which Miss Leblois reported ("Research on the Origin and Development of the Secretory Canals," An. des Sc. nat. Bot., 7th series, Vol VI, 1887, page 247) in other organs and in other plants inside similar canals. This author uses the term "thalli" for the cells composing it, pointing out quite correctly that their development is not entirely comparable to that of the thalli of the vessels since they are not forced to traverse any bordered pits.)

The proliferation of the epithelial cells here begins on the level of the ligno-suberous stratum and continues from there above and below it. The secretory canals are always filled up in this fashion, above the separating stratum, in the petiole, up to a slightly greater distance than below it (th, Figure 64). Very soon, the cells, which constitute veritable thalli, are jammed very closely together due to the reciprocal pressure so that the entire group, especially on the level of the primary cicatrization lamina, assumes the appearance of a parenchymatous tissue with polygonal cells; on the other hand, they usually leave more or less wide channels between them, above and below this lamina.

Once the obstruction of the secretory canal has thus been completed, the filling cells, before the leaf falls, take on the histological characterization of the tissues at whose level they are located; thus we see that they are lignified at the level of the lignified region of the petiole and that they are ligno-suberous (ths, Figure 66) on the level of the ligno-suberous lamina. Generally, however, the cells of these thalli keep their thin walls and differ quite clearly in this respect from those of the bast tissue near-by whose walls are thicker; the lignified portion of the walls here is rather thin.

Above the blocked region of the canal, in the petiole, the epithelial cells die like the other cells of the organ; below, in the pulvinus, they continue their secretory function.

At the moment of defoliation, the entire filling tissue, which is found above the separating stratum, that is to say, its largest portion, is carried away with the leaf; the other part cicatrizes the canal.

In the passage of the secretory canals, the generating zone which forms the scar cork develops due to the subdivision of the thalli (as shown in Figure 63, lic). Sometimes, when the ligno-suberization of the latter descends a little below the lower level of the ligno-suberous lamina in the neighboring tissue, the cork passes below this region and, because of this, describes a slight curve downward, in the same way as it does often cross the bundles.

Rhus Coriaria L.

At the base of the petiole of Rhus Coriaria, we have a swelling inside of which we find the axillary bud (the reader is here referred to Figure 82 which shows a similar arrangement of the base of the petiole in Robinia Pseudo-Acacia). In the upper leaves of the shoots, the swelling, all around the bud, blends with the stem except along an opening which is barely visible in the plane of the leaf and against the surface of the stem; in the other leaves, and especially at the base of the shoots, this opening is widened into a tangential crack; the upper edge of the swelling, however, continues to rest against the stem. In summary, the leaf, in all cases, does not appear to have an axillary bud.

A little above the insertion of the petiole -- and consequently at the base of the cavity containing the bud -- we then have the separating stratum and the cicatrization lamina.

The separating stratum reveals a concave direction downward and we find very few subdivisions here. Above it, we have a very thick subcicatricial lignified stratum.

The primary cicatrization lamina is quite clearly outlined below; it is ligno-suberous at its base and gradually becomes only lignified as we go up; it disappears at a rather great distance from the separating stratum, leaving an average of five to seven layers of sacrificed parenchyma between it and that stratum.

Contrary to what we reported in the case of the preceding species of the type Diospyros, this lamina is differentiated very late, in other words, a short time before the leaf falls; sometimes it is not completely differentiated when the leaf falls. The ligno-suberization of the elements here begins, around the beginning of October, in the same regions as in Rhus Cotinus.

Because of the late formation of the first cicatrization lamina, the differentiation of the separating stratum and later on the lignification of the elements of the petiole above the latter are always found to develop first.

The obstruction of the vessels developes here especially due to the numerous thalli which have grown here before the leaf falls.

The secondary scar cork is very thick and grows across the bundles, following the same procedure as in Aristolochia Sipho. Sometimes, especially in the vicinity of the surface of the pulvinus, the zone that generates this cork dies after having furnished a more or less thick stratum of cells. Below this dead region we have a variable thickness of parenchyma which becomes ligno-suberized; this happens most often after it has subdivided; then a new generating zone is reformed below; this zone obliquely connects the preceding scar cork to the periderm in a manner recalling our illustration in Figure 90 for Gymnocladus canadensis.

The leaf pulvinus is very prominent here. The scar forms a more or less regular ring around the bud which reveals an essentially pentagonal base. It surrounds it completely in the pulvini situated close to the top of the shoots and it surrounds it incompletely in the others (ci, Figure 67).

The terminal leaf scar occupies the end of the stem whose aborted vegetative tit it throws off laterally.

Secretory Canals

In Rhus Coriaria, as in Rhus Cotinus, we have big secretory canals in the bast of the big bundles of the petiole; in this species, however, we have six instead of three at the base of the organ.

The obstruction and the ligno-suberous cicatrization of these canals occurs in the same fashion as for those of Rhus Cotinus; the same is true for the crossing of the scar cork here (lic, Figure 68).

Negundo fraxinifolium Nutt.

The axillary bud of this species, like the one of Rhus Coriaria, is hidden in a swelling at the base of the petiole; in addition, however, the portion of the swelling which thus covers the bud forms, on the inside, a kind of spur which fits very tightly into a corresponding recess in the stem; this depression involves not only the cortical parenchyma of this organ but also its caulinary bast-ligneous system.

The formation of the ligno-suberous lamina begins in the external cortical parenchyma, halfway between the bundles and the circumference of the pulvinus; besides, it developes, as in Diospyros virginiana, before that of the separating stratum.

In Negundo fraxinifolium, and in some of the species which we have examined so far (Pyrus communis and Mespilus germanica, for example), the scar cork often appears before the winter below the ligno-suberous stratum; similarly, the cork formed at this time is always rather thin and has very thin walls. Besides, since most often there is no periderm on the stem during the first year, the sides of this cork end below the epiderm of the pulvinus, descending again a little downward at the expense of the subepidermal layer.

During the second year, the generating zone of the scar cork gives us a new stratum which is much thicker. In the few pulvini where this zone does not exist at the end of the first year, it differentiates at the beginning of the second year. In both cases the cork formed during the second year resembles the periderm of the stem. Each of its cells reveals a suberous framework (su, Figure 69) and a very thick, hard thickening (eps) on its inside half. Later the periderm of the stem, which forms at the expense of the deepest layer, will connect with it.

The leaf scar has the shape of a crescent more or less open toward the surface, on which we can distinguish three or four navels. The axillary bud is located inside and against the top of the crescent. The two scar crescents of one and the same node unite laterally, forming a more or less raised angle between them along the stem (ci, Figure 70). Above each of the scars we can see the depression of the surface of the stem into which fits the petiole swelling spur (emp); it extends in an arc from one end of the crescent to the other, above the bud.

Laticiferous Organs

We find articulated laticiferous organs in the bast of the bundles of Negundo; the cells of these organs are very long in the other parts of the plant but they are shorter at the base of the petiole. These milk-bearing organs, at the level of the ligno-suberous stratum, subdivide several times transversally before the leaf falls; the new cells formed by this subdivision are ligno-suberized like those of the neighboring parenchyma. I reported a similar fact in the case of Aesculus Hippocastanum. As in the case of the latter, the generating zone of the cork crosses them while subdividing them (L L_1, Figure 69). All the new partitions here are always transversal so that -- even when the cork is thick, such as at the end of the second year, for example -- we can still clearly recognize the file of peridermal cells derived from the laticiferous organ; this is even clearer when it is composed of cells that are much larger than those of the neighboring files. In addition, the cork formed by the subdivision of the laticiferous organs is histologically similar to that of the rest of the pulvinus.

Chapter VI. Species Related to the Type Morus nigra

In Morus nigra, as in the preceding type, the ligno-suberous cicatrization stratum is already finished at the time the leaf falls but the tissues of the pulvinus earlier underwent meristematic action; this stratum, by the way, is formed at the expense of these tissues.

Here is a list of species related to that type: Morus alba, Sophora japonica, Menispermum canadense, Chimonanthus fragans, Platanus occidentalis, Fraxinus juglandifolia, F. Ornus, Magnolia acuminata, Catalpa bignonioides, Juglans nigra, Celastrus scandens, Asimina trilobata, Aralia spinosa.

Morus Alba L.

Everything we have said earlier in the case of M. nigra, with respect to the changes that occur in the base of the petiole during the first and second years, also applies to M. alba; this occurs in the same order but about 15 days later.

The cicatrization of the branching milk-bearing organs in this species is likewise the same as in M. nigra.

Sophora Japonica L.

The petiole of Sophora japonica has a swelling at its base which, as in some of the case we studied earlier, conceals the axillary bud. The latter is very flat and this is why the swelling covers it without growing hollow in the form of a cavity which would contain it in the same fashion as in Gleditschia triacanthos (Figure 84).

The separating stratum forms a little above the insertion of the leaf, at the base of the swollen portion covering the bud.

The lignification of the elements of the petiole, above the separating stratum, involves a very thick region; at the time the leaf falls, this region is even thicker than the ligno-suberous lamina.

In Sophora japonica, the partitions in the pulvinus appear later than in Morus nigra, that is, toward mid-October. Moreover, the progress of scar differentiation is not the same here; it is first of all the layer of cells forming the separating stratum that subdivides many times; then this subdivision is propagated in the subjacent cells. Only later on do we observe the lignification of the tissues, above the separating stratum, and even later than that, a short time before defoliation, do we get the ligno-suberization of the meristematic stratum.

After the leaf falls, the first cicatrization lamina often becomes a little thicker as a result of ligno-suberization of the primary elements of the pulvinus below it.

Quite often, during the first year, as a matter of fact, the vascular thalli situated below the ligno-suberous stratum and primarily in the vicinity of the re-entry of the leaf bundles into the bast-ligneous caulinary crown, get considerably thicker walls and these walls are then lignified.

The scar cork -- unlike that of Morus nigra -- is not accompanied by phelloderm and ends rather abruptly against the epiderm without involving it in any way and without curving toward the bottom. Later on, the periderm of the stem, which is formed more deeply between the second and the fifth layers of the cortical parenchyma, connects with it.

The leaf pulvinus is very prominent and the scar is V-shaped (ci, Figure 71); between the branches of this V we have the bud which is very flat and which has very black flaky leaf-bud scales. At the top and at the two ends of the V we have three big fascicular navels. Starting from the lateral extremities of the scar and going on above the bud, we can see the very pronounced pouches of the cortical tissue of the upper internode; the side of the petiole swelling, which covered the bud (br, Figure 71), is supported against this pouch before the leaf falls.

As in the case of Rhus Coriaria, the vegetative aborted top of the shoot is pushed to the side and the axillary bud of the last leaf becomes terminal.

Menispermum Canadense L.

In this species, the base of the leaf is horseshoe-shaped around four superposed axillary buds (B, Figure 72) whose size increases as we go from the bottom to the top one. These buds are very flat and the first three (Figure 72) are covered with a swelling of the petiole, in the same way as the one and only bud of Sophora japonica; the fourth bud is in the open air and consequently appears to exist only in the axilla of the leaf.

The ligno-suberous lamina is not at all thick; its one special feature is represented by the fact that it grows not only across the constriction of the petiole (ss, Figure 72) but that it is extended beyond that point, into the petiole swelling, along its inside face, opposite the buds (lp, Figure 72). In this latter region it is made up of a group of a two to four layers of cells adjoining the epiderm which does not undergo any change.

The separating stratum (cs, Figure 72), which in this case is not of meristematic origin, is contiguous to the ligno-suberous lamina and likewise consequently is prolonged into the petiole swelling. Above it there is no lignification of tissues.

The arrangement just described means that, after the leaf falls, the ligno-suberous cicatrization stratum is prolonged, opposite the lowest three buds, by a thin lamina which covers them and which protects them during the winter; I have called this the leaf-bud scale lamella (lp, Figure 73).

(I used the term "leaf-bud scale" because it protects the buds during the winter and because it can be compared to the flakes of the same name. However, in using the term "lamella," I wanted to differentiate it quite definitely from the ordinary flakes whose origin is quite different. This is the kind of lamella that was found by Mr. Wiesner, G., " Investigations on Autumn Defoliation of Ligneous Plants," Sitz. d. k. Akad. d. Wissench. zu Wien, 1871, page 506, in the case of Philadelphus coronarius and by Mr. Mikosch, K., "Contributions to the Anatomy and Morphology of Bud Covers of Dicotyledonous Ligneous Plants," idem, 1876, page 751) in the case of Berberis and Robinia, which the latter author has given the name "Articulartegmente" /Joint covers/.)

Thus we see that, although the insertion of the petiole has the shape of a horseshoe inside which we find the buds, the fresh scar (ci, Figure 74) is almost circular and slightly cord-shaped in its upper portion and is topped by only one bud. On the other hand, the direction of the separating stratum above the pulvinus and the direction of this stratum in the swelling of the petiole are inclined against each other and toward the stem and this is why the surface of the scar is slightly folded in the form of a semi-circular groove (Figure 73).

In the cortical parenchyma of the petiole and of the stem of Menispermum canadense, we have enormous sclerites with very thick walls and with branching punctures in which the thickening and lignification of the walls begin rather late, around July. They are rarer at the level of the cicatrization stratum.

At the time when this stratum is differentiated, there are some sclerites which no longer contain any protoplasm or any apparent nuclei; these sclerites then do not undergo any change. The others, in which the nucleus and the protoplasm are still quite visible, may, on the other hand, reveal the following transformations. A few of them simply lose their content. The others split like the cells of the parenchyma of the pulvinus once, twice, or three times, depending on their size (a, Figure 75). The new partitions thus formed remain thin and do not acquire any bordered pits but they become lignified like the walls of the mother cell. In addition, the daughter cells thus formed may -- although rarely -- be covered by a suberous film (sub, Figure 75) which penetrates to the bottom of the branching bordered pits, just as it happens in the cells of the neighboring parenchyma.

What I have just said with respect to the sclerites of Menispermum canadense applies to the majority of them, that is to say, to those which already have very thick walls at the beginning of the differentiation of the cicatrization stratum. It sometimes happens, however, that some of these enormous cells destined to form sclerites at that time are still in the beginning stage of their differentiation; their walls still have the same thickness as those of the neighboring tissue and they are cellulosic or they are simply equipped with a very thin lignified thickening. After that they split many times in a wide variety of directions, forming a parenchymatous tissue which takes on the histological characterization of the neighboring tissue. We can however still recognize the cells derived from this subdivision by the fact that their size is a little greater than that of the elements of the enveloping parenchyma. In addition they constitute a group which is always surrounded by the wall of the mother cell; this wall, as I indicated earlier, might already contain a beginning of the lignified thickening at the time the subdivision or partitioning starts.

In the elements of the ligno-suberous stratum near these sclerites, the new partitions very often run parallel to the walls of these sclerites.

Let us go back now to cicatrization. During the second year a thick scar cork develops below the ligno-suberous stratum; this thick scar cork, however, does not extend into the leaf-bud scale lamella.

Very often we have a second cork forming near the outside of the pulvinus; this second cork runs obliquely to the first and reminds us of the one in Rhus Coriaria; however, the parenchyma intercaleted between them does not undergo any lignification here.

In almost all cases, the zone that generates the scar cork at the same time produces a thick phelloderm. The cells of this phelloderm are parenchymatous and they are strongly amyliferous; after growing longitudinally, each of them may subdivide transversally once or twice; in this fashion we can count as many as 15 layers of phelloderm in certain pulvini; these layers of phelloderm are formed either directly by the generating zone or after the subdivision of the cells derived from this zone. In the region furthest away from the generating zone [in the most distant region of the generating zone], these cells are found further and further apart in a more or less angular pattern; they become quite roundish although they continue along a longitudinal file.

When the buds in the axilla of the leaf abort during the second year, their scar is closed by a thick cork which continues almost directly that of the leaf pulvinus. In this case, the phelloderm which accompanies it is likewise very much developed opposite the buds and continues that of the leaf scar which, at that time very thick on the side of the buds, gradually diminishes toward the outside of the leaf pulvinus where it ceases to exist. On the other hand, when all of the buds or at least the lowest one of them remain dormant, the scar cork does not extend beyond the axilla and the corresponding phelloderm has its maximum thickness in the center of the pulvinus and extends along all of its circumference.

During the second year, the leaf-bud scale lamina, which we earlier saw covering the lowest three buds, splits longitudinally under the influence of the diametral growth of the stem or of the axillary shoot, if it produces one.

Chimonanthus Fragrans Lindl.

The ligno-suberous lamina here includes only four or five layers of cells. In contrast to what we have in Morus nigra, the cell partitions here appear first of all in the internal cortical parenchyma of the pulvinus and against the bundles; they are, furthermore, less and less numerous as we go from the base of the scar stratum toward the separating stratum.

The lignification of the tissues of the petiole, above the separating stratum, involves an average of four or five layers of cells.

Platanus Occidentalis L.

At its base the petiole has a swelling which houses the axillary bud, as in the case of Rhus Coriaria.

The changes which occur at the base of the petiole are the same as in Chimonanthus fragrans. The lignification of the tissues, above the separating stratum, is, however, much less accentuated, as in the case of Morus nigra.

After the leaf falls, the ligno-suberization of the elements of the bundles often descends very low inside the leaf pulvinus.

The scar cork, which develops during the second year, grows across the entire pulvinus; sometimes, however, when the hard bast of the bundles is very thick at the level of its formation, this cork does not manage to grow across it and descends more or less deeply into the pulvinus, forming a sleeve around it. It then looks very much like the cork we described during the second year of Robinia hispida (lic$_2$, Figure 83).

The leaf scar forms a tight pentagonal band almost completely surrounding the bud; it is wider opposite the angles [corners] in which we find the navels (ci, Figure 76). As in the case of Rhus Coriaria, the axillary bud of the scar becomes terminal at the top of the shoots.

Fraxinus Ornus L.

The cells of the ligno-suberous stratum split rather early, in August, as in the case of Morus nigra; however, the ligno-suberization of the elements of this lamina occurs only around mid-September and it is preceded by the subdivision of the separating stratum as well as by the differentiation of the subcicatricial lignified region.

The secondary scar cork is not at all thick and, like the periderm of the stem, each of its cells (lic, Figure 77), has a thin suberous framework (su) which is reinforced (doubled) by an internal cellulosic thickening (cel) which is likewise not very thick. Opposite it there almost always develops a phelloderm (ph) as in the case of Menispermum canadense; this phelloderm may include as many as 12-15 layers at the level of rupture of the bundles.

Fraxinus Juglandifolia Lamk.

In this species the cicatrization lamina is thicker than in F. Ornus; here the partitions are, moreover, less numerous and they appear much later, toward the end of July. Besides, as in the case of Morus nigra, the division of the cells is followed almost immediately by their ligno-suberization.

We may also have a phelloderm below the zone that generates the scar cork but it is always less thick than in the case of Fraxinus Ornus and it includes four or, at most, five layers of cells.

Asimina Trilobata Dun. and Magnolia Acuminata L.

The ligno-suberous stratum is differentiated a short time before the leaf falls, around the end of September; nevertheless, it reaches the bundles almost completely before the leaf falls.

There is no subcicatricial lignified stratum and the separating stratum consists of two layers which most frequently are subdivided only in the external region of the petiole.

At the end of the second year, the secondary scar cork has a thickness of only two or three layers; it is not accompanied by phelloderm.

These secreting cells -- which generally are widespread throughout the cortical parenchyma of the stem and the petiole -- are rare at the level of the ligno-suberous lamina. They do not undergo any change of a cicatricial nature inside this lamina; their wall remains cellulosic and their content dries out.

Catalpa Bignonioïdes Wal.

In this Catalpa, the ligno-suberous lamina, which exists already at the time the leaf falls, is very thick, at least with respect to the lamina in the previously mentioned species; its size turns out to be in a direct ratio to the great width of the insertion of the petiole. The partitions here are still numerous in the external region of the petiole where the cells composing it are big; they are much less numerous in the internal region where the cells of the parenchyma are very small.

There is no lignification in the tissues above the separating stratum.

We know that the bundles are distributed, in the base of the petiole, on the pattern of an almost complete circle; the biggest among them are located in its external region. Around the three or five biggest bundles, the ligno-suberous stratum, which invades them almost completely a little before the fall of the leaf, is almost always thicker than anywhere else; besides it rises very high in the petiole (ss, Figure 80), forming one or more cones which envelop all of these bundles together or each one of them. The separating stratum follows the upper limit of this ligno-suberous lamina and as a result of this the partitions, which constitute and which are always parallel to its direction -- in the raised region around the bundles -- turn out to run considerably oblique and sometimes even completely longitudinal.

This prominence of the separating stratum and of the ligno-suberous lamina around the bundles produces the following situation after the leaf falls: in the external region of the leaf scar, which is elliptical (ci, Figure 81), we then either have a single big conical crest (em) or several smaller ones which are more or less widely joined together by their base. On the largest scars -- that is to say, on those in the middle region of the shoots -- these kinds of thorns may protrude as much as 4 mm above the surface of the scar.

I did not observe anything in the constitution of the bundles in this region that might explain this particular feature of the ligno-suberous stratum. Perhaps it develops under the influence of the lignified marrow of the stem which, itself, in some points advances into the base of the pulvinus (m, Figure 80), along the inside of the leaf bundles in this region. It seems, as a matter of fact, that its presence prevents the cicatrization lamina from transversally cutting the base of the leaf and it seems that it forces it to move up parallel to its surface.

The ligno-suberization of the elements of the pulvinus appears in many points at the same time, toward mid-September. Around mid-October the separating stratum differentiates and the vessels are filled with thalli.

The scar cork is not at all thick here. At the level of the protrusions of the ligno-suberous stratum, it follows the lower boundary of this stratum and as a result of this describes a curve at whose top it cuts the bundles.

Juglans Nigra L.

In J. nigra, the meristematic partitions exist only in the lower portion of the ligno-suberous lamina. The separating stratum is formed here at the expense of the cells of the petiole which have not subdivided earlier.

The ligno-suberization of the cells of the pulvinus occurs toward mid-September. The scar cork is very thick and finds it very difficult to grow across the hard bast when the latter extends all the way to its differentiation level.

The crystal-bearing cells are extremely numerous in the entire cortical parenchyma of the plant and especially in that of the pulvinus, below the cicatrization strata. Those that are inside the primary scar lamina are ligno-suberized like the other elements of the cortical parenchyma.

Celastrus Scandens L.

Here everything happens the way it happens in the case of Morus nigra but we do not have any subcicatricial lignified stratum here and the ligno-suberization of the pulvinus reaches almost all of the bundles before the leaf falls. The separating stratum most often describes a slight curve downward as it moves across the bundles.

Aralia Spinosa L.

Between the separating stratum and the primary scar stratum we have a medium stratum of two to four layers of sacrificed parenchyma.

As in some of the earlier species, the partitions in the ligno-suberous lamina are more numerous in the lower portion.

The cortical parenchyma and the bast of the bundles contain numerous secreting channels. Some time before defoliation, those in the base of the leaves are filled with gummy lignin. This obstruction occurs first of all at the level of the ligno-suberous stratum; but it descends a little below this stratum when the latter extends up to a rather considerable distance above it, in that part of the leaf which is going to fall. In other words, the gummy lignin is produced here in the same region as the thalli inside the channels in the case of Rhus Coriaria and Cotinus (th, Figure 64). As for the elongation of the epithelial cells, such as we described it in these latter species, we can say that it occurs only sometimes in A. spinosa and then only at the lower level of the ligno-suberous stratum where the partitions of this stratum are most numerous. But this elongation, preceded by several subdivisions (c, Figure 79), is always arrested early by the appearance of the gummy lignin (lig) inside the canal. During the second year these secreting canals are constricted under the influence of the scar cork which eventually winds up traversing them completely.

Chapter VII. Species Relating to Type Aesculus Hippocastanum

We recall that this type differs from the two preceding types, Diospyros and Morus, by the fact that the scar stratum here is already equally formed before defoliation and is made up only of a secondary cork.

I found very few species that are related to this type: here they are: Aesculus rubicunda and parviflora, Salix caprea and repens, Populus alba, Viburnum opulus and Lentago, Sambucus nigra and racemosa.

Aesculus Rubicunda Lodd. and Ae. Parviflora Wall.

In these two species the modifications which occur at the base of the leaves before they fall and those which follow the fall of the leaves are the same as in the case of Ae. Hippocastanum. However, in Ae. parviflora, the formation of scar cork begins in August, instead of July.

Salix Caprea L. and Populus Alba Link.

In these two species, the scar cork, already formed before the fall, has essentially the same thickness throughout the entire width of the pulvinus. It is in direct contact with the separating stratum and the thin ligno-suberous region, which tops it in Aesculus, is completely absent here.

We no longer observe any trace of lignification above the separating stratum.

The progress of differentiation of the scar cork is not the same as in the Aesculus types where it is formed primarily across the cortical parenchyma and continues for a long time without connecting with the periderm of the stem. On the other hand, in S. caprea, the cork begins to differentiate along the circumference of the pulvinus; besides, it appears only toward the middle of September, in other words, much later than in the case of Aesculus Hippocastanum.

At the moment the leaf falls, this cork is histologically constituted like the cork of the stem, that is to say, its cells have thin walls, except in the vicinity of the generating zone where they have a strong suberous thickening on their outside walls.

Salix Repens L.

This species differs especially from the preceding Salix caprea by the fact that its scar cork is not as thick and by the fact that they thalli are less frequent in the vessels before the leaf falls.

Sambucus Racemosa L. and Sambucus Nigra L.

At the moment the leaf falls, in both of these species, the scar cork exists only in the external region of the pulvinus whereas it is topped by two or three layers of lignified parenchyma in its internal region. As in the case of Salix caprea, there is no subcicatricial lignified stratum here.

The process of differentiation of the scar cork is the same as in Salix caprea but, in contrast to what we have just seen for this species and the preceding ones, this cork stops around the bundles; it no longer climbs up toward the petiole but this time descends lower and lower toward the pulvinus. It is not as thick in S. racemosa as in S. nigra.

Viburnum Opulus L.

At the moment the leaf falls, the scar cork, in V. opulus, is missing most frequently in the regions of the cortical parenchyma which are situated opposite the bundles; here it is replaced by a ligno-suberous stratum which is formed at the expense of the primary tissue and which has earlier undergone a slight meristematic action.

The cells of the separating stratum reveal numerous partitions; sometimes we have as many as six here which are oriented transversally in a more or less regular fashion. Between the separating stratum and the cicatrization stratum we have two or three layers of sacrificed parenchyma which are likewise heavily partitioned.

All of these different strata are differentiated quite a bit later than in the case of Aesculus Hippocastanum, that is, around the middle of September. Moreover, their order of appearance is different. The subdivisions of the separating stratum come first here; next comes the subcicatricial lignification of the separating stratum. A little later the subdivisions reach the subjacent layers of the sacrificed parenchyma and finally a generating zone appears further down which rapidly gives rise to the scar cork prior to defoliation.

Although the separating stratum here is thick, the actual separation occurs here only in its upper portion.

Viburnum Lentago L.

In this species, as in the preceding species, the cells of the separating stratum are heavily subdivided; this also applies to those which separate it from the scar cork; however, at the time of defoliation, the latter exists throughout the entire width of the pulvinus and even in the internal cortical parenchyma, opposite the bundles. Besides, the partitioned region, which corresponds to the sacrificed parenchyma of V. opulus, is lignified before the differentiation of the subjacent cork.

In this species we do not have a subcicatricial lignified stratum.

Chapter VIII. Species Related to the Type Forsythia suspensa

The type Forsythia suspensa is characterized by the presence -- at the time the leaf falls -- of a double cicatrization lamina in which a well developed ligno-suberous stratum tops a stratum of secondary cork. The ligno-suberous stratum is formed at the expense of the cells of the pulvinus which have not subdivided in advance.

Here are the species related to this type: Acer campestre, Rhamnus catharticus, Myrica Gale, Robinia hispida and Pseudo-Acacia, Gleditschia triacanthos.

Acer Campestre L.

The cork of the cicatrization lamina includes only three or four layers of cells; most often it cuts slightly into the side or edge of the bundles even before the leaf falls. The ligno-suberous portion also cuts into them but much more deeply.

Contrary to what we have in Forsythia suspensa, we do have lignification of tissues above the separating stratum -- although this lignification, to be sure, is not at all intensive.

The separating stratum is very thin and consists of one layer of cells that have split once or twice. The cells are then doubled on the inside here, as well as in all the other species which I related to the type Forsythia, as in the case of Amorpha fruticosa.

The scar strata differentiate very early, around the beginning of August. As in the case of Forsythia, the ligno-suberous portion appears first but its differentiation begins in the external cortical parenchyma in the vicinity of the bundles.

The crystal-bearing cells, which are numerous at the base of the leaf, here behave like their neighbors, in this respect recalling those of Alnus glutinosa (Figure 50).

In the bast of the bundles of Acer campestre we have a few rare articulated milk-bearing organs. At the level of differentiation of the scar cork, these milk-bearing organs split transversally and contribute to its formation (1a, Figure 78).

The cicatrization of the vessels here occurs primarily through the thalli which develop before defoliation throughout the entire base of the leaf.

Myrica Gale L.

The double cicatrization lamina is not at all thick here and, in the inside half of the pulvinus, the ligno-suberous portion exists ordinarily by itself. On the other hand, above the separating stratum, the lignification of the tissues is very intensive and involves a very thick region above all in the internal cortical parenchyma. We have several layers of sacrificed parenchyma below the separating stratum.

The ligno-suberous portion of the scar strata differentiates first around the middle of September but the cork appears below it even before it has been completely formed.

Rhamnus Catharticus L.

In this species the cicatrization lamina is very thick when compared to the diameter of the petiole and it has the same thickness throughout its entire extent; its lower limit is found exactly at the level of the axillary angle (corner) of the leaf. Its secondary cork is not thick but in its vicinity the cells of the ligno-suberous stratum sometimes have completely suberized walls.

The separating stratum is formed as a result of the subdivision of a single primary layer; this subdivision occurs once or twice. The subcicatricial stratum is not thick but it is heavily lignified.

The crystal-bearing cells inside the primary scar stratum are ligno-suberized like its other elements.

Robinia Pseudo-Acacia L.

As in some of the other species which we studied earlier, the petiole has, at its base, a hollow swelling consisting of a conical cavity which contains the two to four superposed axillary buds (B, Figure 82). Inside this cavity, the epiderm of the petiole is doubled by a secretory hypoderm comprising one or two layers of cells that are larger than the other parenchymatous elements of the organ. The lime oxalate crystals are abundant in the parenchyma at the base of the petiole swelling and especially in contact with the hypoderm.

The separating stratum is made up of one layer of cells which have earlier been subdivided transversally several times. It is located rather far from the leaf insertion and, as in Menispermum canadense, it grows not only across the constricted part at the base of the petiole but it also extends across its swelling, opposite the buds and a little above the secretory hypoderm I mentioned earlier; however, the thin lamella between it and the epiderm of this latter region here remains cellulosic (lp, Figure 82).

As a result of the position of the separating stratum, the axillary buds remain protected, during winter, by a leaf-bud scale lamella as in the case of Menispermum; here, however, this lamella, instead of continuing the ligno-suberous stratum, as in this latter case, prolongs the stratum of sacrificed parenchyma which, in effect, is very thick in Robinia Pseudo-Acacia.

Immediately after defoliation, the leaf scar, flanked by its two stipulary thorns, has a more or less trilobed shape, with three fascicular navels between which the surface rises in the form of a cone indicating the presence of the buds below the leaf-bud scale lamella. Above this scar we can observe -- in many pulvini -- another one which is smaller and which seems to represent the scar left over from a bud that aborted very early.

At the level of the ligno-suberous stratum, the cells of the articulated milk-bearing organs are shorter than elsewhere. Very frequently they subdivide and they become ligno-suberized like the neighboring elements. This latter change also occurs in most of the crystal-bearing cells.

The stratum of scar cork is completed, as in the type, during the second year. It grows directly across the wood of the bundles and the soft bast but it can cut only the hard bast which has a certain thickness at this level; very often, likewise, it will descend very low, inside the pulvinus, passing along the two faces of this tissue and gradually disappearing, as illustrated for the case of Robinia hispida (lic_2, Figure 83).

During the second year and sometimes during the first year, the leaf-bud scale lamella splits longitudinally and is gradually detached. This latter modification is speeded up by the vegetation of the buds, provided they do develop here.

At the end of the shoots, the abortion of the principal bud causes it to be pushed aside and this means that the leaf scar here appears to be terminal.

Robinia Hispida L.

The arrangement of the axillary buds here is the same as in R. Pseudo-Acacia. The scar stratum is a little thicker especially in the ligno-suberous portion.

The separating stratum crosses only the constricted portion of the petiole so that we do not get any leaf-bud scale lamella here and as a result of this the buds are visible after the leaf falls between the branches of the V formed by the scar.

The changes which these articulated milk-bearing organs and the crystal-bearing cells undergo are the same as those in the preceding Robinia. The arrangement of the scar cork across the bundles is likewise the same; this is also true of the sleeve which the cork forms around the hard bast (lic_2, Figure 83).

Gleditschia Triancanthos L. v. inermis

In this species we still have a swelling, at the base of the petiole, which covers the axillary buds ordinarily numbering five here -- however without creating a cavity in which to hold them (P, Figure 84).

The separating stratum, consisting of three or four layers of cells, sometimes subdivided a few times in advance, forms [illegible] above the most constricted region of the petiole (cs, Figure 84); it [illegible] penetrates into the base of the petiole swelling and here occupies a position which causes its inside edge to be located opposite the space between the two upper axillary buds.

The double cicatrization lamina, which exists at the moment the leaf falls, is very thick here. The ligno-suberization here is very intensive in the vicinity of the secondary cork, especially in the internal region of the petiole. Between the scar strata and the separating stratum we have a thickness of ten to twelve layers of sacrificed parenchyma.

In this particular species, the ligno-suberous portion is the first to differentiate, very early, toward the end of August; in addition, the cork forms below it even before its complete differentiation.

There are very few thalli developing in the vessels whose cicatrization is completed primarily by the gummy lignin. The latter appears already before the leaf falls and continues to grow afterward.

The leaf scar has a more or less trilobed shape (ci, Figure 85). Above it appears only one of the many buds that covered the petiole (B, Figure 85). I was able to observe, in effect, that the separating stratum was established at thellevel of the interval between the two upper buds so that, even though there may be no leaf-bud scale lamella as such, all of the lower buds are covered since they are hidden by the upper portion of the pulvinus. The latter, in reality, plays the role of the leaf-bud scale lamella.

The second-year scar cork (lic$_2$, Figure 86) has an origin different from that found during the preceding year. It is in contact with the latter only in the axillary angle from which it descends very obliquely, across the pulvinus, in order to link up with the periderm of the stem at a level quite a bit below that of the first-year cork. As in the case of Robinia hispida, it cuts the bast-ligneous bundles, except for the hard bast against which it curves downward (ls, Figure 86).

The portion of the pulvinus between the first-year cork and the second-year cork is lignified (s, Figure 86).

Chapter IX. Species Related to the Type Alnus glutinosa

As in the preceding case, this type is characterized by the fact that its pulvinus -- even before the leaf falls -- contains a double scar lamina; it differs, however, by virtue of the fact that the ligno-suberous portion of this double stratum is of meristematic origin.

In the species which have similar scar strata at the moment of defoliation, the suberization, in the ligno-suberous portion which is near the cork, almost always invades, in addition to the usual film, a more or less large portion of the rest of the cell walls.

Here are the species related to this type: Betula pubescens, Ptelea trifoliata, Ailanthus glandulosa, Maclura aurantiaca, Tecoma radicans, Rhodotypos kerrioïdes, Cladrastris tinctoria, Gymnocladus canadensis.

Betula Pubescens Ehrh.

Betula pubescens differs from Alnus glutinosa in that the subdivisions of the ligno-suberous portion of the scar strata here are less frequent; many cells in its upper portion do not even have it.

The subcicatricial lignified stratum is not at all thick. Below the separating stratum we find two or three layers of sacrificed parenchyma.

Ptelea Trifoliata L.

The cork of the double cicatrization lamina is usually absent here during defoliation in the internal portion of the pulvinus near the leaf bundles (Figure 89). The sacrificed parenchyma includes several layers of cells.

As in some of the preceding species, the petiole has at its base a swelling which conceals two axillary buds and whose upper edge rests on a pouch of the stem (Figure 89).

The separating stratum is differentiated a little above the most constricted region of the petiole; it consists of two layers which have earlier split once or twice.

On the inside surface of the petiole swelling, opposite the buds, we find a subepidermal stratum (cp, Figure 89), made up of two or three layers characterized by a dense protoplasm and numerous grains of starch. This stratum, which reveals the same characteristics as the separating stratum, is located in the extension of this latter stratum although it is not absolutely continuous with it; as a matter of fact, we have a short interruption, between the two strata, opposite the lower bud (a, Figure 89). The subcicatricial lignification (rs) occurs not only above the separating stratum but also above the specialized subepidermal layer; it is this layer which, when coming into contact with the epiderm at a certain point (a, Figure 89), interrupts the continuity of the two strata. The separation of the cells, which causes the leaf to fall, occurs only in the separating stratum and does not affect the specialized layer which is its prolongation; despite this rough outline of the formation of the leaf-bud scale lamella, the buds are thus exposed after defoliation.

(In a single one of the many specimens which I examined, the separation extended also into the specialized subepidermal layer and thus left a very thin leaf-bud scale lamella above the buds. This particular case supports the opinion expressed above, to the effect that the specialized stratum in reality represents a prolongation of the separating stratum.)

The secretory sacs, which are numerous in the cortical parenchyma of the plant, are less frequent at the base of the petiole. When one of these sacs is included in the ligno-suberous lamina, its epithelial cells are reached by ligno-suberization. The scar cork now grows around those of the apparatuses which it encounters on its way.

Ailanthus Glandulosa Desf.

The double cicatrization lamina, which exists at the moment the leaf falls, has a direction that is almost parallel to the axis of the stem and is therefore very oblique with respect to that of the petiole. Its thickness is considerable and is proportional to the very large leaf insertion surface. The cork here includes twelve to fifteen layers.

The separating stratum is made up of two or three rows of cells which very rarely are split before that.

The differentiation of the primary cicatrization lamina occurs very early, toward the beginning of August; ligno-suberization occurs here from the outside toward the inside of the pulvinus. The cork appears below the ligno-suberous stratum much later, toward the beginning of September.

During the second year, the cork grows across the bundles, describing a very pronounced curve toward the stem; in some pulvini, the top of the curve may even reach the region where the leaf bundles are joined to the caulinary bast-ligneous system.

Tecoma Radicans pr. sp. L.

The ligno-suberous portion of the scar stratum is thick; its cork, on the other hand, consists of only two or three layers.

The separating stratum is in contact with the double cicatrization lamina in the inside portion of the pulvinus; it moves away slightly in its outside portion. Made up of one or two layers subdivided transversally three, four, and even five times, it is therefore very thick; however, the separation occurs here always only between its two upper layers. The subcicatricial lignified layer, which tops it, is not thick.

During the second year, a new layer of cork forms across the pulvinus, at a certain distance below the secondary cork of the first year and parallel to it; this new cork layer cuts across the bundles. The parenchyma between the two corks remains cellulosic.

Rhodotypos Kerrioïdes Sieb. and Zucc.

The double cicatrization lamina which contains this species is not thick at the moment the leaf falls. Its ligno-suberous portion is heavily subdivided. Its cork, which consists of five to seven cell layers -- in contrast to what we saw in the preceding species -- is thicker in the internal region of the pulvinus and very often it reaches the outside edge of the latter only after the leaf has fallen.

The separating stratum does not reveal any subdivision and there is no lignified stratum differentiated above it.

Cladrastris Tinctoria Raf.

In Cladrastris tinctoria, the four or five buds, which are superposed and which are strongly pressed against each other, are completely hidden in a vast conical cavity of a basilar swelling of the petiole. The separating stratum develops at the base of this cavity so that the buds are exposed during winter.

The double cicatrization lamina is not thick and is very oblique toward the direction of the petiole. Its cork seems to be an almost direct continuation of the periderm of the stem as in the case of Aesculus Hippocastanum; its ligno-suberous portion consists of only three or four layers.

In almost all of the preceding cases, the gummy lignin, which completes the obstruction of the vessels begun by the thalli or which might even replace this obstruction, appears only rarely before defoliation. In Cladrastris tinctoria, this obstruction by gummy lignin is always an accomplished fact at the moment the leaf falls; this substance is found here over a considerable length of the bundles, after a variable height above the separating stratum all the way into the caulinary bast-ligneous system. Once in a while it is accompanied by a few thalli; however, among those which do exist here, at the level of re-entry of the leaf bundles into the stem, there are some which have acquired hard walls even before the leaf falls.

The leaf scar forms a ring more or less open on the inside around the buds which are covered by a thick felt of hairs and which are so strongly pressed against each other that they appear, when looked at from the outside, as a single whole

The terminal leaf scar of a shoot occupies its top and the aborted terminal bud is already pushed aside.

During the second year a new scar cork stratum forms; as in the case of Tecoma radicans, it develops a short distance below the first. It is this new stratum which grows across the bundles.

Gymnocladus Canadensis Lamk.

The double cicatrization of lamina, which exists at the moment of defoliation, is very thick, especially around the external circumference of the pulvinus and particularly opposite the bundles. Its cork consists of an average of five to eight layers while its ligno-suberous portion includes as many as twenty. In addition, it is topped by a thick sacrificed parenchyma averaging four to eight rows of cells.

The separating stratum is composed of two layers in which some of the cells are subdivided only once.

The scar strata and the separating stratum rise in the shape of a dome and grow across the bundles so that the leaf scar appears mamillated after the leaf falls.

During the time of defoliation the thalli are most numerous especially in the spiral vessels; on the other hand, the gummy lignin often appears in the secondary vessels on the level of the cicatrization strata.

The ligno-suberization of the parenchymatous tissues of the pulvinus begins very early, in July, and involves the external circumference of the pulvinus. Ordinarily, the secondary layer appears below the ligno-suberous lamina as the latter progresses across the base of the leaf; sometimes, however, it forms only after its complete development.

Toward the end of August, the double scar lamina is already in existence so that we can indeed find it at the moment of defoliation. The separating stratum and the subcicatricial lignified stratum which, in this species, is not at all thick, are differentiated sometime before that period, around the beginning of October.

During the second year a new scar cork stratum is formed; this new stratum doubles the preceding one in the internal region of the pulvinus but it moves away from it in its external region and descends very obliquely, connecting with the periderm of the stem which is lower than the cork from the preceding year [at a point lower than the cork of the preceding year] (lic_2, Figure 90). It is this second-year stratum which grows across the bundles, however, without cutting their hard bast against whose circumference it will make contact.

When the axillary bud aborts and is destroyed, a cork is formed below its scar and this cork connects with the second-year stratum of the leaf pulvinus, a little below the axillary angle (Figure 90).

Maclura Aurantiaca Nutt.

In this species, the cicatrization lamina, which exists at the moment the leaf falls, is not double in its entire extent. As a matter of fact, we can observe the cork here only in the external cortical parenchyma (lic, Figure 87) and the ligno-suberous lamina alone cicatrizes the internal cortical parenchyma.

The portion of the scar strata which, in the external cortical parenchyma surmounts the secondary cork, reveals a special arrangement of which I was unable to find another example among the many species studied. In contact with the scar cork it contains a region which is made up almost entirely of a sclerenchyma with very thick and spotted walls (s, Figure 88). (This very thick-walled sclerenchyma makes up a portion of the cicatrization lamina and recalls the one which, according to Brettfeld ("On Cicatrization and Leaf Fall," Pringsheim's Jahrbücher, Volume XII, page 133) constitutes all of the scar strata of most of the monocotyledons.) The rest of the primary cicatrization lamina -- in those of its parts which border on the separating stratum and on the epiderm of the pulvinus -- is normally ligno-suberized (ss, Figure 88). I might add that we often have a few isolated cells in the interior of the sclerenchyma; these isolated cells keep their thin walls (a, Figure 88). Although completely plunged into the sclerenchyma and isolated from the focus of ligno-suberous differentiation, these cells still undergo this differentiation; they also have a suberous film inside.

The cicatrization lamina begins to form toward the beginning of September. The thickening and the lignification of the walls, in its sclerenchymatous portion, occur at the same time as the ligno-suberous differentiation. The thin lamina of subjacent cork develops after the complete differentiation of this sclerenchyma.

The scar cork stratum is completed during the second year as it crosses the bundles and the internal portion of the pulvinus.

The numerous branching milk-bearing organs of the plant are cicatrized, in the same fashion as those of Morus nigra, by finger-shaped partitions (cl, Figure 88). They do not alter the nature of their walls as they cross the sclerenchyma; in addition, they are broken by the cork whose continuity is established at the point of rupture between their ends.

Chapter X. Species Related to Spiraea opulifolia

We recall that the periderm is located very deeply in Spiraea opulifolia. It develops, in contact with the bast, not only in the stem but also in the pulvinus where it folds back even around the bundles, forming a veritable sleeve [muff]. The scar cork is established inside this [illegible] sleeve, close to its base; as a result it crosses only the bundles; the cortical parenchyma of the pulvinus is sacrificed in its entirety, as is that of the stem.

All of the species which we summarized in this chapter also have a deep periderm and certain special features of cicatrization related to that location.

Potentilla Fruticosa L.

In the region where the two stipules are attached, well above its insertion, the petiole has a joint marked by a circular constriction (p, Figure 91). At the level of this constriction, the cells of the cortical parenchyma are very small and the transition from this region to the petiole and to the pulvinus -- which have larger cells -- occurs gradually although rapidly.

Below this joint, the pulvinus grows first of all into a club [sic; "massue" -- mass]; then it stretches out and is flattened around the axillary bud and the stem so that its base envelops all of these two organs almost completely.

The leaf bast-ligneous system which, in the petiole, forms a big strip in the middle, accompanied by two small lateral bundles, is reduced to a single mass in the vicinity of the joint and, besides, reveals a very pronounced constriction opposite these bundles. Further down it resumes its normal volume and once agains separates into three bundles whose course is marked on the outside by three crests which give the pulvinus a pyramidal appearance.

The periderm of the stem is situated deep down -- even deeper down than in Spiraea opulifolia; this is the case because it is located between the hard bast and the soft bast. It is seriated; that is to say, it has cellulose layers which are here and there separated by a suberized layer. (According to H. Douliot ("Research on the Periderm," Ann. des Sc. nat. Bot., 7th Series, Volume X, 1889, page 135), the periderm of the Cinquefoils is never seriated; this author probably did not study my species.) As in the case of Spiraea, it forms a sleeve which surrounds the bundles in the lower half of the pulvinus (mp, Figure 91).

The separating stratum is formed at the end of the long pulvinus, on the level of the joint of the leaf, a short time before defoliation. It consists of two or three rows of small cells of this region and there is no tissue reaction above or below it, before the leaf falls.

After defoliation, a slight lignification develops in the cortical parenchyma of the pulvinus. This lignification is not located immediately below the wound; it develops along the entire length of the pulvinus but especially in the vicinity of the bundles.

The ligno-suberization involves only the living elements of the bundles. Moreover, this modification, as well as the deposit of gummy lignin in the vessels, occurs, as in Spiraea, only inside the peridermal sleeve (g and g_1. Figure 91, indicating the limit of the deposit of this substance).

During the second year, the changes which occur in the leaf pulvinus are the same as in Spiraea opulifolia. The scar cork which likewise grows only across the bundles at the base of their peridermal sleeve, is not seriated; this is an occlusion cork all of whose cells are suberous.

Caragana Altagana Poir.

The constitution of the base of the petiole is the same as in Potentilla fruticosa. The peridermal sleeve of the bundles here occupies an identical position (mp, Figure 94).

In C. altagana, however, a thin lignified stratum (rs, Figure 94) is differentiated, before the leaf falls, above the separating stratum. In addition, the lignification which we were able to observe developing, in the cortical parenchyma of Potentilla fruticosa, only after the leaf falls, in this case turns up before the leaf falls (s, Figure 94). The upper limit of the tissues thus lignified is very neat; above it we have a more or less thin stratum of sacrificed parenchyma.

The changes which follow the fall of the leaf recall those observed in Spiraea opulifolia.

Calophaca Volgarica Fisch.

This species, like the preceding ones, has a joint (Figure 92) at the end of a rather long pulvinus. The periderm, however, is not located as deeply. In the stem it surrounds the central cylinder, passing a short distance from the isolated masses of the hard bast; in the base of the pulvinus it approaches this hard bast; it then even comes into contact with it, forming peridermal sleeves around the bundles (mp, Figure 92). The latter climb up very high, almost into the immediate vicinity of the joint of the petiole, and often they are even enlarged on the inside, below the sacrificed parenchyma, moving a little away from the bundles.

In the region adjoining the articulation, where the three re-entering bundles are united, they are surrounded only by a single peridermal sleeve which results from the fusion of the three preceding ones (mp, Figure 93). We also find two small stipular bundles at this same level (fst, Figure 93); they combine with the lateral re-entering bundles of the leaf a little above the base of the pulvinus; these two bundles do not have any peridermal sleeve.

The anatomical changes which precede and follow the fall of the leaves are the same as in Caragana altagana.

Symphoricarpos Racemosus Michx

As in the case of Spiraea opulifolia, the petiole does not reveal any articulation but the peridermal sleeve of the bundles is shorter here.

In the leaf, the cortical parenchyma of the pulvinus reveals very thickened and spotted walls which however remain entirely cellulosic. (I might point out here that the cortical parenchyma of the stem below the pulvinus looks the same although it is, in addition, heavily lignified.) Above the pulvinus it yields rather abruptly to a tissue whose walls are thin; the separating stratum develops a short time before the leaf falls at the level of transition, in the first layers with the thin walls, without any advance subdivision.

Before the formation of this stratum and at a very early stage, a ligno-suberous stratum is differentiated, below it, at the expense of the tissue cells with the very thin walls. In the bundles, the ligno-suberization occurs only after the leaf has fallen; then the wound surface develops up to the base of the peridermal sleeves.

Philadelphus Coronarius L.

At its base and on its inside face, the petiole has a not very noticeable swelling in which we find the axillary bud (B, Figure 95). In addition, it reveals, a little below its insertion, an articulation or joint indicated by a circular groove which is not readily visible and which passes over the swelling, above the bud. A longitudinal section shows -- at the level of this groove -- a stratum of two or three layers of small, flat cells with thin walls which are definitely different from the cells of the pulvinus and of the petiole and which recall those which we illustrated in Azalea sinensis (art, Figure 99). This stratum, specialized at a very early stage, is located at the base of the adult leaf and grows across the entire petiole, forming a line broken at an angle and turning upward. It is this stratum which, without any subsequent alteration, will constitute the separating stratum. There is no subcicatricial lignified stratum being differentiated above it in autumn.

As in the case of Symphoricarpos racemosus, the peridermal sleeve of the bundles remains short (mp, Figure 95); similarly, the ligno-suberous stratum is differentiated very early, around August. This stratum, which is contiguous to the separating stratum, consequently extends against the inside edge of the petiole swelling up to a point above the bud (lr, Figure 95). After the fall of the leaf, this results in a leaf-bud scale lamella which covers the latter in the manner of a candle snuffer [upside down funnel] and gives the surface of the scar a conical appearance (bc, Figure 96). Later on, under the influence of the diametral growth of the stem or the elongation of the bud into the shoot, this lamella regularly breaks up into three parts.

The crossing of the bundles by the second-year cork occurs in the same fashion as in Spiraea opulifolia.

Chletra Alnifolia L.

This species is even closer to the Spiraea type because of the deep position of its periderm in the stem and in the leaf pulvinus; however, the separating stratum is here developed excessively close to the insertion of the leaf and almost parallel to the surface of the stem (cs, Figure 97), so that the pulvinus here is remarkably short. As a result of this arrangement, the peridermal sleeve of the bundles here is barely indicated.

The subcicatricial lignified stratum cannot be found in this species; as for the ligno-suberous stratum, it exists only in the internal region of the pulvinus (ss, Figure 97) and, through its lower face, even makes contact with the periderm.

Among the very few crystal-bearing cells, which we can find in the cortical parenchyma of the pulvinus, those that are included in the ligno-suberous portion only undergo lignification; on the other hand, their cavity is often filled with gummy lignin around the crystal, as I described it for Amorpha fruticosa.

After the leaf falls, the pulvinus does not undergo any further changes during the first year except for the ligno-suberization of the living elements of the bundles and the deposit of gummy lignin in the vessels. During the second year, the scar cork forms across the bundles and closes the sleeve, as in Spiraea opulifolia.

Azalea Sinensis Lood.

Very close to its insertion the petiole reveals a joint marked by a circular groove that is not very easy to see. At that level the cells are clearly differentiated from those of the petiole and the pulvinus by their small size, the relative thinness of their walls, and their flat form (art, Figure 99); this differentiation occurs even before the petiole has developed completely. The separating stratum will form in autumn (cs, Figure 98) at the expense of two or three layers of this specialized tissue.

As in the case of Diospyros virginiana, the dissolution of the walls of the separating stratum, which leads to the dehiscence of the leaf, involves only their primary membrane.

As in the case of Chletra alnifolia, the separating stratum is very close to the surface of the stem which it almost continues. Here, likewise, the periderm is deep and is in contact with the bast; it is interrupted around the bundles, at the base of the pulvinus, without forming any sleeve. As in the case of Chletra alnifolia, we have a thin ligno-suberous lamina here before the leaf falls; this lamina, however, extends over the entire width of the pulvinus (ss, Figure 98); likewise situated against the separating stratum, it is in contact with the periderm only in its internal region and only opposite the bundles. Finally, the scar cork crosses the bundles only during the second year.

Ribes Nigrum L. and Deutzia Scabra Thumb.

These two species recall Azalea sinensis, except for the absense of the joint at the base of the leaf. However, the ligno-suberous lamina exists here only in the external cortical parenchyma; the periderm is in contact with the separating stratum in the internal cortical parenchyma.

Chapter XI. Species Related to the Type Hamamelis virginiana

We recall that the distinctive characteristics of this type consist in the fact that the first-year scar strata are removed during the second year due to the "revival of cicatrization" caused by the formation of a new separating stratum. This ties in with the case of the "marcescent leaves" whose fall is caused by similar revival.

I therefore combined here the several species that have both of these characteristics or only one of them.

Parrotia Persica A.M.

The fall of the leaves and the cicatrization of the wound occurs here in the same fashion as in H. virginiana.

During the second year, the revival of cicatrization, which, by the way, occurs in the same fashion, appears sooner than in this latter species, starting in February and during March. We also noted that, in this species, it occurs more rapidly in the pulvini above which a flower bud developed, although the development of this bud did not break the pulvinus. Perhaps this is due to the fact that the circulation and supply of nutritive substances is more considerable in the vicinity of the buds thus developed; this would mean that the separating stratum involved in this environment would differentiate faster.

The few marcescent leaves, which we encounter sometime in Parrotia persica reveal the same process of cicatrization and fall as those in Hamamelis virginiana.

Sorbus Aucuparia L., S. Aria Crantz. and S. Hybrida L.

The phenomena which precede and follow the fall of the leaves during the first year recall those of Hamamelis virginiana. However, the separating stratum reveals a broken surface at the level of the bundles similar to that of Spiraea opulifolia (cs, Figure 51). In addition, it develops at a distance from the axillary angle which varies with the position the leaf occupies on the shoot. For those at the top, this distance may amount to as much as 4 mm whereas for those at the base it may be reduced to less than 1 mm. The length of the pulvini therefore varies considerably depending on the leaves (Figures 100 and 101).

The ligno-suberous stratum, which forms only after the fall in the vicinity of the wound, reveals a lignification and a suberization which are not at all intensive; besides, it is not at all thick. In some cases, we note the beginning of the formation of the scar cork, before the winter, below and against the ligno-suberous stratum.

The changes which occur in the leaf pulvini, during the second year, recall those which we pointed in Hamamelis virginiana. The separating stratum involved in this revival always develops right at the base of the pulvinus and consequently very often far from the first scar lamina (cs_2, Figures 100 and 101). It forms in the same fashion as that connected with the autumn fall of the leaves in this same species, that is to say, due to transversal subdivision of one cell layer; however, its surface is perfectly level. We can then watch the development, above it, in the soft tissue of the pulvinus, of a lignified stratum similar to the subcicatricial lignified stratum which I pointed out above the autumn separating strata in most of the leaves (rsc, Figure 100). This stratum is differentiated even in the somewhat short pulvini whose live tissue, above the revival separation stratum, consists of no more than four or five cell layers (rsc, Figure 101).

Dehiscence, inside the separating stratum, ordinarily occurs first in the middle region of the pulvinus; more rarely it occurs in its lateral parts. In all cases, this dehiscence and the revival of cicatrization resulting from it occur progressively and slowly during the second year. These phenomena result in the replacement of the first scar with another one which is much closer to the stem.

The cicatrization of the new wound occurs in the same fashion as that of Hamamelis virginiana.

In the Sorbus studies, there is no marcescence of the leaves.

Quercus Hispanica L. and Q. Pedunculata Ehrh.

In these two species there are many more marcescent leaves than deciduous leaves. The transformations which occur in the pulvini of these two types of leaves during the first year are the same as those in Hamamelis virginiana; however, most often, the marcescent leaves do not reveal any trace of the autumn separating stratum at their base.

On the other hand, the revival of the cicatrization, during the second year, occurs only in the pulvini of the marcescent leaves, whereas in the others it is found roughly outlined here only exceptionally.

The base of the petiole, especially in Quercus pedunculata, contains isolated sclerites or groups of sclerites. These do not undergo any modification when they are contained inside the ligno-suberous stratum.

(It was certainly these sclerites which Ledeganck, K., ("Histochemical Research on the Autumn Fall of Leaves," B. de la Soc. roy. bot. de Belgique, Volume X, 1872) mentioned in Q. Robur as example of diffuse suberification. Here is what he has to say about this (page 158): "In the green parenchyma we can see disseminated several transparent points which indicate the existence of one or more cells with thick walls whose cavity has been almost entirely obliterated"; further on he has the following to say about these same cells (page 159): "The use of the sulfuric iodine-containing reagent gives the same hue to the thickened cells disseminated in the parenchyma and to the stratum of the periderm; without in any way prejudging their physiological functions or the origin of these cells, we can thus consider the thickening of their walls as the result of a deposit of suberous substance inside their cavity; this formation replaces the stratified periderm, such as we have observed it so far." The use of the differential reagents of lignin and suberin, such as Phloroglucin and tincture of alcan, etc., showed me that the thick walls of these elements are not at all suberous but simply lignified.)

Cornus Mas L.

During the first year, the fall of the leaf and the cicatrization of the wound reveal all of the characteristics of the type Paulownia imperialis.

The leaf pulvinus is more or less elongated, like that of the Sorbus and the modifications which occur in their base, during the second year, here also reveal the same features; but the revival of cicatrization here occurs sooner, at blossoming time, which, as we know, is very early. In addition, it often happens, in the pulvini at the base of the shoots, that the subcicatricial lignified layer is absent because the revival separating stratum is developing in contact with the first scar lamina whose base is at the level of the axillary angle.

Cornus Sanguinea L.

In this species, the first-year ligno-suberous stratum resembles that of the type Diospyros virginiana and occurs like it, before the leaf falls.

The revival of cicatrization and the changes which follow are the same as in C. mas; however, below the scar cork closing the new wound, we often get a parenchymatous phelloderm with a thickness averaging five to six layers.

Cotoneaster Melanocarpa Lood.

Cotoneaster Melanocarpa reveals the same variations of the Hamamelis type as the Sorbus but the revival of cicatrization here is less regular and the separating stratum, which causes it, instead of developing right at the base of the pulvinus, forms between it and the first cicatrization lamina. Moreover, it does not always grow across the bundles, especially in the middle bundle, so that the latter are broken very slowly and so that the revival occurs more or less belatedly, sometimes only during the third year. As a result of this, the new scar stratum is completed almost always before the first leaves fall (lic_2 and ss_2, Figure 102).

The final scar stratum includes a ligno-suberous lamina which is quite thick and which extends just to the base of the pulvinus; it also includes a secondary cork which doubles [reinforces] it.

Sometimes the first revival separating stratum develops only incompletely; we then get a second stratum which is complete and further down. Above each of them, a thin lignified stratum is differentiated. The final double cicatrization lamina then develops below the lowest separating stratum, that is to say, below the one that will produce the revival.

Carpinus Betulus L.

This species has deciduous leaves and marcescent leaves. The changes which occur here at the base of the former recall those of Hamamelis virginiana; the subcicatricial lignified stratum here, however, is thicker and consists of about six to eight cell layers.

The revival of cicatrization involves a process that differs very little from the one we described so far.

At the beginning of the second year, a scar cork develops below and against the first-year ligno-suberous stratum; but the first cells formed by its generating zone, instead of remaining flat and suberizing like the following layers, are very much elongated in the longitudinal direction; their walls remain cellulosic and, in addition, become very thin and very fragile (a, Figure 103). It is these delicate layers which act as the revival separating stratum and dehiscence occurs here, from the outside of the pulvinus toward the inside, due to the rupture of their walls, following the procedure employed by the autumn separating stratum of the leaf of Aristolochia Sipho. The detachment of the first scar strata occurs very slowly during the entire second year and often ends only during the third year. The growth of the scar cork (lic, Figure 103), above the new dehiscence surface, is independent of the greater or lesser speed of revival.

Except for the absence of the autumn separating stratum, the changes which appear in the pulvini of the marcescent leaves are the same as those which we described in those of the deciduous leaves. However, the first-year ligno-suberous stratum here appears later and develops gradually as the leaves die. Furthermore, the revival of cicatrization, which at the same time causes the marcescent leaf to fall, here occurs more rapidly; the action of the separating stratum here is aided by the weight of the leaf and the action of the wind.

Fagus Sylvatica L.

In Fagus sylvatica, the changes, which occur at the base of the deciduous leaves and in the marcescent leaves, recall those of Carpinus Betulus, with this difference: at the base of the deciduous leaves, the ligno-suberous lamina is differentiated before the leaf falls.

Staphyllea Trifoliata L.

This species does not have any marcescent leaves. As in Carpinus

Betulus, the first layers of second-year scar cork remain cellulosic but their cells do not extend as much in the longitudinal direction. The ruptures which here cause the revival of cicatrization occur in the same manner; however, they occur more slowly during the following years.

We might add, however, that the revival of cicatrization sometimes does not occur at all because, in this case, the first layers of scar cork have become suberized like the others.

Staphyllea Pinnata L.

The conditions under which the revival of cicatrization of S. pinnata occurs are roughly the same as those in S. trifoliata; nevertheless, it occurs in a very inconstant and very incomplete fashion. The first layers of the scar cork may remain cellulosic only very rarely and then only in the lateral parts of the pulvinus. This means that the separation, when it does come about, remains local and that the revival of cicatrization is never general.

Summary of Part I

In our study of the phenomena connected with the fall of leaves there are two types of facts which we must consider: the detachment of the organ and the cicatrization of the wound.

Detachment of Leaf

Separating Stratum

The leaf is detached by means of a mechanism involving a special stratum, the separating stratum, which exists in all cases and which ordinarily is differentiated a short time before defoliation.

This stratum develops most often some distance above the axillary angle of the leaf and rarely almost at the level of that angle (Ribes nigrum, Deutzia scabra, Azalea sinensis, etc.) or at a great distance above it (Sorbus, Cotoneaster melanocarpa, Calophaca volgarica, etc.).

As a general rule, the hard tissues are particularly reduced in size at the base of the petioles, in the region where the separating stratum will develop. The walls here are less thick and the only lignified elements which we find here are the ligneous vessels. Frequently, moreover, the entire bast-ligneous system is more or less constricted (Aristolochia Sipho, Potentilla fruticosa, Caragana altagana, etc.).

The separating stratum is ordinarily quite noticeably perpendicular to the axis of the petiole but it may also be very oblique toward that axis and it may be almost parallel to the axis of the stem (Aesculus, Deutzia scabra, Ribes nigrum, etc.). In the majority of cases it reveals a level surface. There are exceptions, however: sometimes it is more or less concave toward the stem (Rhus Coriaria, Xanthoxylon fraxineum, etc.); in Sorbus and in Spiraea opulifolia it forms a broken surface whose angle is, instead, turned upward. Whether it is level or not, it almost always rises a little as it grows across the leaf bundles so that, after defoliation, the fascicular navels are slightly in relief. This rise is quite exaggerated at the level of the external bundles of Catalpa bignonioïdes where the navels of these bundles form, on the scar, one or more conical teeth. In Gymnocladus canadensis, there is a less pronounced rise leading to the surface of the mamillated scar.

The separating stratum is always distinguished from the neighboring tissues by the fact that it reveals the characteristics of a strongly vegetative tissue. Here the protoplasm is denser, the starch is more abundant, and the cell turgescence is stronger.

Contrary to opinions accepted in the past, it is not always of meristematic origin, that is to say, formed by a cell subdivision. There are, as a matter of fact, many species where it consists of nonsubdivided cells

(Aristolochia Sipho, Amorpha fruticosa, Aesculus Hippocastanum, Forsythia suspensa, etc.). In other cases it is formed only in part as a result of cell subdivision (Gymnocladus canadensis, Alnus glutinosa, Rhus Coriaria, etc.). Nevertheless, there are species where it is entirely derived from a cell division (Morus nigra, M. alba, Viburnum Opulus, V. Lentago, etc.). In the latter case, the number of subdivisions is highly variable; it generally involves two or three per cell but we may have as many as four or five (Paulownia imperialis, Morus nigra, etc.) and there may also be as many as eight or nine (Spiraea opulifolia).

Ordinarily -- when the separating stratum is thus derived from cell subdivisions -- the latter are oriented almost regularly and parallel to the direction of the stratum although they are small in number; in the opposite case, their orientation is very irregular.

The separating stratum grows across the leaf bundles, taking over their parenchymatous cells and avoiding only the ligneous vessels and the sieve-like tubes. When it is of meristematic origin, the subdivisions here are less numerous than otherwise and they are oriented more regularly.

Very rarely the separating stratum is made up of only one layer of cells (Aristolochia Sipho); most often it involves two or three when it is formed without prior cell subdivision and it consists of a larger number in the opposite case. In some species its thickness is not equal at all points; thus it may consist of several layers in the entire external region of the petiole and only a single layer in its internal region (Alnus glutinosa, Rhus Cotinus, etc.)

Ordinarily there is nothing at the base of the adult leaf that would indicate the future position of the autumn separating stratum. In some cases, however, the leaf has, at its base, a joint marked by a circular constriction or a groove at whose level the parenchyma cells are very small and gradually, although rapidly, make the transition to the largeer cells of the petiole and the pulvinus. The separating stratum is thus differentiated through this joint and generally at the expense of its most constricted region (Hippophae rhamnoïdea, Crataegus monogyna, Caragana altagana, etc.). In Diospyros virginiana, the Syringa, Azalea sinensis, etc., we can observe a special feature of the same kind although it is even more pronounced here. The stratum of small cells, located at the level of the joint, consists of only three or four layers which neatly and abruptly separate the leaf from its pulvinus. It is this entire stratum, already indicated before the complete development of the leaf, which in autumn is transformed into the separating stratum, thus recalling what Brettfeld described for the monocotyledons.

Leaf Detachment Mechanism

Except in the few special cases we will discuss later on, the leaf is detached as the cells become separated from each other inside the separating stratum. In this process, the cell walls here are transformed into a pecto-cellulosic mucilage -- which, by the way, is primarily cellulosic here; ordinarily this change involves the entire wall with the exception of a thin stratum adjoining the cell cavities. The mucilaginous portion is first of all slightly swelled, especially in the upper layers of the stratum; after that it is finally dissolved under the action of the cell juice [sap] into [in] the cells which will border on the dehiscence surface. These border cells are thus isolated from each other; their protoplasm is from then on enveloped only by the thin, unmodified stratum of the original walls.

The size of the mucilaginous portion of the walls varies with the thickness of the latter; it is ordinarily very small when the separating stratum, derived from a cell subdivision, has only thin walls. In some cases however (Forsythia suspensa, Diospyros virginiana, etc.), the mucilage is poorly developed although the walls may have a certain thickness; this is the case because only the primary membrane of the cells is dissolved here.

In general, separation occurs inside the separating stratum in a rather regular fashion between two layers of its upper region and in a manner causing the majority of the cells of the stratum to remain attached to the pulvinus.

This separation produces a crack across the base of the leaf; the leaf now falls due to its own weight, provided it was not still helf by the vessels and the sieve-like tubes, although the resistance offered by the latter is soon broken due to the effect of the following phenomena. On either side of the dehiscence surface, the border cells grow longitudinally in the opposite direction, pressing against each other, so as to remove the leaf from its pulvinus. The resisting elements of the bundles cannot follow this growth and are subject to increasing traction which causes them to break and as a result of this the leaf, now no longer held by anything, falls due to the effect of its own weight.

When the separating stratum is made up of more than two layers, all of its cells contribute to bringing about the rupture of the last elements of the bundles in this fashion. In effect, all of them are more or less swelled; in this fashion, and even before the separation as such takes place, they produce a noticeable thickening in the entire stratum and they thus contribute in a noticeable fashion to the removal of the petiole from its pulvinus.

In most cases, dehiscence progresses from the outside toward the inside of the petiole; more rarely, it follows the inverse order (Koelreuteria paniculata, Gymnocladus canadensis, etc.); sometimes it begins at several points in the stratum at the same time (Paulownia imperialis, Hamamelis virginiana, Catalpa bignonioïdes, etc.).

Although, as I said above, the separating stratum and the weight of leaf are capable, by themselves, to bring about defoliation, we must add that the wind and the frost may noticeably speed up this process by triggering it even before the completion of the dehiscence crack. I might even add that the majority of leaves fall primarily due to the effect of these latter two factors.

In Aristolochia Sipho, the mechanism of leaf detachment differs from the mechanism which we have just described. The single cell layer which constitutes the separating stratum here grows very much in the longitudinal direction; the longitudinal cell walls here become very thin and delicate and they are gradually broken due to the weight of the leaf and due to the action of the wind and the frost. A similar structure may also be produced, although locally, in species subject to the first mode of defoliation, when a part of their separating stratum happens to consist of only one cell layer (Rhus Cotinus, Alnus glutinosa, etc.).

Subcicatricial Lignification

The vitality of the elements of the petiole diminishes rapidly above the separating stratum as the time for the fall of the leaf draws near and at the moment the leaf falls the protoplasm has disappeared. In some cases these are the only changes which we can observe in this region; more generally, however, the cells here also undergo a parietal lignification which begins a little after the appearance of the separating stratum. This lignification always decreases in intensity as we go up and the cell walls, which it involves, are not thickened in advance.

This lignified tissue, which I called subcicatricial because of its position, generally consists of only two or three layers. In some cases it may however be quite thick (Spiraea opulifolia, Tilia europaea, Corylus Avellana, etc.). In Spiraea opulifolia, it is furthermore the seat of cell subdivisions occurring before lignification.

Cicatrization

After the end of the season there is always a recovery of protoplasm vitality which appears as the first phase of the scar reaction; this happens in the pulvinus, as in the separating stratum; the recovery of vitality however is of lesser intensity at that time.

I. Cortical Parenchyma. Anatomical Characteristics of Scar Tissues

There are four defensive measures which the plant may use to cicatrize the parenchymatous tissues under the wound resulting from the fall of the leaf; these are the following: subdivision of the primary tissues of the pulvinus, ligno-suberization of these tissues (with or without deposit of gummy lignin in channels), their sclerification, or the formation of a secondary scar cork below them.

a. The primary tissues are subdivided along a more or less considerable stretch of the pulvinus, thus forming a stratum with variable thickness and position.

The new partitions are oriented in various directions in each cell; however, the transversal directioniis the most frequent one here, especially in the parenchymatous elements of the bundles. The cells, which are thus subject to meristematic action, do not undergo any diametral growth, that is, neither before nor after their division.

The intensity of subdivision is usually unequal throughout the thickness of the stratum involved; sometimes its maximum is located in the upper region and sometimes it is located in the lower region. We will come back to this peculiarity later on.

b. Ligno-suberization involves the primary tissue which did not earlier undergo the meristematic action which we just discussed; this ligno-suberization always operates in the following way. The cell walls are lignified without being thicker; this is followed by the addition of a very thin suberous film which covers the entire cell cavity, including the bordered pits, that is to say it develops in a discordant stratification on the preceding parietal strata.

I called this the "ligno-suberous stratum" because of the presence of lignin and suberin in this stratum of the pulvinus. These two substances are rarely equally distributed here and they are rarely distributed more or less uniformly over the entire thickness of the stratum (Diospyros virginiana, Forsythia suspensa). Ordinarily, the lignification, very intensive at the base, and clearly delimited, progressively decreases in intensity toward the upper part. The suberous film, on the other hand, reveals a great deal of uniformity in all cells and it is always more or less thin here; often, however, it is missing in the upper part of the stratum where we then observe only the last traces of lignification.

The ligno-suberization of the cells is always followed by their death.

In the region where the ligno-suberous lamina is differentiated, the intercellular channels are often absent or they are very small. In the rare cases where they still have a middle (average) inside diameter (opening), they are frequently obstructed by gummy lignin (Paulownia imperialis, etc.).

c. Cicatrization by simple sclerification of the elements of the pulvinus is very rare; I encountered it only in Maclura aurantiaca although even here it forms only a portion of the cicatrization lamina and then only in the external and lateral regions of the pulvinus. The cells of the pulvinus which constitute this hard part of the primary scar stratum get stronly thickened walls before these walls are lignified. This special feature of Maclura aurantiaca recalls the primary cicatrization of many monocotyledons which, according to Brettfeld, thus have a very thick sclerenchyma, however, over the entire width of their pulvinus.

d. The secondary scar cork is then connected all around the leaf pulvini with the periderm of the stem and it is always histologically constituted like the latter, except sometimes, when the constitution is somewhat different in those of its layers that are formed first. In addition to this cork, which always develops between its generating zone and the surface of the wound, we may also have, on the opposite side, a more or less thick phelloderm, even though the periderm of the stem does not have it. This phelloderm is most frequently cellulosic and amyliferous (Menispermum canadense, Fraxinus Ornus, Morus nigra, etc.); at the same time it may also be hard and crystal-bearing (Celtis occidentalis). Its maximum thickness generally is found along the bundle passage [where it grows across the bundles].

These, then, are the four types of scar reactions which we may get in the leaf pulvini as part of the cicatrization of the wound. There is only one among them which seems indispensable to complete cicatrization and which appears in all cases; this is the formation of the secondary cork which I called "scar cork," this cork may even develop by itself but that is rare. Often, the formation of the cork is accompanied only by the differentiation of a ligno-suberous stratum. At other times, finally, we may also have a meristematic subdivision of the cells of the pulvinus before ligno-suberus differentiation.

The size of the cicatrization strata is usually in a direct ratio with the width of the wound and the strata are thickest in those species where the petioles are the biggest [widest].

Time of Scar Strata Differentiation

The factor that distinguishes the different species from each other, more than any other factor, is -- not so much the final state of cicatrization -- but rather the time the latter appears. This is why I selected my types in this study primarily on the basis of this period.

a. In the simplest cases, cicatrization is completed before defoliation (Mispilus germanica, Amorpha fruticosa, Koelreuteria paniculata, etc.). A ligno-suberous stratum is then differentiated, at the expense of the tissues of the pulvinus, below the wound and always before winter; this stratum is doubled by a scar cork during the second year.

At other times, cicatrization occurs after the fall and resembles the one which I have just described; in that case the tissues of the pulvinus, which constitute the ligno-suberous stratum, have been the seat of a cell subdivision before the leaf fell. Let us note that, in this case, the subdivision is always more active in the upper part of the stratum than at the base (Broussonetia papyrifera, Ficus Carica, etc.).

b. Cicatrization may begin even before defoliation but it is then represented only by a single scar stratum, that is, either the ligno-suberous lamina or the cork. In the first of these cases, the cork appears below the ligno-suberous lamina only during the second year.

When the ligno-suberous lamina exists only before defoliation, the ligno-suberization may, either, not have been preceded by any cell subdivision (Diospyros virginiana, Cornus sanguinea, Fagus sylvatica, etc.), or, on the other hand, this subdivision may turn out to be more or less active here (Morus nigra, Catalpa bignonioïdes, etc.). In this latter case, the new subdivisions are generally numerous, particularly in the upper part of the stratum and more rarely in its lower part (Magnolia acuminata, Juglans nigra, Chimonanthus fragrans).

The species in which the cork exists only or almost only before the leaf falls are very small in number (Aesculus, Viburnum, Salix, etc.).

c. The two scar tissues, ligno-suberous stratum and cork, may coexist before defoliation; in this case the primary tissue, at whose expense the ligno-suberous stratum will be differentiated, may or may not have been the seat of a prior subdivision.

When we do have subdivision, it is more active at the base of the stratum and the partitions here are oriented more transversally so that we have a gradual transition of this region to the subjacent cork.

Ligno-suberization always appears before the time the cork is formed; it may even be completely terminated at that time although, more often, it has only begun by then.

We therefore see, quite generally, that the cell subdivision of the primary parenchymatous tissues of the pulvinus -- providing there is any -- appears always prior to defoliation and before any other scar differentiation. Ligno-suberization comes next /in second place/ and always during the first year. The formation of the cork may also begin during the first year; however, more often, it occurs during the second year. When, during the first year, the scar cork appears belatedly after the fall of the leaf, which is not at all frequent, it is always quite thin and its cells differ from those of periderm of the stem in that their walls are always very thin.

When the ligno-suberous stratum is differentiated before defoliation, it happens sometimes that the suberization, at its base, will extend beyond the ordinary suberous film of each cell and into the neighboring parietal strata.

When the two scar strata or only one of them exist before the leaf falls, they will begin to differentiate, however, sometimes very long before defoliation, in July or August (Gymnocladus canadensis, Aesculus, Ailanthus glandulosa, Acer campestre, etc.); most often, however, this happens one or two months or, rarely, less than that, prior to defoliation (Viburnum, Sophora japonica, etc.).

In all cases, cicatrization avoids the bundles almost entirely so long as defoliation has not been completed.

Let me add at this point that -- when cicatrization occurs only after the fall -- it is never carried out by a single scar cork.

In most cases, the latter, once established, only thickens during the following years. In some species, however, this cork tends to develop more and more, starting in the second year, along the prolongation of the periderm of the stem. We can then see the second-year stratum -- in contact with that of the one from the preceding year in the internal region of the pulvinus -- moving away and heading obliquely toward the bottom in its external region (Gymnocladus canadensis, Menispermum canadense, etc.). Sometimes this oblique direction is even more pronounced when the second-year cork stratum is only in contact with that of the preceding year in the axillary angle of the pulvinus (Gleditschia triacanthos). Finally, it may also be altogether deeper than the first (Cladrastris tinctoria, etc.).

Points of Departure for Scar Differentiation

In the ligno-suberous strata, the modification of the cell walls begins either in the upper part of the stratum (Morus nigra, Ficus Carica, Evonymus latifolia, etc.), or in its lower portion (Chimonanthus fragrans, Gymnocladus canadensis, Negundo, etc.). Furthermore, it appears more often in the external region of the pulvinus but it may also begin around the leaf bundles (Forsythia suspensa, Fagus sylvatica, Fraxinus juglandifolia, etc.) or at the level of the cortical parenchyma (Xanthoxylon fraxineum, Negundo fraxinifolium, etc.); sometimes it may begin in several places at the same time (Morus nigra, Ficus Carica, Catalpa bignonioïdes, etc.).

In most cases the scar cork appears then also in the external region of the pulvinus and progresses toward its internal region; the opposite case occurs much more rarely (Aristolochia Sipho, Paulownia imperialis, Diospyros virginiana, etc.). This cork may also begin in the interior of the cortical parenchyma (Xanthoxylon fraxineum, Aesculus, etc.) or against the leaf bundles (Sorbus, Cotoneaster melanocarpa, Mespilus germanica, etc.).

Sacrificed Parenchyma

Regardless of the time of scar stratum differentiation, we often have -- above these strata, between them and the surface of the wound (or the separating stratum before the leaf falls) -- a more or less thick portion of pulvinus tissue which, after defoliation, remains cellulosic; I called this "sacrificed parenchyma." This tissue, in effect, is flattened on the scar strata, thus augmenting the relief of the fascicular navels. Moreover, it is often invaded by the mycelium of various fungi which never penetrates into the subjacent ligno-suberous stratum.

II. Bast-Ligneous Bundles

The cicatrization of the bundles, which sometimes starts shortly before the leaf falls through the ligno-suberization of the tissues of their circumference, eventually ends before the winter through the completion of the ligno-suberization of all of their elements, except the sieve-like tubes and the vessels. After this first cicatrization, a secondary cork develops, below and against the ligno-suberized region which it has produced.

Inside the ligno-suberous stratum, the sieve-like tubes are most often flattened by the neighboring cells; although their walls are lignified more or less like the walls of the latter, this process takes place without the development of a suberous film inside them. Along with the ligneous vessels, these are the only elements of the bundles where we can observe this peculiarity.

The ligneous vessels are blocked either by thalli or by gummy lignin or, most often, by both of them together at the same time. However, while the thalli always develop in the vessels and in the entire base of the petiole, before the leaf falls, the gummy lignin, on the other hand, is ordinarily deposited in the pulvinus only and then, only, after defoliation.

Earlier I showed that the substance which I called "gummy lignin," instead of "wound gum," as did my predecessors, in effect only looks like a gum, whereas it reveals all of the microchemical and coloring reactions of lignin. This is why I called it "lignin"; I added the qualifying adjective "gummy" only to indicate its appearance.

The ligno-suberous differentiation of the bundles progresses from their edge toward their center and it almost always descends lower inside the pulvinus than in the cortical parenchyma.

After the scar cork has been developed across the base of the leaf, before the leaf falls, it never crosses the bundles from that time onward; it then disappears around them, climbing up slightly toward the separating stratum. The bundles are cut by the cork only after the leaf has fallen and, except for some rare exceptions, during the second year, only; the generating zone of this cork, by the way, is formed at the expense of their /bundles/ living elements. The sieve-like tubes and the vessels are broken due to the effort of the cork, as it grows. Although the vessels are obstructed by thalli, the former often subdivide at the level of the generating zone and contribute to the formation of the cork (Aesculus, Aristolochia Sipho, Juglans nigra, etc.).

In most cases, the cork thus grows across the bundles, describing a curve toward the stem, along the lower surface of the ligno-suberous lamina.

The hard bast which, as we saw earlier, is always missing at the level of the separating stratum, may, on the other hand, in certain species, exist at the level of the scar cork. In this case the latter never grows across it; it may either be stopped abruptly around it (Gymnocladus canadensis), or it may curve back toward its surface and gradually disappear, enveloping it with a sleeve which will sometimes plunge toward the stem (Robinia hispida, Platanus occidentalis, Gleditschia triacanthos, etc.), or climb back up again toward the surface of the scar (Amorpha fruticosa).

III. Secretory Tissue

1. Crystal-Bearing Cells

The crystal-bearing cells never subdivide, even when they are included in a region where the cell division is very active. Those that are included in the ligno-suberous lamina may be dead; but that does not prevent their walls from becoming more or less lignified (Amorpha fruticosa, Aristolochia Sipho, etc.). However, when they still contain protoplasm, they are capable of becoming ligno-suberized and the suberous film, which they produce, will then cover not only their walls but also the outside of the thin envelope of crystals and the outside of the bridges which often connect this envelope to the walls (Alnus glutinosa, Castanea vulgaris, etc.)

2. Secretory Cells

The isolated secretory cells appear incapable of any reaction related to the fall of the leaf; their content dries out (Magnolia acuminata, Benzoin odiferum, etc.).

3. Articulated Laticiferous Organs

The articulated laticiferous organs of Amorpha fruticosa, of the Robinia, of Caragana altagana, etc., are broken by the separating stratum and by the cork in the same way as the sieve-like tubes. Ordinarily their walls are lignified in the passage of the ligno-suberous stratum.

In the case of the Aesculus, Negundo, Acer campestre, etc., these same elements subdivide transversally several times, and sometimes also longitudinally, at the level of the primary cicatrization stratum; then the newly formed cells are ligno-suberized. These laticiferous organs then subdivide again, later and further down, in order to become involved in the composition of the generating zone of the scar cork and in order to contribute to the formation of the latter.

4. Branching Laticiferous Organs

In Morus nigra, M. alba, Ficus Carica, etc., the branching laticiferous organs are first of all plugged up, in each of their branches, by two plugs consisting of modified latex, and then by two partitions, one above the separating stratum in the petiole and the other below it in the pulvinus. These partitions are finger-shaped and have convexities turned toward each other, that is to say, two of them, at a time, are turned toward the separating stratum /both of them toward the separating stratum/. In Periploca graeca it may also happen that only the two latex plugs are formed.

These laticiferous organs are then broken at the level of the separating stratum, in their sacrificed region, that is to say, between the two partitions; later on they are crushed and cut by the scar cork either above or below the lower partition.

5. Secretory Sacs

The secretory sacs of Tilia europaea and Ptelea trifoliata, which often are contained inside the ligno-suberization, undergo no change other than the ligno-suberization of their epithelial cells. Those which are found at the level of the separating stratum or of the scar cork are shaped (twisted) by these two tissues.

6. Secretory Canals

The secretory canals of Aralia spinosa are plugged by gummy lignin befor the leaf falls, from a point at a certain distance above the separating stratum in the petiole all the way to a point a little below the scar strata in the pulvinus.

Those of Rhus are blocked by their epithelial cells which are developed into thalli inside the canal. These thalli are ligno-suberized at the level of the ligno-suberous lamina and are transformed into the generating zone which will produce the zone that generates the secondary cork. In this fashion, the first and the second scar lamina establish their continuity across [through] the canals.

Some Special Features Pertaining to the Separating Stratum or the Cicatrization

Leaf-Bud Scale Lamella

In some species the axillary bud or buds of the leaf are hidden under the more or less swollen base of the petiole (Platanus occidentalis, Rhus Coriaria, Ptelea trifoliata, etc.). Ordinarily, the separating stratum is then formed below this swelling so that the buds are exposed after the leaf falls (Sophora japonica, Cladrastris tinctoria, Robinia hispida, etc.). In some species, however, this stratum is formed higher up and extends across the petiole swelling. After the leaf falls, a portion of this swelling then remains above the buds; I have called this portion "leaf-bud scale lamella," in comparison with the scales by the same name, whose role is likewise to protect the buds during the winter. While the only bud of Philadelphus coronarius and all of those of Robinia Pseudo-Acacia are thus hidden, only three out of the four in Menispermum canadense are thus protected.

In Ptelea trifoliata the separating stratum extends into the petiole swelling above the buds; but this happens in a fashion preventing the dehiscence from extending into this region and similarly preventing the formation of a leaf-bud scale lamella. Does not this arrangement recall the existence of an ancestral state which might have disappeared?

In Gleditschia triacanthos v. inermis, the separating stratum is arranged in such a way that four out of five buds are hidden by the enlarged extremity of the pulvinus without the latter otherwise taking on the appearance of a leaf-bud scale lamella.

Species With Deep Periderm

In the species where the periderm is normally situated deeply in the stem, it is also similarly situated in the pulvinus. It then forms a sleeve around the leaf bundles; this sleeve surrounds the bundles completely over a more or less considerable distance (Potentilla fruticosa, Caragana altagana, Calophaca volgarica, etc.).

In these species the scar cork does not develop across the cortical parenchyma which constitutes a veritable sacrificed tissue; it grows only across each of the bundles, plugging their peridermal sleeve near the base.

Revival of Cicatrization

In certain species the scar tissues, which are formed before the winter of the first year (ligno-suberous lamina), are removed during the second year due to the establishment -- below them -- of a new separating stratum similar to the one which triggered the autumn fall of the leaves (Hamamelis virginiana, Parrotia persica, Sorbus, etc.).

In the Sorbus, Cornus mas, Cornus sanguinea, etc., the pulvinus, which results from defoliation, is rather long in size. Between the revival separating stratum and the ligno-suberous lamina (first scar lamina), there also continues to exist a more or less thick parenchyma. Above the new separating stratum we then find differentiated a lignified region similar to the one which was formed earlier in the base of the petiole above the autumn separating stratum (subcicatricial lignified stratum).

In Fagus sylvatica and Carpinus Betulus, the exfoliation of the first-year scar strata is produced by a slightly different process. The first layers, supplied by the secondary cork generating zone, below the ligno-suberous stratum, remain cellulosic and grow very much in the longitudinal direction; their walls then become very thin. After that, these delicate walls are broken progressively -- due to the action of external factors -- in the same fashion as in the autumn separating layer in Aristolochia Sipho. We may encounter a similar arrangement in Staphyllea trifoliata; however, since this is often local, the revival which it produces may only be partial.

Marcescent Leaves

We find marcescent leaves primarily in those species which feature a revival of cicatrization.

The feature distinguishing these marcescent leaves from the deciduous leaves of the same species is nothing more than the absence or incomplete development of the autumn separating stratum. The marcescent leaves are, in effect, leaves that are developed later than the others; they are leaves that have not yet terminated their vital cycle at the ordinary defoliation time, so that the bad-weather season kills them before the plant has had time to terminate or even begin here the establishment of the separating stratum.

The ligno-suberous stratum, furthermore, is differentiated, in the base of these leaves, before winter comes, in the same way as in the case of the diciduous leaves; but this happens only after their death. Moreover, it is ordinarily not as thick and its thickness decreases even further, the later its differentiation comes about.

During the second year, it is a revival of cicatrization which brings about the fall of the marcescent leaves (Hamamelis virginiana, Fagus sylvatica, etc.) and which, aided by the weight of the leaf and the wind, then occurs much faster than that of the pulvini of the diciduous leaves.

In the Quercus hispanica and pedunculata, the revival of cicatrization occurs only in the pulvini of the marcescent leaves. It is, at most, rough /approximate, vague/ in the others.

PART II

FALL OF FOLIOLES AND CICATRIZATION OF WOUND

In the historical review at the beginning of this work we saw that only two, out of all the authors who studied the phenomenon of autumn defoliation, concentrated on the fall of the folioles in a joint project; I am talking here about Mr. Van Tieghem and Mr. Guignard ("Observations On the Mechanism of Leaf Fall," _Bull. de la Soc. Bot. de France_, Volume XXIX, 1882, page 312). They studied only one case -- the case of Gymnocladus canadensis -- and then only under artificial conditions. We will recall that, according to these authors, the wound left by the fall of the folioles is never cicatrized.

The results, which I will present in this second part, like those pertaining to the leaves, were obtained on the basis of a study of organs normally falling in autumn. They involve several species which I will now describe in succession.

Before we go any further, I would like to point out a general fact: there is no lignified element other than the vessels, at the base of the folioles, as at that of the leaves, before the beginning of the phenomena that prepare the way for the fall of the leaf; furthermore I want to state that the bast-ligneous bundles here are frequently constricted.

Sorbus Aucuparia L.

At the base of the folioles of Sorbus aucuparia, we can observe a slight constriction a little above its insertion and on the inside face only. The separating stratum for the foliole develops at its [this] level, sometime before the separating stratum of the leaf. This stratum [foliole separating stratum] is made up of two or three layers of cells which -- in contrast to those making up the leaf separating stratum in the same species -- are not subdivided in advance. Above it we have a subcicatricial lignified stratum undergoing differentiation here, similar to the one we encountered at the base of the leaf.

The foliole separating stratum mechanism -- in this species and in the following ones -- is the same as the mechanism for the leaf separating stratum in the same species.

This separating stratum is established at the base of all folioles but it does not always manage to function before the detachment of the leaf, especially when we have an abrupt or sudden heavy wind or frost. Thus we see that some folioles may be involved with the petiole in its fall [may be forced to fall with the petiole].

In the pulvinus of the folioles there is never any trace of cicatrization that might occur prior to their fall but it may occur afterward. As a matter of fact, among the folioles which fall early, many do so while the petiole is still quite alive and while, therefore, the tissues of the little leaf pulvinus still have sufficient vitality to react against the irritation resulting from the fall of the foliole. This leads to the formation of a cicatrization stratum under the wound, although this stratum appears perfectly useless to the plant since the fall of the petiole -- which comes a short time afterward -- will involve it [carry it away] likewise.

This cicatrization stratum, by the way, is more or less complex, depending on whether the fall of the foliole occurs more or less shortly before the fall of the leaf.

In the most complex cases of cicatrization which I observed, I found -- below the remnants of the separating stratum -- not only a lamina consisting of two or three layers of ligno-suberous cells (ss, Figure 104), but also, below and against it, a secondary cork. The latter, which might even completely grow across the bundles (lic, Figure 104), was, however, more than two or three layers thick. The ligneous vessels were plugged by gummy lignin.

This kind of state of cicatrization of the wound left by the folioles is not rare in this species; I observed it many times. I might also point out here that it turns out to be more complete than that of the first year at the base of most of the leaves since, in this latter case, the cork grows across the bundle only in very exceptional instances. When the cicatrization of the foliole pulvini is less complete, the cork may be absent and may reveal only the rough outline of its generating zone. Most often, the ligno-suberous stratum exists here all by itself; at other times it is represented only by a few lignified cells. Finally, in yet other cases, there may be no trace of cicatrization whatever.

I have often found several degrees of cicatrization in one and the same leaf, that is to say, in the different foliole pulvini carried by one and the same petiole.

Juglans Nigra L.

The leaf of J. nigra generally drops its folioles a long time before its fall.

The separating stratum of these folioles differs from that of the leaves in that it is not of meristematic origin. Its formation is accompanied by the characterization of a more or less thin lignified stratum which is established above it, in the base of the foliole, and [accompanied by] the production of numerous thalli in the ligneous vessels of the same region.

Since the folioles fall rather prematurely or quite a bit earlier than the leaves, we find that the cicatrization of their [the folioles] wound is frequent; the process involved here most often involves the following steps. A ligno-suberous lamina is formed below the debris of the separating stratum and against this debris (ss, Figure 105); the thickness of this ligno-suberous lamina averages five to seven layers of cells, the lower ones of which are often subdivided once or twice, even before the foliole falls. The ligno-suberization here involves always the parenchymatous elements of the bundles, including the thalli. Below this ligno-suberous stratum I was never able to observe anything more than the rough outlines of a cork; these outlines are found especially in the internal cortical parenchyma, in the vicinity of the bundles.

As in Sorbus aucuparia, we can encounter all of the intermediate variations, along with this most complete state of cicatrization; these variations might even include the complete absence of cicatrization; this, of course, would depend on the greater or lesser precociousness of the fall of the folioles.

An odd terminal foliole will never be detached because there is no separating stratum developing at its base, nor will there be any scar tissues. This peculiar feature is explained probably by the fact that its median vein directly continues the petiole without articulation and without modification of tissues of any kind whatever.

Gymnocladus Canadensis Lamk.

The leaf of Gymnocladus canadensis is composed of two stages. The folioles are the first to fall rather long before the leaf falls. The secondary petioles, on the other hand, are detached only a short time before; some of them are even still attached to the primary petiole at the moment it falls.

The tissue changes which occur at the base of the folioles and at the base of the secondary petioles, before their fall, are of the same nature in both cases. These two types of organs have an articulation at their base; this articulation is marked by a circular constriction at whose level the elements of the cortical parenchyma gradually become smaller in size. The separating stratum is formed at the expense of the small cells of this articulation, without the separating stratum being first the site of cell subdivisions; dehiscence here occurs by the same method as at the base of the leaf, that is to say, through the separation of the cells. A more or less thin subcicatricial lignified stratum is differentiated above the separating stratum.

There is generally no cicatrization below the wounds left behind by the fall of the secondary petioles. On the other hand, below the wounds left by the folioles,we can often observe a more or less pronounced cicatrization, depending on the precociousness of the fall of these folioles. This cicatrization most often consists of the ligno-suberization of a layer of four or five cells; this ligno-suberization also involves the bundles.

On the basis of what I have just said, I might note that I do not agree with Messrs. Van Tieghem and Guignard (loc. cit., p. 312); these two authors maintain that the separating stratum is a meristematic layer revealing two or three new thin partitions and that a middle layer is resorbed during the detachment of the foliole. I likewise disagree with them when they say that the wound left by the folioles on "the primary petiole" (since the leaf is composed of two stages, there is no doubt that we are actually dealing here with the secondary petioles) is never cicatrized.

I would also like to point out again the artificial conditions under which these authors studied the fall of the folioles and of the leaves; I thought that these conditions might cause a variation in the process of defoliation and this is why I tried to repeat their experiment. I thus put detached branches of Gymnocladus canadensis in cans at the same time, in July, that is, and I kept them there as much as possible under the same environmental conditions.

In this experiment I noted, first of all, that -- even under normal conditions and under the conditions observed by Mr. Van Tieghem and Mr. Guignard -- the separating stratum appeared successively at the base of the folioles, then at the base of the secondary petioles, which these authors do not mention at all, and finally at the base of the leaf itself. I, on the other hand, found that, despite these special experimental conditions, the mechanism of detachment of the different parts of the leaf remained similar to that of natural defoliation, that is to say, that the formation of the separating stratum was not preceded by any subdivision and that its cells were separated without ever being resorbed. Like Messrs. Van Tieghem and Guignard, I did not observe any trace of cicatrization either in the base of the folioles, or in that of the secondary petioles, or, for that matter, at the base of the leaf. This shows how the process of artificial fall differs in this respect from autumn fall.

I might also add that, in this experiment, there is a subcicatricial lignified stratum above the separating strata of the different parts of the leaf; the characterization of this subcicatricial lignified stratum is similar to that which forms in autumn and I found that the former here is much more lignified.

<u>Staphyllea Pinnata L.</u>

In this species the separating stratum is formed right at the base of each foliole at the expense of the two layers, some of whose cells have split earlier transversally and only once, differing in this respect from the separating stratum of the leaf which reveals numerous subdivisions. We note here a weak lignification of the tissues above it.

After the foliole falls, we may or may not get a scar stratum made up of two or three layers whose walls undergo ligno-suberous modification.

We know that the folioles of Staphyllea pinnata are opposite [opposed] and inserted on petiole swellings which constitute veritable nodes. Now, the lignified tissues which are abundant in the bundles and the pith of the internodes of the petiole are reduced at the level of the nodes to the point where they are represented only by the ligneous vessels; this can be found also to exist at the base of the folioles and the leaves. Moreover, a separating stratum is formed in autumn across each of these nodes; this separating stratum cuts across the entire cortical parenchyma, the medullary parenchyma, and even the bundles (cs, Figure 107). This separating stratum is developed for each node around the same time as that of the corresponding folioles but the cell subdivisions here are more abundant. The lignification of the tissues which occurs above it is likewise more accentuated.

Although there may be a separating stratum at all of the nodes of the petiole, the internodes of the latter are not always disarticulated [disjointed]. Generally, as a matter of fact, these types of strata act sometime after those of the folioles and only a short time before the fall of the petiole itself, so that the terminal internodes only have time enough to become detached. (Mer, E., "Vegetative Phenomena Preceding or Accompanying the Loss and Fall of Leaves," Bull. de la Soc. bot. de France, Volume XXIII, 1876, page 188, found a similar disarticulation of the internodes of the petiole in the leaves of Mahonia whose fall he managed to bring about while keeping a leaf-bearing branch in a closed space saturated with humidity.) I never observed -- below the scars thus produced -- any formation of scar strata similar to those which I pointed out in certain foliole pulvini of the same species.

Caragana Altagana Poir.

At the base of the folioles of Caragana altagana (Figure 106) we have an articulation as at the base of the leaves but the circular groove, which indicates it, is not as deep although it is very clearly indicated. As in the case of the base of the leaves, the separating stratum is differentiated here at its level. This stratum is topped by a more or less thin subcicatricial lignified layer; besides, it tops another lignified layer even before the leaf falls (rs and s, Figure 106).

In the C. altagana, the cicatrization of the foliole pulvini has already begun before the folioles fall. Sometimes -- although very rarely -- the lignified scar stratum may be completed later on through the characterization of some ligno-suberous elements further down. The vessels are almost always filled with gummy lignin up to a certain distance below the surface of the scar.

All of the folioles generally fall before the petiole.

Calophaca Volgarica Fisch.

The folioles of this species, like those of the preceding one, has a basilar articulation; however, in autumn, the lignified scar strata are the only ones we encounter here. There is no modification in the foliole pulvini after the folioles fall.

Xanthoxylon Fraxineum Willd.

The folioles of X. fraxineum all fall before the petiole; however, since they generally fall only a short time earlier, we get a scar reaction below the wound only rarely. In some cases, however, I four some lignified strata or even some ligno-suberous strata here.

A separating stratum, similar to that of the folioles and topped, like it, by a rather thin subcicatricial lignified stratum, develops across the latter [ligno-suberous stratum] and often also across the two last nodes of the petiole, as in the case of those of Staphyllea pinnata. Despite the presence of these separating strata, it is very rare to find this disarticulation of the two last internodes of the petiole. Ordinarily, the latter falls before their disarticulation.

Aralia Spinosa L.

We know that the leaf of Aralia spinosa is composed of two stages. The different parts of this leaf are attached, in pairs, to one and the same node of a primary petiole or a secondary petiole, depending on the part we are considering.

Before the separating stratum at the base of the leaf, we can observe the formation of similar separating strata not only at the base of the folioles and the secondary petioles, as in the case of Gymnocladus canadensis, but also across all of the nodes of the secondary petioles as well all of those of the primary petiole. All of them are made up in the same fashion as a result of the subdivision of one or more cell layers. A thin subcicatricial lignified stratum is differentiated above each of them; in addition, thalli penetrate into the interior of the big vessels in their vicinity.

These separating strata appear successively and roughly regularly in those regions that are furthest away from the leaf, toward its base. The detachment of the different parts of the leaf follows the same progression. Sometimes, however, as a result of an oabrupt fall of a secondary petiole or the primary petiole, these organs take with them all or a part of their appendixes.

The scars resulting from the fall of the folioles and the secondary petioles are slightly concave; they result from the fall of the internodes of the secondary petioles and those of the primary petiole; they are deeply cut in the form of a groove running along the plane of symmetry of these organs.

Below these different scars and especially below those of the folioles, we sometimes can observe the formation of a scar stratum which may be ligno-suberous or simply lignified.

At the level of the disarticulation of the folioles, the secondary petioles, and the primary petioles and before their fall, the secretory canals are plugged, as in the case of those at the base of the leaves, by the gummy lignin which, likewise, is deposited especially above the separating stratum.

Robinia Pseudo-Acacia L.

Like those of some of the preceding species, the foliole of R. Pseudo-Acacia has at its base an articulation at whose level the separating stratum is established. The crystals of calcium oxalate, which are very numerous in the rest of the secondary petiole and the primary petiole, are missing at the level of these articulations.

No lignified stratum is differentiated above the separating strata; often, however, a few thalli penetrate into the vessels in their vicinity and before the folioles fall. The latter generally fall all together before the petiole. After their fall, the wound may be cicatrized by a rather thin ligno-suberous lamina which sometimes completely grows across the pulvinus but which more frequently is formed only in its internal cortical parenchyma. Moreover we can sometimes note the deposit of gummy lignin in the vessels below the wound.

Robinia Hispida L.

The articulation of the foliole of this Robinia is similar to that of Robinia Pseudo-Acacia; the circular groove here is however less accentuated.

In this species the cicatrization, after the fall of the folioles, is rarer than in the preceding species; it is also less pronounced and it is most often tied in with the formation of the lignified strata. Here we still have some thalli at the moment the foliole falls and the gummy lignin likewise generally manages to block the vessels in the vicinity of the scar.

Amorpha Fruticosa L.

The separating stratum is differentiated in this species likewise at the level of a joint in the base of the foliole. The lignification above it is very slight. The majority of the wounds produced by the fall of the folioles does not involve any cicatrization. I observed a thin ligno-suberous stratum only in a small number.

Aesculus Hippocastanum L. and Ae. Parviflora Walh.

In both of these species with their palm-shaped leaves, the changes which occur at the base of the folioles are the same as those that occur at the base of the folioles of Amorpha fruticosa. The cicatrization here is likewise very reduced and rather infrequent.

Cladrastris Tinctoria Raf.

As in the two preceding species, C. tinctoria recalls Amorpha fruticosa. We might note, however, that, in general, the terminal foliole does not fall although it is equipped, like the others, with a basilar separating stratum; as the petiole falls, it takes the foliole along with it.

Staphylea Trifoliata L.

The separating stratum here is differentiated at the base of the folioles; as in the case of the leaf, it is made up of one or two rows of cells which have earlier split two to four times. The subcicatricial lignified strata are quite thick here. However, although the three folioles fall quite some time before the petiole, there is generally no cicatrization below the wound.

Sophora Japonica L.

The detachment of the folioles of S. japonica occurs at the level of an articulation in their small petiole [leaflet petiole]. Contrary to what happens when the leaves of the same species fall, the formation of the separating stratum for the foliole is not preceded by a cell subdivision. Ordinarily we do not have any wound cicatrization below it.

Koelreuteria Paniculata Lamk.

The separating stratum of the foliole is of meristematic origin, like that of the leaf; however, the subdivisions here are less numerous; ordinarily there is only one per cell.

In the base of the folioles we have numerous thalli developing inside the vessels, before the folioles fall. Wound cicatrization is rare in the pulvinus. Although the separating stratum may be well constituted at the base of all of the folioles, the latter do not always fall before the petiole and often they are taken along by the latter, at least those from the top.

Ptelea Trifoliata L.

The separating stratum of the foliole in this species is made up of two or three successive subdivisions of one cell layer, as in the case of the leaf.

All three leaves fall a short time before the petiole so that the cicatrization of the wourd is not at all frequent. Sometimes, however, I was able to find lignified strata below the wound.

Gleditschia Triacanthos L. var. inermis

The big leaves of this species are made up of two stages; the smallest ones are made up of only one sometimes.

The fall of the folioles and of the secondary petioles occurs in the same fashion. The separating stratum here is never of meristematic origin;

it is established at the level of an articulation marked by a circular groove which is not deep and which is found on the folioles; it may be quite accentuated but it exists only on the inside face of the organ in the case of the secondary petioles.

When the leaf falls, a more or less large number of its secondary petioles are very often still attached to the primary petiole and even more frequently they may still be provided with bare folioles. I never encountered any trace of cicatrization in the foliole pulvini.

Inside the vessels at the base of the folioles we cannot see anything that would remind us of the considerable deposit of gummy lignin which we encountered earlier at the base of the leaves of the same species, before their fall.

Tecoma Radicans L. p. sp.

The separating stratum at the base of the folioles of T. radicans is made up -- like that of the base of the leaf -- by a layer of cells which have split earlier three or four times. Above it we have a rather thin sub-cicatricial lignified stratum. Below the wound we generally do not note any cicatrization.

As in the case of some of the preceding species, a separating stratum develops here across the nodes of the petiole; this separating stratum is constituted by the subdivision of a cell layer; however, only those at the top are completely traversed, so that only the last internodes are disarticulated.

Fraxinus Ornus L. and F. Juglandifolia Lamk.

In these two species we still have a separating stratum at the base of all of the folioles but the latter do not begin to fall until a short time before the leaf and many of them are taken down with the leaf.

As in the case of Tecoma radicans, we have separating strata also forming in the nodes of the petiole, especially in those that are closest to the top of the leaf; but these strata only grow across the cortical parenchyma; they avoid the bundles and even the medullary parenchyma although the latter may remain cellulosic at that level. This means that the separating detachment occurs only in the outside tissues and that the petiole of these Fraxinus is never completely disarticulated.

Ailanthus Glandulosa Desf.

The folioles of A. glandulosa fail like those of the earlier Fraxinus; in this case we very often find numerous thalli in the large vessels before their detachment. In some cases we even observe the formation of a cicatrization stratum, under the wound; the differentiation of this stratum does not go beyond the state of the lignified strata.

Negundo Fraxinifolium Nutt.

Negundo reminds us of Ailanthus glandulosa but the number of folioles which do not fall here -- despite the presence of their separating stratum -- is greater.

We must also note that the articulated laticiferous organs of the bast of the vessels are often subdivided here at the level where the foliole will become detached and in the small subjacent pulvinus; in this respect they recall what happens at the base of the leaf before defoliation.

Rhus Coriaria L.

A short time before the leaf falls we can observe a separating stratum at the base of each of the folioles of R. Coriaria and, above it, we can observe a lignified stratum consisting of four to five layers. More than in Negundo, the foliole separating strata here ordinarily do not function before those of the leaf so that the leaf, in falling, takes along a larger number or perhaps even all of its folioles. There is no trace of cicatrization below the separating strata.

At the base of each of the folioles the secretory canals, which are located in the bast, are -- sometime before the fall of the organ, like those at the base of the leaf -- plugged by thalli which form epithelial cells, proliferating on their inside. Similarly, likewise, these thalli are produced not only below the separating stratum but also and above all above it, up to a certain distance into the secondary petiole.

Summary of Part II

Fall of Folioles

The fall of the folioles of a composit leaf is brought about by the establishment, in their base, of a separating stratum similar to the one which we find at the base of the leaf but in which the meristematic subdivision, when it does exist, is less active.

The majority of the folioles have an articulation marked by a circular groove at whose level the cells of the cortical parenchyma gradually become smaller; this occurs even in those species where the leaf does not have such an articulation. The separating stratum is established in this tissue.

The mechanism of foliole detachment is the same as that of leaf detachment.

The separating stratum is differentiated at the base of the folioles ordinarily a short time before that of the leaf. However, the folioles are not always detached at the moment of defoliation and the leaf may then take a more or less large number of these folioles along with it as it falls (Koelreuteria paniculata, Rhus Coriaria, Negundo fraxinifolium, etc.).

In the species whose leaves are composed of two stages (Gymnocladus canadensis, Gleditschia triacanthos, Aralia spinosa), the secondary petioles are detached in the same fashion as the folioles and their fall occurs quite regularly, after that of the latter and before that of the primary petiole.

Subcicatricial Lignified Strata

In the majority of cases we get a lignification -- above the separating stratum -- of the neighboring tissues which is comparable to the lignification which we described earlier, in the base of the leaves.

Cicatrization of Wound

It is wrong to say -- as has been done to this very day -- that the wound left by the fall of the folioles is never cicatrized. However, contrary to what we said in the case of the base of many leaves, the scar tissues at the base of the folioles are almost never differentiated before their fall. In two species, only, among all of those which I studied (Caragana altagana and Calophaca volgarica), do we have a cicatricial lignified stratum -- even before that time -- similar to the one which we encounter in the base of the leaves in these same species.

The scar strata which may differentiate after the fall of the folioles are always quite thin. They develop against the rests of the separating stratum and they consist only of a few layers which often only lignify but which may also be ligno-suberized (Juglans nigra, Gymnocladus canadensis, etc.); their ligno-suberization may often even invade the bundles. In the somewhat more complex but less numerous cases, we may also have -- below this ligno-suberous stratum -- either very simply the rough outline of a cork generating zone or perhaps even a cork; to be sure, this cork is not at all thick but it, likewise, will ordinarily grow across the bundles (Juglans nigra, Sorbus aucuparia, etc.).

It is not at all rare to find foliole scars -- on one and the same tree and often even on the same leaf -- which are accompanied by a more or less complex scar stratum and we may also find others which do not have the slightest trace of such a stratum.

Thalli develop frequently in the vessels, at the base of the folioles and before their fall, in the same way as at the base of the leaves; they are, however, less abundant (Aralia spinosa, Koelreuteria paniculata, Juglans nigra, etc.). Similarly, a gummy lignin may be deposited here.

Although ordinarily related to the relative time of foliole and leaf fall, the intensity of cicatrization, at the base of the deciduous folioles, nevertheless does appear to a certain extent to be related to the specification because, in certain species, the scar strata are very rare (Ailanthus glandulosa, Negundo fraxinifolium, Rhus Coriaria, etc.), whereas in other species, on the other hand, they exist frequently (Juglans nigra, Sorbus aucuparia, Gymnocladus canadensis, etc).

Sometimes, the articulated laticiferous organs are subdivided at the base of the folioles and before their fall in the same way as at the base of the leaves, but this is somewhat rarer (Negundo fraxinifolium, etc.).

As in the case of those at the base of the leaf, the secretory canals at the base of the folioles of Aralia spinosa are plugged, before their fall, by gummy lignin. Like those of Rhus Coriaria, they are blocked by their epithelial cells which are developed in the form of thalli.

Disarticulation in the Nodes of Certain Petioles

In some species, whose folioles are opposite, the petiole forms veritable nodes at the level of their insertion; there is no hard bast in these nodes and the ligneous and bast fibers are likewise missing; in these nodes, the medullary parenchyma, lignified everywhere else, has remained cellulosic. A separating stratum may be differentiated in autumn across these nodes and above this stratum, the tissues may react and form a thin lignified stratum, as at the base of the leaves and the folioles. In Aralia spinosa, such a separating stratum is established not only in the nodes of the primary petiole but also in those of the secondary petioles. In Staphylea pinnata it exists in all of the nodes of the petiole; the same is true of Tecoma radicans, but it traverses completely only the terminal nodes; in Xanthoxylon fraxineum, it is produced only in the latter; finally, in Fraxinus, it is incomplete in all of the nodes.

Often these separating nodal strata prove capable of disarticulating the petioles a short time before defoliation; often, however, the leaf falls before this disarticulation.

General Discussion

On the basis of what we have just said we can say that the opinion of some of my predecessors -- who attribute the cause of the fall of the leaves to the development of a cork across the tissues of the leaf pulvinus -- is in error. This cork is indeed missing at the moment of the fall much more often than it can be found. Moreover, it is sometimes developed a very long time before defoliation, without the leaf as a result suffering from this; this can be understood when we realize that it then does not affect the bundles and does not prevent the circulation of sap between the stem and the leaf. I might add that such a stem is constantly absent in the base of the folioles and that, however, most of them still fall in autumn.

Defoliation is certainly brought about by nonanatomical but rather by physiological causes. The habit of deciduousness in the leaves of the current epoch has probably been developed under the influence of periodically renewed conditions, similar to the development of their life cycle during a certain period of time; their fall is therefore the result of their decay and death. Under the influence of the same environmental conditions, the plant has also adopted the habit of itself practicing the amputation of this dead or dying leaf -- before winter; after all, this leaf will very soon not only become useless but also harmful to it; it prepares itself here by establishing a specialized stratum called a separting stratum.

Our research has been almost exclusively anatomical and we can therefore discuss very little on the physiological causes of the fall of leaves and our discussion will therefore deal mainly with the anatomical facts accompanying it.

Coincidence of Position Existing Between Separating Stratum and Articulation of Certain Leaves

I showed that the future position of the separating stratum, in the base of the adult leaf, is only rarely indicated by an articulation marked by a small circular groove at whose level we find a stratum of more or less specialized tissues, whereas this fact is much more general in the base of the folioles. On the other hand, the presence of this articulation, particularly at the base of the folioles, coincides most of the time with the existence of movements which have been discovered in these organs, so that it seems above all to have been established in order to promote them [the movements]. These findings have caused me to think that the establishment of the separating stratum in the articulations, whenever they do exist, probably is nothing more than a secondary peculiarity of the existence of the latter [articulations] and that -- if this establishment occurs here sooner than anywhere else, in autumn -- this is only because the articulations constitute regions of lesser resistance.

Agents Involved in the Fall of Leaves

a. We showed that the triggering of the activity of the separating stratum and particularly the formation of the dehiscence surface were accompanied by a major longitudinal growth of the cells of the stratum and that this growth occurred in a certain way so as to aid in the fall of the leaf. In reality, we should probably compare this cell elongation to the one that occurs frequent[illegible] at the expense of the cells in the tissues irritated by a natural or artificial [illegible] constitute a veritable means of [illegible] tum, however, the cell [illegible] pulvinus and the base of [illegible] petiole [illegible] influence -- also triggers the rupture of the [illegible] elements ([illegible] vessels, etc.) which only hold the debris of the leaf after the formation of the hehiscence surface.

However, the weight of the leaf, the wind, and the frost also turn out to be powerful agents in defoliation.

b. The action of the weight of the leaf and especially the action of the wind, working on a large surface, are certainly very powerful. To realize what is involved here we need only compare, in one and the same species, on the one hand, the speed with which the marcescent leaves fall in the spring; as we have seen earlier, this fall is caused by a revival in cicatrization; on the other hand, we might look at the slow speed with which the valves fall; these are likewise formed by a similar revival at the tops of the pulvini of the deciduous leaves.

c. It seems probable that the frost likewise is a strong factor in the fall of leaves. But how does it act? It is probable that it causes turgescence water to freeze in the cells and that this water -- while expanding more or less quickly under the action of this freeze -- speeds up the slow action of the separting stratum and breaks the last parietal resistance while keeping the leaf or the follicle in its position. Following the thaw caused by the morning sun, the ice melts and the leaf, which is no longer held by anything,falls to the ground. Following a frost, many of us, I am sure, have been able to watch these organs being detached in large numbers, in the morning due to the action of the first rays of the sun, while the atmosphere was perfectly calm.

d. As regards the valves (flaps) due to the revival of cicatrization, we must add that desiccation is added to the other factors. This latter factor acts on the heterogeneous tissue of the valves and tends to cause them to curve back more or less upward and to enlarge the dehiscence crack in this manner.

On the basis of a study of the facts, I might finally add that the action due to the elongation of the cells in the separating stratum develops only very sl[illegible] was not, as almost always, [illegible] even replaced by the [illegible] action of the outside agents.

Dehiscence Surface Considered as Free Surface

Regardless of the causes that bring about the fall of the leaves and the folioles and the formation of the separating stratum, it seems obvious to me that the place where the dehiscence surface is established turns out to be a source of irritation, a wound, against which not only the subjacent but even moreso the tissues above want to react. In my opinion, we have here the formation of what Mr. Bertrand (Bertrand, Eug., "Law of Free Surfaces," Bull. de la Soc. bot. de France, Volume XXXI, 1884, page 2) has called a "free surface"; it is this surface which, above, causes the formation of the subcicatricial lignified stratum and, below, in the pulvinus, the changes in the primary tissues (ligno-suberous strata) as well as the formation of the secondary tissues (scar corks) whose lowest ones terminate the cicatrization by plugging the window of the caulinary periderm opposite the leaves. This is also the factor whose action leads to the development of the thalli, the deposit of gummy lignin, etc., in the two directions.

The frequent presence of cicatrization strata in the base of the leaves, in full activity, may seem to be in contradiction with the opinion I have just stated, to the effect that it is the wound which causes the scar differentiation. But this peculiarity of the production of the effect before the cause is probably the result of an advance adaptation. (Here, for instance, we might mention the adaptation which, in the embryo sac of the Gymnosperms, causes food substances to be placed for the nutrition of the not yet formed young individual.) Although we might admit that the plant, originally, developed its defensive tissues only after the death of the leaf and under its influence, it is easy to understand how -- gradually and from generation to generation -- this plant could develop the habit of forming, in advance, a region of dehiscence and to prepare the cicatrization even earlier. This adaptation could be accomplished especially easily since, on the one hand, it would be undeniably useful to the plant which is already, at the moment the leaf falls, isolated from the external agents and, since, on the other hand, the phenomenon, under whose influence it is produced, was periodic.

Significance of Marcescence of Leaves and of Revival of Cicatrization

In the case of the marcescent leaves it seems, at first sight, that it is the dead leaf itself which becomes the stimulating cause and leads to the formation of the scar tissues as well as the formation of the separating stratum. However, let us keep in mind that this particularity of marcescence occurs especially in late-developed leaves which have in some way been surprised by the appearance of winter; let us keep in mind that, furthermore, this particular feature is due to the fact that the customary separating stratum has not had time to develop or, at least, has not had a chance to develop fully; when we keep these thoughts in mind, we are led to think that this marcescence in reality, in present-day leaves, constitutes nothing more than a new phenomenon grafted onto that of the habitual fall of the leaves.

However, the marcescence of present-day leaves is particularly interesting because of the conditions under which the new separating stratum is formed below the usual level of the first [stratum]. It seems, in effect, very probable that the differentiation of this second stratum is brought about by the plant's need for getting rid of an organ which has not managed to fall /by itself/ by any normal processes. Now, are these conditions, to which it owes its existence, not precisely the same which, in the beginning, caused the plant to develop the habit of leaf fall? Is it not also because the leaves, until now persistent, became the site of accidents due to increasingly cold winters, that the plant has developed the habit of cicatrizing itself at their base and then dropping them?

As far as the revival of cicatrization is concerned -- a cicatrization which is located in the pulvini of the deciduous leaves of some species -- we might say that it recalls, anatomically speaking, very much the situation we have in the case of the marcescent leaves, which is one reason why I was tempted to separate them. But must we admit, in this connection, that this revival recalls an earlier marcescence? Must we admit this on the basis of facts other than the fact that the revival of cicatrization and marcescence of leaves coexist in some species? I do not think so and I would be tempted to approach this phenomenon from the phenomenon of the formation of successive rhytidomes /wrinkles/.

Relationship Between Nature of Scar Reaction and Time At Which It Occurs

The nature of the scar reaction is in proportion to the state of vitality of the tissues at whose expense it occurs. Thus we see that the meristematic subdivision of the primary tissues of the pulvinus -- which sometimes precedes their transformation into a ligno-suberous stratum -- always occurs more or less long before the leaf falls and never afterward, that is to say, at a time when the life of the cells is not yet slowed down by the approach of winter. For the same reason, the secondary cork appears almost always either well before defoliation, if it is a first-year cork, or at the time of the return of vegetation, if it is a second-year cork. On the other hand, the cicatrization -- at the base of the marcescent leaves -- which always occurs later than in the pulvini of the deciduous leaves, is ordinarily less developed than in these latter cases; the later it begins, the less developed it will be, that is to say, assuming it begins at a time when the vegetation has already been slowed down noticeably.

The fact that the cicatrization rarely occurs below the wounds left by the folioles may be attributed to the same cause since, in effect, at the time these folioles fall, the leaves themselves are getting ready to fall and very often are just about to fall, so that there is certainly a considerable reduction in the vitality of the petiole at that time. Moreover -- and this tends to prove this point -- the scar reaction in the foliole pulvinus occurs in an evident and tangible fashion only when the folioles fall prematurely, that is to say, when they fall a rather long time before the petiole, at a time when the latter still has enough of the necessary vitality to react against the excitation of the wound.

In order to take place, ligno-suberous differentiation does not seem to require a state of cell vitality as well developed as the state required for the meristematization and formation of a secondary cork generating zone; it may occur not only rather late, after the fall of the leaf or the foliole, but it may also turn out to be the consequence of a last effort of reaction made by the tissue which is just about to die. I showed, in effect, that, in the formation of the ligno-suberous strata, lignification appeared first and that it represents the result of a reaction that is still common to all tissues: on the other hand, the production of the suberous film reveals all of the characteristics of an individual defense put up by each of the elements and representing their last vital act. The lignin does not remain located in the special membrane of each of the cells; it spreads into all of the tissues and here reaches even the walls of the dead cells, such as those of the more or less crushed sieve-like tubes, as well as those of certain latex-bearing organs and certain crystal-bearing cells which are devoid of protoplasm; it may exude in the form of gummy lignin, either into the intercellular channels which it blocks or into the ligneous vessels. The suberous film, on the other hand, is lacking in all of these dead elements, as in the ligneous vessels, whereas it does develop in all of the still living elements of the parenchyma and even in the crystal-bearing cells or in the cells which are already heavily differentiated, such as certain sclerites of Menispermum canadense; here these elements, which still contain protoplasm, are still capable of individually reacting before dying. This suberous reaction of the cells is only rarely capable of producing a weak diffusion of suberin outside the film into the neighboring parietal strata; this can barely be observed only at the base of the ligno-suberous strata and, only when these strata develop early, [it can be observed] a long time before the fall of the leaf.

Cicatricial Function of Ligno-Suberous Strata

I indicated that the formation of a ligno-suberous stratum never constitutes a means of definite cicatrization for the wound; but this stratum is often the only defense mechanism which the plant has during the winter following defoliation. We might therefore ask ourselves how the plant is protected during that span of time. Here we might first of all consider that the lignification of the cell walls -- by lending consistency to the ligno-suberous stratum -- prevents the subjacent tissues from being crushed and crumpled; but it is obvious that it also serves, to a considerable extent, for the protection of these tissues against outside agents by forming a kind of impermeable screen. In particular, it stops the invasion of fungi. We know, in effect, that the mycelian filaments usually grow into [in] the tissues either by circulating among the cells through the channels or in the membranes, or by growing across the latter, penetrating into the cell cavities. Now, at the level of the scar strata, these filaments cannot circulate through the channels because these channels most often are either excessively reduced in size [diameter] or they are frequently obstructed by gummy lignin; from then on, the lignification of the walls becomes the real obstacle to the circulation of the mycelian filaments between the cells. Now, what about the penetration of the fungi through the pits and across the cell cavities? This penetration is prevented by suberin -- an excellent protective substance -- which accompanies the lignin in the ligno-suberous strata and which, although in a small quantity, is here arranged in the form of a film around each cell so as to isolate and protect its cavity.

As further confirmation of what I have just said about the scar function of the ligno-suberous strata with respect to the invasion by fungi, I might also point out that the sacrificed parenchyma, which often separates the strata of the surface of the wound, is frequently invaded by an abundant mycelium; this mycelium, however, never penetrates into the subjacent ligno-suberous tissue.

The same qualities of impermeability of the ligno-suberous lamina very probably permit them to prevent also the loss of interior liquids.

Deeper Cicatrization of Tissues in Bundles

In connection with the cicatrization of the leaf bundles I said that the ligno-suberization descends further down in their interior than in the neighboring parenchyma.

This deeper penetration of ligno-suberization into the bundles probably, on the one hand, comes from the fact that their elements, very much elongated longitudinally, enable the excitation due to the wound to be propagated further along; on the other hand, it probably comes from the fact that this excitation [stimulation] is exerted over a longer period of time since the bundle tissues are always those in which the ligno-suberization continues to develop most slowly and most belatedly.

This extension of the ligno-suberous lamina inside the bundles explains the sometimes very pronounced curve which the scar cork describes at that point toward the stem. Its generating zone, in effect, can develop only in living elements; it is, from that point onward, forced to perform a downward movement in going around the ligno-suberous region of the bundles whose elements are dead.

Conditions Under Which Thalli and Gummy Lignin Appear

I explained earlier that the exudation of gummy lignin, through the cells of the scar tissues, turns out to be one of the results of the collective defense of these tissues through lignification. I must, however, also point out that this gummy lignin seems to be deposited particularly in special places of excitation: for example, in the vessels, in certain glandular canals, in the intercellular channels, etc. In addition, we must note that the thalli develop in the same regions of the vessels and of the glandular canals and that they do so before the appearance of lignin. We might therefore say that gummy lignin is deposited in openings established across the cicatrization tissues, at a point where the proliferation of the border cells does not manage to fill them up, that is to say, it does not manage to block them completely.

It seems quite obvious that the formation of thalli and the production of wound lignin are due to the slowdown in the vital activity of the leaf and the excitation of the separating stratum. However, if we remember that the production of these substances may also be encountered in the tissues of the petiole and of the pulvinus up to a distance from the separating stratum which is considerably greater than in the case of the other scar tissues, we must admit that the holes, in which they are formed act rather in the manner of folds of the exciting surface which would penetrate into the interior of the tissues of the petiole and those of the pulvinus; or, in other words, we might say that the cavity of these holes permits the transmission of excitation over a greater distance along /[from/] the separating stratum than the neighboring tissues would permit.

Physiological Significance of Subcicatricial Lignified Stratum

In the phenomenon of leaf fall, the role of the changes which we have just pointed out (development of thalli, gummy lignin, formation of successive scar strata) is quite clear: it is to protect the plant against the consequences of defoliation.

The same, however, cannot be true for lignification which often occurs in the tissues above the separating stratum; this lignification is expressed by the establishment of the subcicatricial lignified stratum. This stratum, in effect, disappears upon defoliation since it is involved in the fall of the organ at whose base it has developed. Is it, then, of some use or any use whatever to the plant? What is its significance?

We might ask ourselves, first of all, whether its presence, at the base of the petiole and the folioles, might not help to speed up the decay and subsequent fall of these organs. Well, I do not think so because, in addition to the fact that it is generally more or less thin, it usually avoids the bast-ligneous bundles, that is to say, it does not in any way interfere with the circulation of the sap. This is even more likely to be the case since, as we showed earlier, we have scar strata which are much better insulating agents than this particular stratum, without the leaf suffering as a result; these scar strata often exist almost immediately below this lignification stratum, in the pulvinus, and a long time before defoliation. I might also add that a similar lignified stratum may develop, not only above the separating stratum formed in autumn in the base of the leaves and the folioles, as well as in the internodes of certain composite petioles, but also above the separating strata which produce flaps in the case of revival of cicatrization, that is to say, under conditions when the above assumption is no longer admissable.

Nor do I think that the establishment of the lignified stratum is the result of a reverse reaction. I showed, in effect, that -- by way of preparation of the defense required in response to the coming fall of the leaf -- the pulvinus is the site of great vital activity whose upper portion is indicated by the separating stratum at the same time that it also represents maximum intensity here; we furthermore know that an organ, whose vital activity is, on the contrary, in the process of diminishing, begins immediately above the separating stratum. In the upper region of the separating stratum we thus have a boundary between two tissues with very different activities; in other words -- as I indicated earlier -- we have a free surface, such as Mr. Eug. Bertrand sees it (loc. cit.). On either side of this free surface, the tissues react because of their vitality; I showed earlier how vigorous the reaction is here, below this surface, in the pulvinus. Above it, the vitality of the tissues of the petiole is greatly reduced and the reaction is much less. Here it suffices only to produce the general lignification of a stratum of tissues sometimes preceded by meristematization; it is, however, inadequate to bring about the individual suberization of its cells and, even moreso, the formation of the secondary tissues. If we use the nomenclature proposed by Mr. Lignier (Lignier, O., "Contribution to the Nomenclature of Secondary Tissues," Bull. de la Soc. Linn. de Normandie, 4th Series, Volume IX, 1895, page 40), then the subcicatricial strata in the petiole are strata that have been "epicinicized" [seasoned] at the same rate as the scar strata in the pulvinus and they differ only in the intensity of the reaction.

We must furthermore note that, in the base of the leaf, the subcicatricial epicinization is much less than the one formed below the scar; this is easily explained by the excessive difference in the vitality of the reacting tissues; in some cases, however, it may be greater than it. This, then, is the situation at the base of certain folioles and even moreso in the petiole nodes, probably because the vitality of the chlorophyll region is capable of lasting longer than that of the petiole regions.

In support of this opinion on the physiological significance of the subcicatricial lignified stratum, I might add that the symmetry of the epicinizing reactions on either side of the free surface (dehiscence surface) is furthermore manifested by the following facts: at the lower end of the petiole, which is in the process of becoming detached, we have a variable stratum of cells that are physiological similar to those of which the separating stratum at the tip of the pulvinus is made up; the vessels and gland canals in the base of the petioles and the folioles here are blocked by thalli and sometimes even by the gummy lignin, like those in the pulvinus; these latter reaction manifestations sometimes occur with even greater intensity above than below the dehiscence surface.

Our opinion here is further supported by what happens in the case of Cotoneaster melanocarpa. Here we might remember that, in this particular species, we may have one or two separation revival strata which are more or less complete and which can grow here successively in the pulvinus, below the primary scar lamina; now, each of them is topped by a lignified stratum although they are very close to each other.

Finally, I might say the following to anyone who would object to my explanation of the uselessness of this subcicatricial epicinization as far as the plant is concerned (although, of course, I do admit this uselessness): this is not the only case where we can observe the development of a tissue that is obviously useless to the plant. In effect, the scar strata which sometimes develop below the wounds left by the folioles are no good to the plant and help only the petiole; but even their usefulness to the petiole is debatable since the petiole falls very soon after the foliole.

Conclusions

We can arrive at the following conclusions on the basis of the observations which I have reported on here and which I made on roughly a hundred species of dicotyledons with deciduous or marcescent leaves, as well as on the basis of the discussion and interpretation of the facts recorded.

The impending death of the leaf brings about certain anatomical changes in its base which often appear before the visible symptoms of this death. These [changes] are the formation of a separating stratum and the differentiation of the cicatrization tissues. One or the other of these two types of changes occurs in all cases.

Detachment of Leaf

Separating Stratum

The separating stratum is the place where the leaf dehiscence surface is formed during defoliation. It develops not far from the base of the organ, above its axillary angle, and it is always characterized a short time before the leaf falls.

In leaves which have an articulation at their base, an articulation at whose level the tissues are more or less specialized and offer less resistance, the separating stratum is located in this articulation.

The separating stratum almost always involves several cell layers although sometimes it consists of only one. The layers constituting it are either of primary origin, that is to say, they do not have any prior subdivisions, or they are of meristematic origin. The dead cells or the too heavily specialized cells, such as the ligneous vessels, the sieve-like tubes, the crystal-bearing cells, etc., are not involved in its formation.

Dehiscence of Leaf

The dehiscence of the leaf may occur according to one of the following two distinct processes.

1. When the separating stratum consists of only one layer, we can observe the elongation of the cells and the consecutive thinning of the walls; after this comes the dehiscence as a result of the rupture of these thinned walls.

2. When the separating stratum consists of several layers, that is to say, in the most frequent case, the dehiscence is, on the other hand, the result of a separation or detachment which develops between certain cells of this stratum, near its upper face.

In this connection, the cell walls are transformed, in the entire stratum, into a pecto-cellulosic mucilage, exclusive of a thin membrane which directly limits the cell cavities. Then the mucilage is dissolved in such a manner that the protoplasm of the cells here remains covered only by this thin membrane; however, this last phase occurs only in the region of dehiscence and, between two of its layers, the cells involved remain attached, at least along one of their sides, either to the tip of the pulvinus or to the base of the petiole.

The dead or too heavily specialized cells (ligneous vessels, sieve-like tubes, etc.) are then broken as a result of the elongation -- in the opposite direction -- of the cells bordering on the dehiscence crack, provided they have not already been broken by the longitudinal growth of the entire stratum which often precedes the detachment. This mechanical action is furthermore aided and often entirely replaced by the mechanical action of the weight of the leaf, the wind, and the frost.

Cicatrization

The separating stratum appears in the base of the leaf as a source of excitation for the neighboring tissues. Above it, the elements of the petiole react in the majority of the cases in the fashion of those which are below, in the pulvinus, although ordinarily with a considerably smaller intensity. Below, the stimulating action of this separating stratum appears to occur concurrently with the action due to the impending death of the leaf and it seems to precede the action which results from the wound produced by its dehiscence; the result of these various actions then leads to cicatrization.

We might also remark that, probably as a result of progressive adaptation, this cicatrization in many species begins to develop more or less shortly before the apparent development of these various stimulating causes.

The size of the scar strata is generally in a direct proportion with the size of the scar, that is to say, we have thick scar tissues corresponding to big scars.

Nature of Tissues Produced by Subcicatricial Reaction

The anatomical peculiarities which result from the subcicatricial reaction of the base of the petiole are the very frequent formation of a lignified stratum, the proliferation of thalli in the vessels and in the secretory canals, the formation of finger-shaped partitions in the branching laticiferous organs, the deposit of gummy lignin, etc.

Nature of Scar Tissues of Pulvinus

The cicatrization of the pulvinus occurs in different ways, depending on the nature of the elements and of the tissues which are involved.

a. In the parenchymatous tissues we may have the following, separately or concurrently:

A region of primary meristematization with variable extent and position, that is to say, a region in which the cells undergo more or less intensive and more or less regular subdivision.

A ligno-suberous stratum whose cells may or may not be the site of a primary meristematization.

A sclerous area, in other words, an area made up of cells with very thick and lignified walls, at the level of the ligno-suberous stratum (only in Maclura aurantiaca). (Let us remember here that, according to Brettfeld (loc. cit.), these sclerous tissues often become involved in the cicatrization of the leaf pulvini of the monocotyledons.)

A cicatricial periderm, most frequently represented only by a secondary cork, which, however, may also contain a more or less thick phelloderm. This periderm is always deeper than the preceding scar tissues; it is never absent and it terminates the cicatrization.

b. In the ligneous vessels we either have a proliferation of thalli on their inside, or a deposit of gummy lignin, or both of them together. The lignin here always turns out to develop relatively later than the thalli.

c. In the sieve-like tubes, as in certain dead or dying secreting cells (certain crystal-bearing cells, certain articulated laticiferous cells, etc.) or, generally, in the dead elements, the remaining walls are probably lignified due to the influence of the secretion from the neighboring elements.

d. In the same secreting elements — that is to say, when they are still due to a certain protoplasm activity — cicatrization occurs due to ligno-suberization of their walls.

e. In the branching laticiferous organs, cicatrization occurs through the formation of solidified latex plugs, generally followed by the establishment of finger-shaped partitions.

f. In the secretory sacs through ligno-suberization of the epithelial cells.

g. In the secretory canals due to the formation of thalli at the expense of the epithelial cells or due to deposit of gummy lignin in their cavity.

Description and Discussion of Significance of Scar Strata

a. The primary meristematization is always preceded by a recrudescence of protoplasm activity and it appears in the base of the leaf as the earliest means of defense.

b. The characterization of the ligno-suberous stratum is marked by two successive transformations:

1. The general lignification of the walls in all the tissues, without these walls having undergone any prior thickening.

2. The formation, in each cell, of a suberous film which fills its entire cavity, including those [cavities] of the pits and which then is expressed in the form of discordant stratification on the preceding parietal strata.

Lignification appears to be a process of collective defense put up by the cells of the stratum and suberization appears to be a process of individual defence. Whenever the latter exists, it more or less rapidly follows the former and constitutes the last vital act of the cell. The completely characterized ligno-suberized cells are, in effect, dead tissues.

In summary, despite the energy of its cicatricial action, ligno-suberization constitutes only a transitory defense making it possible [for the plant] to wait for the intervention of definite cicatrization through the secondary cork.

c. The cicatricial periderm, which is the cicatrization tissue par excellence, develops in the pulvinus in various ways, depending on the time and the place of its appearance and also depending on the mode of surface cicatrization of the neighboring regions in the stem.

If the cicatricial periderm is formed before the caulinary periderm or well above and at some distance from it, it develops across all of the tissues of the pulvinus and it does not connect up with it until much later. If, on the other hand, the caulinary periderm exists already before the appearance of the scar cork and if it rises sufficiently high in the pulvinus, then this cork merely closes the opening which the former presents in the base of the leaf. Likewise, in the case where the caulinary periderm is deep in the stem and is wound around the bast-ligneous bundles that come out here, enveloping them like a sleeve, the cicatricial periderm extends only across these bundles.

The cicatricial periderm generating zone is established in all of the parenchymatous elements which it encounters, including the thalli and even the articulated laticiferous organs in some species. This periderm is capable of breaking, through lateral compression and of blocking the ligneous vessels as well as most of the laticiferous organs; it rarely manages to grow across the hard tissues in the external part of the bast -- in the same fashion, that is -- when it is located in its way.

d. The thalli are particularly interesting as cicatrization means. They are formed either in the ligneous vessels at the expense of the parenchymatous cells which are contiguous to them or in the secretory canals at the expense of their epithelial cells; they serve primarily to fill up the cavity of these tube-shaped openings. Then they participate in the formation of the separating stratum, in that of the lignified strata and of the ligno-suberous strata and, while subdividing, in that of the secondary scar cork, in the same way as the parenchymatous tissues in the rest of the organ that is to be cicatrized.

e. The gummy lignin is lignin which has exuded through the neighboring cells into the cavity of certain vessels, certain secretory canals, and into the cavity of some of the intercellular channels; it is deposited here in a variable quantity; it looks like a gummy and sometimes more or less granulated mass. This substance blocks these cavities.

f. Very often, we have a zone of barely modified tissue above the well-characterized defense tissues, between them and the wound stimulating surface; this barely modified zone is flattened at the surface of the wound and is often invaded by fungi. I called this zone "sacrificed parenchyma."

Cicatrization Periods

The great variety which I observed in the ways of cicatrization results above all from the time at which the means of cicatrization, which we have just described, go into action.

During the first year, cicatrization can occur only after defoliation; in this case it involves almost always only the ligno-suberous stratum.

If, on the other hand, it develops before defoliation, it can then either include only the ligno-suberous stratum or only the cork; in that case, we ordinarily do not have any more variations until the following year; or it may already have the two strata at the same time.

The parenchymatous tissue of the bast-ligneous bundles is in all cases almost entirely avoided by cicatrization, so long as the leaf has not fallen, regardless of the state of the scar lamina in the neighboring tissues. It is in turn invaded only after the fall, that is to say, after the cessation of its conducting functions. Only the ligneous vessels may have been earlier blocked either by the thalli or by the gummy lignin, or by both of them at the same time.

Regardless of whether cicatrization begins before the leaf falls or whether it begins only after the leaf has fallen, it is never completed during the first year; it is completed through the formation or termination of the secondary cork only during the second year.

Special Features

a. When the petiole has, at its base, a swelling which covers the axillary buds, the separating stratum sometimes is established in a way permitting the attachment, to the pulvinus, of a portion of this swelling; this portion of the swelling continues to protect the buds after the leaf has fallen. It is this portion which I called "leaf-bud scale lamella."

b. In certain species we can observe something which I have called the "revival of cicatrization," that is to say, the first scar tissues are removed, during the second year, by a new separating stratum established below them; the final cicatrization then develops below the new wound.

c. The marcescence of the leaves results from the fact that, as a result of their belated development, the autumn separating stratum has not had time to develop completely here before the winter or it may not develop at all. In the pulvinus of these leaves we can also observe the development of a primary scar stratum, such as the one we have in the deciduous leaves, and, during the following spring, we have a revival of cicatrization which then causes defoliation.

Fall of Various Parts of Composite Leaves

a. The fall of the folioles and of the secondary petioles (bipinnate leaves) occurs in the same way as in the case of the leaf itself. But they cause the cicatrization of the subjacent pulvini only when they come relatively earlier than the fall of the leaf. The cicatrization thus produced is, furthermore, always less forceful; most often it is accomplished by a thin ligno-suberous stratum which, however, may, in some cases, be accompanied by a rather underdeveloped cork. We might point out, furthermore, that, at the base of these folioles and these secondary petioles, the subcicatricial lignifying reaction is more frequent than the cicatricial reaction of the immediately subjacent pulvinus.

b. When the petioles of the composite [complex] leaves have nodal swellings, these may be the place where the transversal separating strata are formed; these strata, by the way, are similar to those at the base of the leaf and of the folioles and they sometimes bring about their disarticulation.

Although they may sometimes give us some information that would help us in specific or sometimes even generic determination, we can say that defoliation and cicatrization generally cannot give us any information that would be important in the description of the system involved. These are purely physiological phenomena whose phases may resemble each other in species belonging to different families and which, on the other hand, may differ within the species or related genera.

Plate Captions

Legend

cs -- separating stratum
rs -- subcicatricial lignified stratum
ss -- ligno-suberous stratum
lic -- secondary scar cork
zn -- scar cork generating zone
pd -- stem periderm
bo -- wood
lm -- soft bast
ls -- hard bast
ep -- epiderm
th -- thalli
scl -- lignified portion of walls
sub -- suberous film
ce -- sacrificed parenchyma
tcr -- sieve-like tube
lig -- gummy lignin
ci -- leaf scar
cif -- fascicular navel
P -- petiole
B -- bud
C -- leaf pulvinus

Plate VII

Fig. 1. Aristolochia Sipho. Diagram of longitudinal section of base of petiole several days before defoliation. 9X. H -- lower limit of ligno-suberous stratum which is differentiated after the leaf falls.

Fig. 2. Portion of a longitudinal section of base of leaf in region of separating stratum: beginning of longitudinal growth of walls of layer which will form this stratum. 200X. m -- wall beginning to thin out.

Fig. 3. Same section as before in more advanced state of separating layer, short time before rupture of its walls. 200X.

Fig. 4. Leaf scar. 2/3X.

Fig. 5. Longitudinal section of a portion of the ligno-suberous stratum of cicatrization in the leaf pulvinus. 320X. po -- pit into which penetrates the suberous film; cu -- cuticle; cc-- cuticular strata; cr -- crystal-bearing cells (the crystal is dissolved).

Fig. 6. Portion of transversal section of leaf bundle at level of ligno-suberous stratum of pulvinus. 140X. l -- bast; bs -- secondary wood; bp -- primary wood; tcr -- lignified sieve-like tube; th -- ligno-suberized thallus; z -- ligno-suberized zone of change [exchange zone].

Fig. 7. Longitudinal section in leaf pulvinus showing mode of propagation of scar cork across wood of bundles. 140X. thp -- thallus about to become involved in composition of cork.

Fig. 8. Diagram of longitudinal section of pulvinus at end of second year. 9X.

Fig. 9. Amorpha fruticosa. Diagram of longitudinal section in base of petiole some days before the leaf falls. 9X.

Fig. 10. Portion of a longitudinal section of the base of the leaf in the region of the separating stratum at the moment the cell walls become mucilaginous. 160X. mu -- mucilaginous walls.

Fig. 11. Same separating stratum in more advanced state, at beginning of partial dissolution of walls. 140X. ci -- portion of walls which is not dissolved and which continues to envelop the protoplasm.

Fig. 12. Same separating stratum in even more advanced phase. Dehiscence has taken place and border cells begin to grow longitudinally. 140X. mu, ci -- as in preceding figures.

Fig. 13. Leaf scar. 4X.

Fig. 14. Diagram of longitudinal section of leaf pulvinous at end of first year. 9X.

Fig. 15. Portion of transversal section of leaf bundle at level of ligno-suberous stratum of pulvinus. 140X. l -- bast; bo -- wood; tcr -- crushed and lignified sieve-like tubes; la -- groups of lignified laticiferous organs; z -- ligno-suberized exchange zone.

Fig. 16. Longitudinal sections of vessels showing the different ways in which gummy lignin is deposited inside them. 250X. lga -- amorphous gummy lignin; lgg -- granualr gummy lignin.

Fig. 17. A crystal-bearing cell of the leaf pulvinus before differentiation of ligno-suberous stratum (crystal dissolved). 360X. ev -- envelope of crystal; es -- lignified thickening of cell wall.

Fig. 18. Crystal-bearing cell taken from same region as preceding one but after formation of ligno-suberous stratum (crystal dissolved). 360X. ev, es -- as in preceding figure; scl -- belatedly lignified portion of cell wall; sub -- suberous film; lig -- gummy lignin deposited in cell cavity.

Fig. 19. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X. H -- base of first-year scar lamina; s-- lignified strata.

Fig. 20. Koelreuteria paniculata. Leaf scar. 2X.

Plate VIII

Fig. 21. Koelreuteria paniculata. Diagram of longitudinal section of base of petiole several days before the leaf falls. 9X.

Fig. 22. Portion of longitudinal section of petiole in region of separating stratum before dehiscence. 80X.

Fig. 23. Same separating stratum at moment of dehiscence inside it. 120X.

Fig. 24. Diagram of longitudinal section of leaf pulvinus at end of first year. 9X.

Fig. 25. Portion of longitudinal section of leaf bundle at level of ligno-suberous cicatrization stratum. 280X. lgg -- granular gummy lignin; lga -- amorphous gummy lignin; th -- ligno-suberized thalli.

Fig. 26. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X.

Fig. 27. Paulownia imperialis. Portion of longitudinal section at base of petiole several days before leaf falls. rm -- meristematic region of leaf pulvinus.

Fig. 28. Cells of external cortical parenchyma of pulvinus at level of ligno-suberous stratum; intercellular channels more or less blocked by gummy lignin lig. 150X.

Fig. 29. Diospyros virginiana. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 30. Portion of longitudinal section of adult leaf at level of its articulation. 120X. art -- articulation tissue.

Fig. 31. Same region as in preceding figure at moment of dehiscence of leaf: separating stratum is formed by specialized leaf articulation stratum. 120X.

Fig. 32. Leaf scar. 2.5X.

Fig. 33. Morus nigra. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. la -- laticiferous organ; cl -- finger-shaped partitions.

Fig. 34. Portion of longitudinal section of base of petiole several days before leaf falls. 60X. la, cl -- as in preceding figure.

Fig. 35. Leaf scar. 4X.

Fig. 36. Diagram of longitudinal section of leaf pulvinus at end of second year. 4X. ph -- phelloderm.

Fig. 37. Portion of longitudinal section of base of petiole: occlusion of laticiferous organs. 120X. la -- laticiferous organ; cl -- finger-shaped partitions.

Fig. 38. Beginning of cicatrization of laticiferous organ. 250X. bl -- mass of modified latex; la -- ordinary latex.

Fig. 39. More advanced cicatrization of laticiferous organ. 250X. cl -- finger-shaped partition developed against mass of modified latex bl.

Fig. 40. Several special forms of finger-shaped partitions in laticiferous organs. 120X.

Plate IX

Fig. 41. Aesculus Hippocastanum. Diagram of longitudinal section of base of petiole several days before the leaf falls. 9X.

Fig. 42. Portion of longitudinal section of base of petiole several days before leaf falls. 40X.

Fig. 43. Passage of scar cork across ligneous vessel of leaf bundle. 200X. thp -- thallus becoming involved in composition of cork.

Fig. 44. Forsythia suspensa. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 45. Portion of a longitudinal section of base of petiole several days before leaf falls. 65X.

Fig. 46. Leaf scar. 2.5X.

Fig. 47. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X.

Fig. 48. Alnus glutinosa. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. H -- lower limit of ligno-suberous transformation of parenchymatous elements of bundles after leaf falls.

Fig. 49. Portion of longitudinal section of base of petiole several days before leaf falls. 150X.

Fig. 50. Crystal-bearing cell inside ligno-suberous cicatrization stratum (crystal dissolved). 300X. ev -- envelope of crystal.

Fig. 51. Spiraea opulifolia. Diagram of longitudinal section of base of

petiole several days before leaf falls. 9X. pa -- cortical parenchyma; mp -- periderm sleeve surrounding leaf bundles in pulvinus.

Fig. 52. Diagram of transversal section of base of leaf before defoliation. 9X. pa, mp -- as in preceding figure.

Fig. 53. Portion of longitudinal section of base of petiole in region of separating stratum. 100X. rm -- meristematic region of pulvinus.

Fig. 54. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X. pa -- cortical parenchyma; mp -- periderm sleeve of leaf bundles.

Fig. 55. Hamamelis virginiana. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. H -- lower limit of ligno-suberous lamina which will develop after the leaf falls.

Fig. 56. Longitudinal section of ligneous vessels of base of petiole before defoliation, showing passage of a thallus (th) from one vessel to the other. 300X.

Fig. 57. Diagram of longitudinal section of leaf pulvinus in spring of second year and at moment of revival of cicatrization. 9X. H -- dehiscence crack produced inside separation revival stratum of cicatrization.

Fig. 58. Diagram of longitudinal section of base of petiole of marcescent leaf in spring of second year, several days before it falls. 9X. cs -- rough outline of autumn separating stratum; cs_2 -- cicatrization revival separating stratum at the same time causing marcescent leaf to fall.

Fig. 59. Hippophae rhamnoïdes. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 60. Celtis occidentalis. (Idem). crs -- crystal-bearing hard tissue.

Fig. 61. Portion of longitudinal section of scar cork. 350X. ph -- hard and crystal-bearing phelloderm; ev -- envelope of crystals (the latter have been dissolved).

Plate X

Fig. 62. Paliurus aculeatus. Portion of longitudinal section of base of petiole at level of separating stratum and of secreting cell E. 140X.

Fig. 63. Xanthoxylon fraxineum. Diagram of longitudinal section of base of petiole several days before leaf falls. 12X.

Fig. 64. Rhus Cotinus. (Idem). 16X. ca -- secretory canal; th -- portion of this canal which is blocked by thalli.

Fig. 65. Transversal section of secretory canal at base of petiole a little above separating stratum. 140X. th -- epithelial cells developed into thalli.

Fig. 66. Longitudinal section of secretory canal in vicinity of base of ligno-suberous lamina. 140X. ths -- ligno-suberous thalli at level of primary cicatrization lamina.

Fig. 67. Rhus Coriaria. Leaf scar. 2X.

Fig. 68. Longitudinal section of secretory canal in region where scar cork crosses it through subdivision of thalli. 140X.

Fig. 69. Negundo fraxinifolium. Longitudinal section of file of laticiferous cells in region where scar cork crosses it. 160X. su -- suberous framework of cork cells; eps -- lignified thickening of same cells.

Fig. 70. Scar cork. 2X. emp -- impression of portion of petiole which covered the bud before the leaf fell.

Fig. 71. Sophora japonica. Leaf scar. 2X. br -- cortical pouch on which portion of petiole, which covered bud before leaf fell, was supported.

Fig. 72. Menispermum canadense. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. lp -- prolongation of ligno-suberous lamina which will form the leaf-bud scale lamella after leaf falls.

Fig. 73. Diagram of section of leaf pulvinus at end of first year. 9X. lp -- leaf-bud scale lamella protecting lower buds after leaf falls.

Fig. 74. Leaf scar. 9X. Only the upper bud B is in the open air; the others are hidden under the scar.

Fig. 75. Group of sclerites inside ligno-suberous lamina; two of them have an internal suberous film (sub). 140X.

Fig. 76. Platanus occidentalis. Leaf scar almost completely surrounding axillary bud. 2.5X.

Fig. 77. Fraxinus Ornus. Portion of longitudinal section of phelloderm (ph) formed by scar cork generating zone. 140X. su -- suberous framework of cork cells; cel -- cellulosic thickening of same cells.

Fig. 78. Acer campestre. Crossing of a file of laticiferous cells (la) by scar cork. 100X.

Fig. 79. Aralia spinosa. Transversal section of secretory canal at level of lower region of ligno-suberous stratum. 100X.

Fig. 80. Catalpa bignonioïdes. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 81. Leaf scar. 1X. em -- conical protrusion formed by external leaf bundles.

Fig. 82. Robinia Pseudo-Acacia. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. lp -- leaf-bud scale lamella.

Fig. 83. Robinia hispida. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X. lic_1 -- first-year scar cork; lic_2 -- second-year scar cork.

Fig. 84. Gleditschia triacanthos. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 85. Leaf pulvinus whose upper portion hides the lowest axillary buds. 3X.

Plate XI

Fig. 86. Gleditschia triacanthos. Diagram of longitudinal section of leaf pulvinus at end of second year. 9X. lic_1 -- first-year scar cork; lic_2 -- second-year scar cork; s -- lignified tissue.

Fig. 87. Maclura aurantiaca. Diagram of longitudinal section of base of petioles several days before leaf falls. 9X. s -- hard portion of scar strata.

Fig. 88. Portion of longitudinal section of external region of petiole several days before leaf falls. 100X. s-- hard portion of scar stratum; a -- isolated ligno-suberous cell at level of this portion; la -- branching laticiferous organs; cl -- finger-shaped partition.

Fig. 89. Ptelea trifoliata. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. cp -- stratum specialized as separating stratum placed in prolongation of this original stratum but inside of which there is no dehiscence.

Fig. 90. Cymnocladus canadensis. Diagram of longitudinal section of leaf pulvinus at end of second year. 3X. lic_1 -- first-year scar cork; lic_2 -- second-year scar cork.

Fig. 91. Potentilla fruticosa. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. mp -- periderm sleeve of bundles in leaf pulvinus; pa -- cortical parenchyma; g, g_1 --

limits of deposit of gummy lignin after leaf falls.

Fig. 92. Calophaca volgarica. (Idem).

Fig. 93. Diagram of transversal section of leaf pulvinus in its upper portion, made before leaf falls. mp -- periderm sleeve common to the three re-entering connected bundles; fst -- stipular bundles ; pa -- cortical parenchyma; sc -- hard tissue.

Fig. 94. Caragana altagana. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X. pa -- cortical parenchyma; mp -- periderm sleeve of bundles; s -- lignified scar tissue.

Fig. 95. Philadelphus coronarius. (Idem). lr --leaf-bud scale lamella; mp -- periderm sleeve of bundles.

Fig. 96. Leaf scar. 2.5X. bc -- conical elevation of surface of scar indicating presence of axillary bud hidden below the latter.

Fig. 97. Chletra alnifolia. Diagram of longitudinal section of base of petiole several days before leaf falls. 9X.

Fig. 98. Azalea sinensis. (Idem).

Fig. 99. Portion of longitudinal section of base of petiole of adult leaf at level of its articulation. 200X. art -- specialized articulation stratum of petiole at expense of which the autumn separating stratum is formed.

Fig. 100. Sorbus aucuparia. Diagram of longitudinal section of leaf pulvinus at tip of a shoot, around springtime of second year, when the cicatrization revival separating stratum has been established. 9X. cs_2 -- separation revival stratum; rsc -- lignified region above this stratum.

Fig. 101. Same diagram as preceding one but for leaf pulvinus of base of shoot.

Fig. 102. Cotoneaster melanocarpa. Diagram of longitudinal section in leaf pulvinus from upper part of shoot, toward end of second year, and in which the cicatrization revival has not yet taken place. 9X. cs_2, rsc -- as in the two proceding figures; ss_2 -- new ligno-suberous lamina; lic_1 -- first-year scar cork; lic_2 -- second-year scar cork.

Fig. 103. Carpinus Betulus. Portion of longitudinal section of leaf pulvinus studied around middle of second year; cicatrization revival has not yet taken place here. 120X. a -- first layers with delicate walls formed by scar cork generating zone; their rupture will progressively lead to the revival of cicatrization.

Fig. 104. Sorbus aucuparia. Portion of longitudinal section of pulvinus of foliole which fell early. 120X. te -- rest of separating stratum.

Fig. 105. Juglans nigra. Diagram of longitudinal section of pulvinus of foliole which fell early. 9X.

Fig. 106. Calophaca volgarica. Diagram of longitudinal section of base of foliole several days before it falls. 16X. s -- lignified scar stratum.

Fig. 107. Staphylea pinnata. Diagram of longitudinal section of node of petiole at time of autumn defoliation. 9X.

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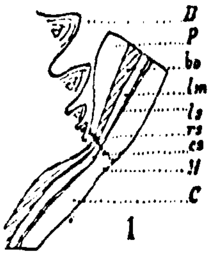

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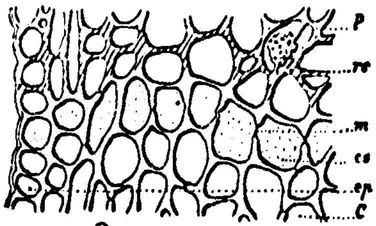

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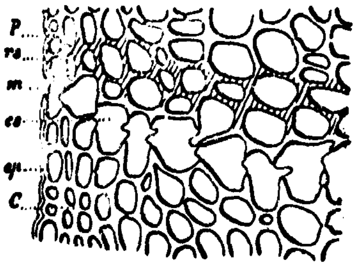

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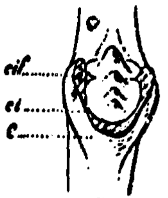

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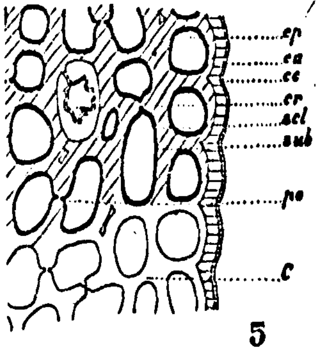

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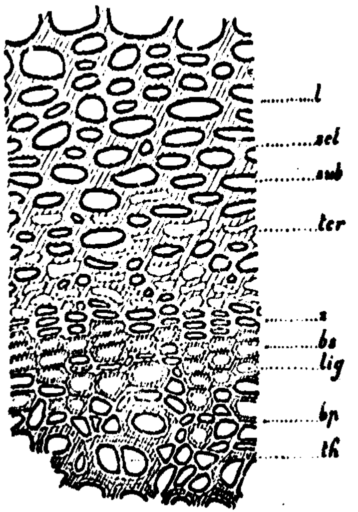

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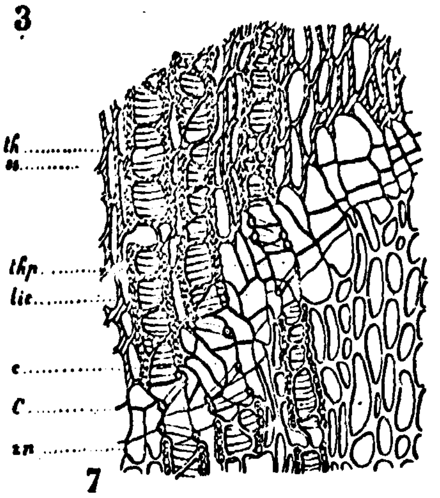

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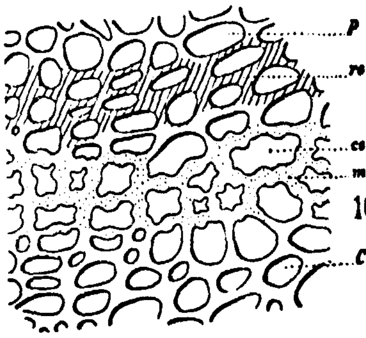

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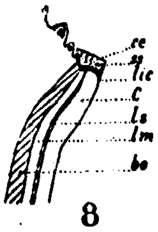

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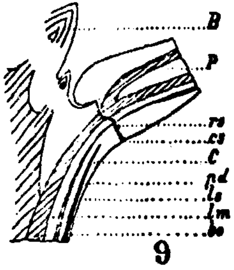

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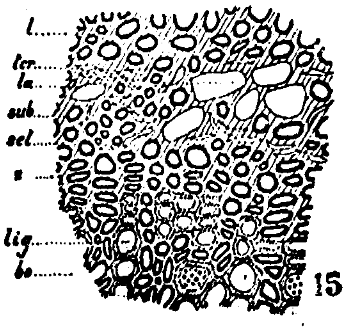

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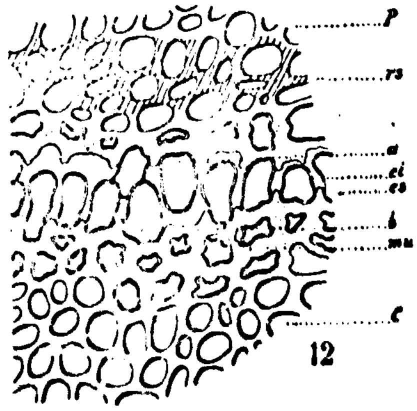

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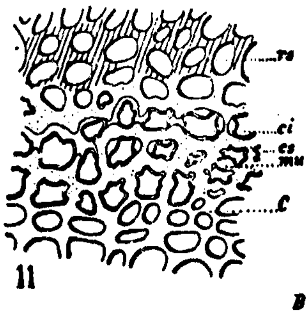

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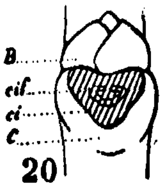

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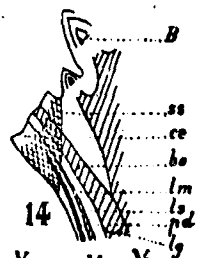

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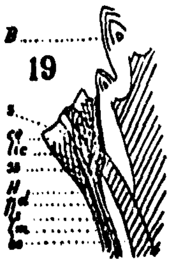

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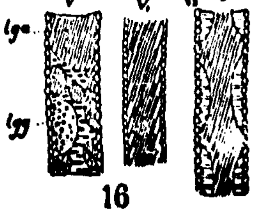

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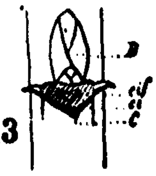

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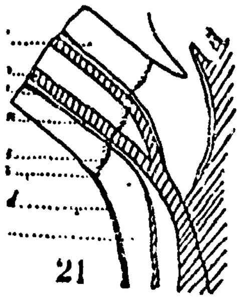

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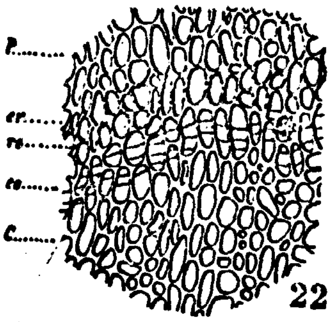

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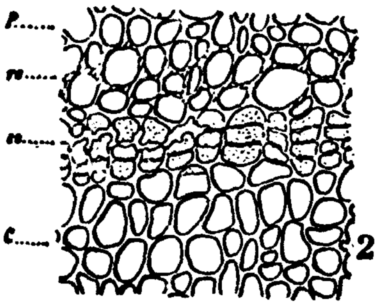

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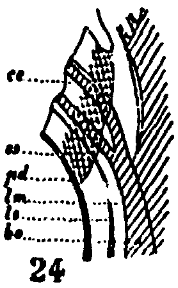

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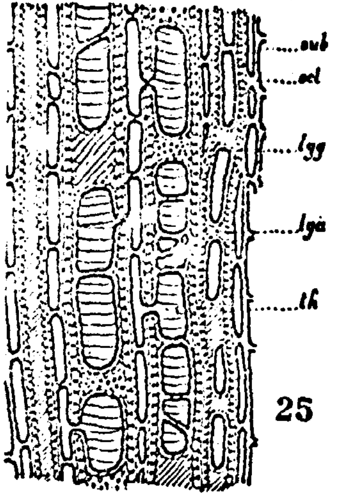

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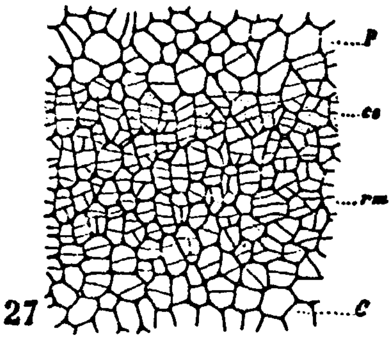

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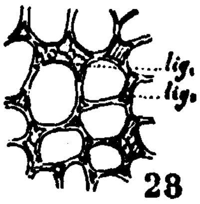

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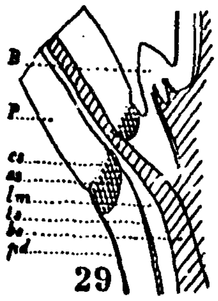

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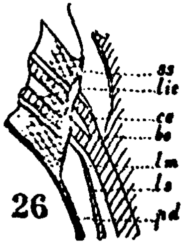

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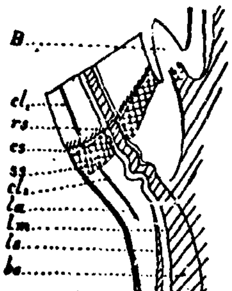

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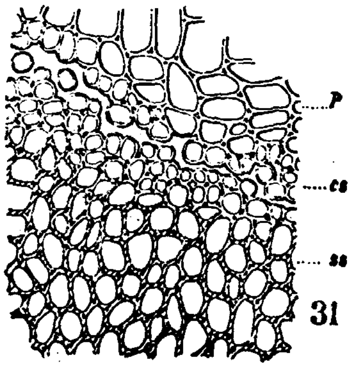

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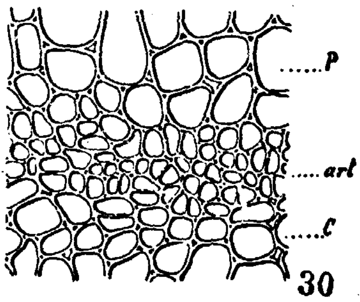

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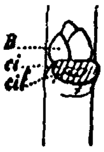

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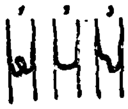

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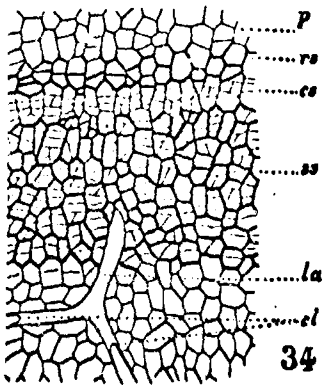

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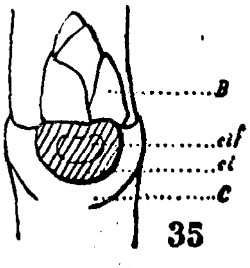

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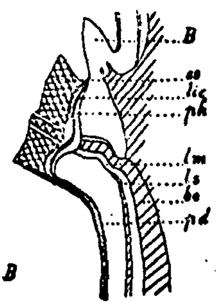

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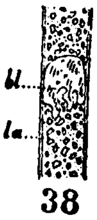

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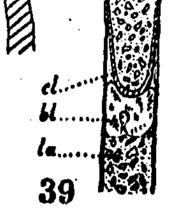

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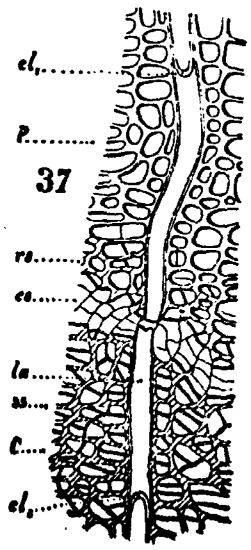

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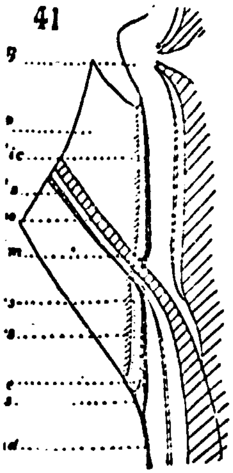
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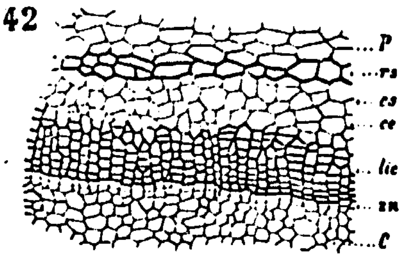
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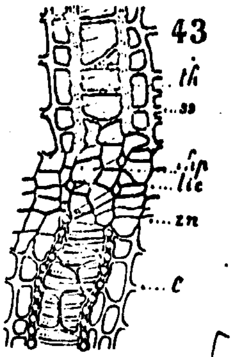
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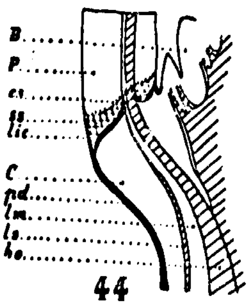
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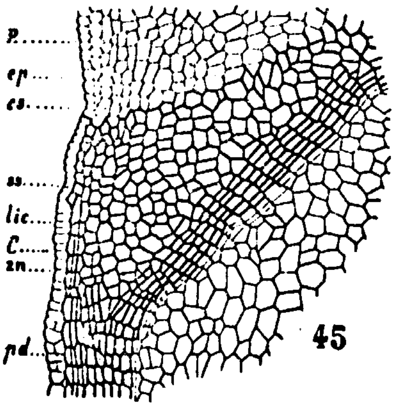
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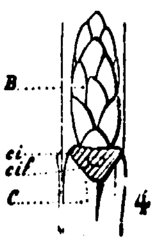
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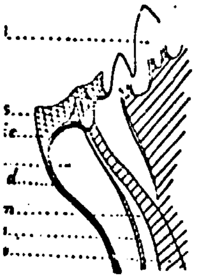
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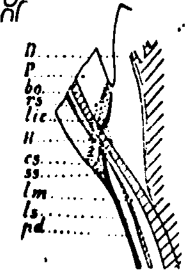
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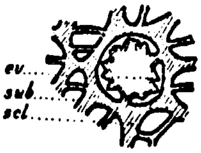
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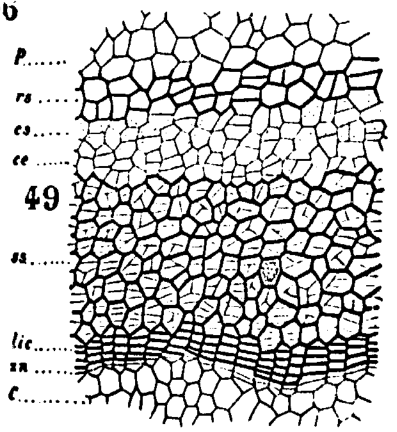
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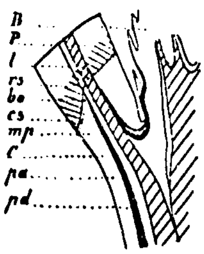
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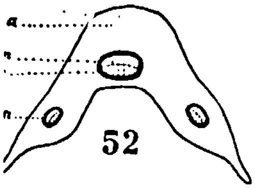
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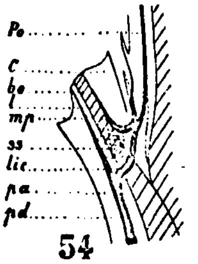
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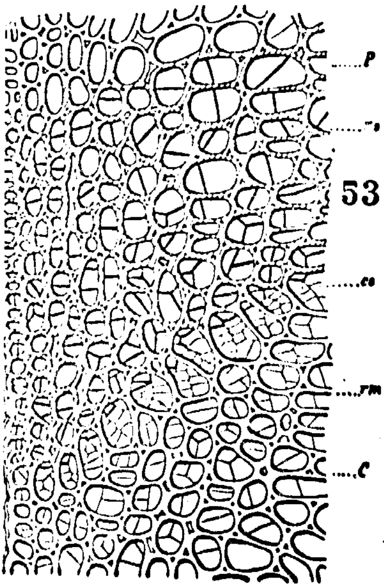
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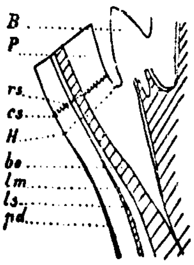
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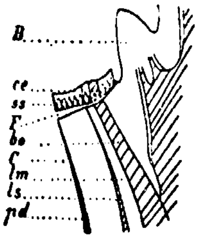
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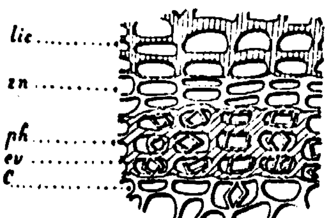
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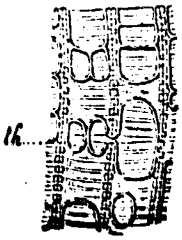
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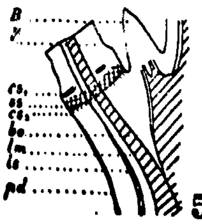
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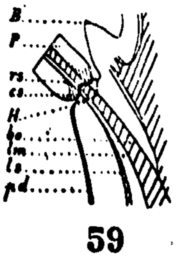
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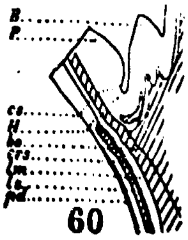
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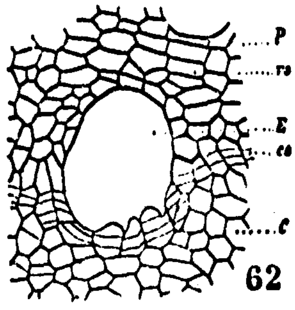

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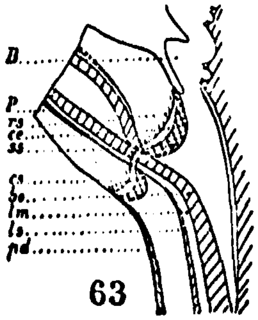

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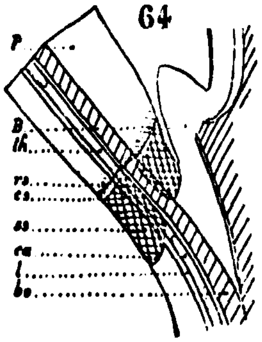

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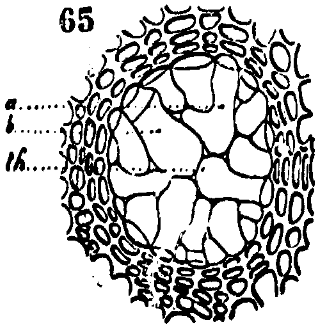

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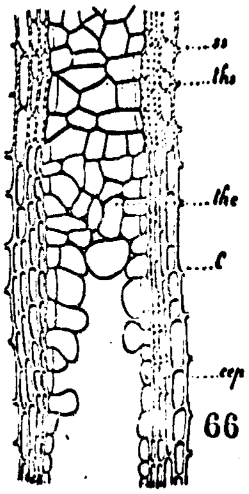

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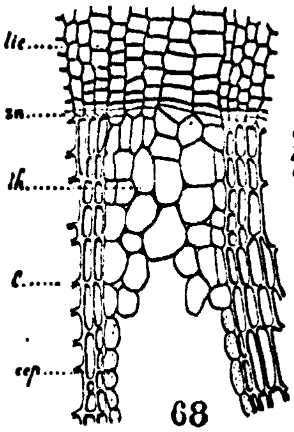

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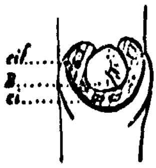

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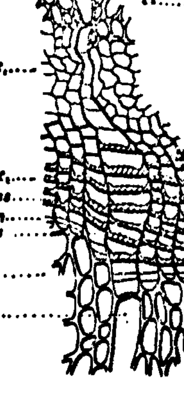

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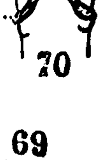

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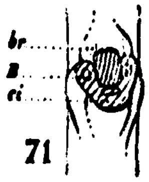

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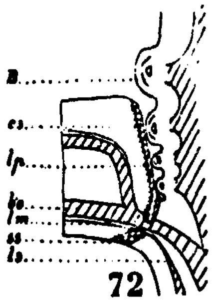

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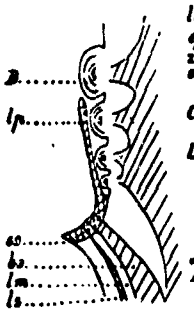

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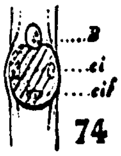

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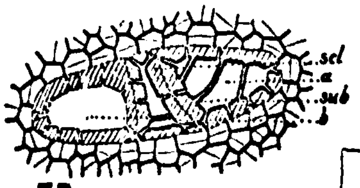

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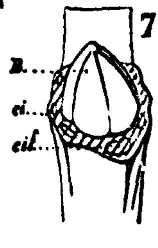

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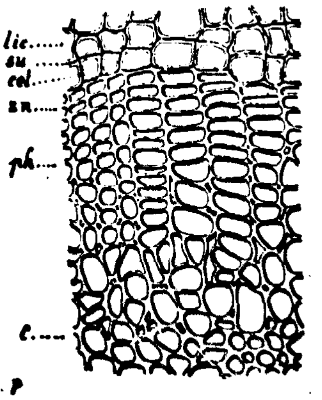

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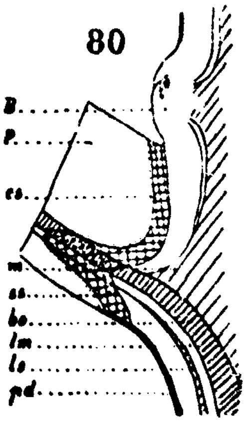

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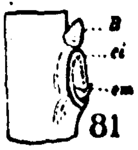

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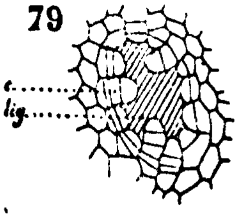

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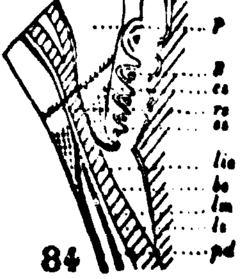

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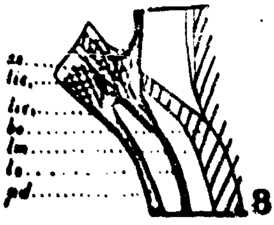

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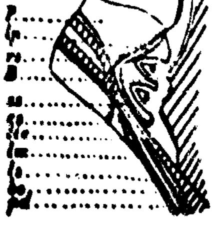

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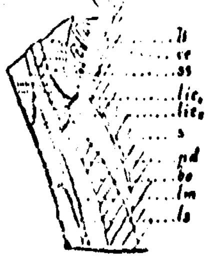

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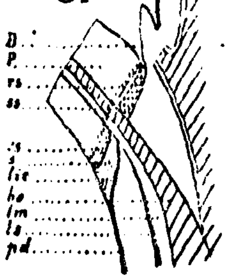

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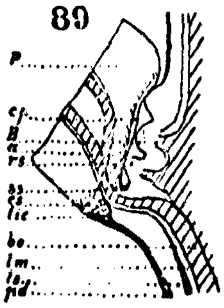

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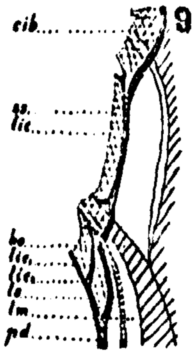

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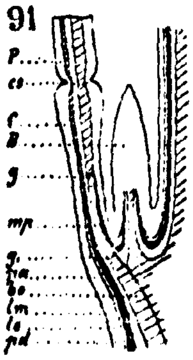

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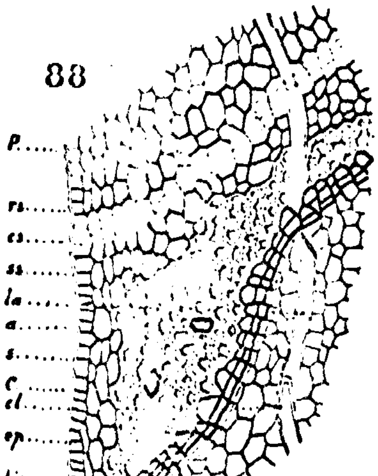

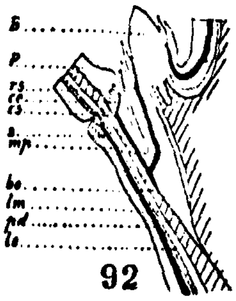

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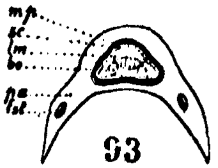

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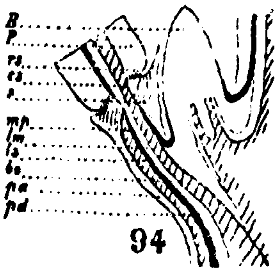

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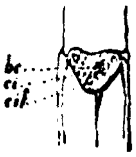

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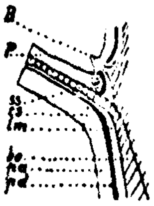

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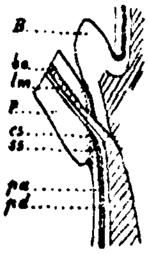

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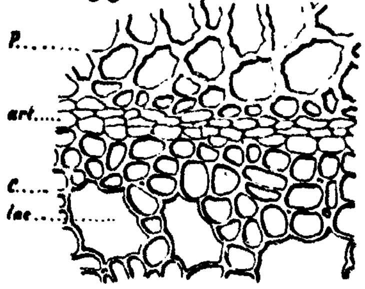

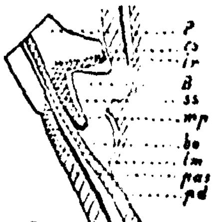

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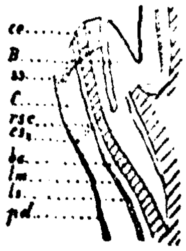

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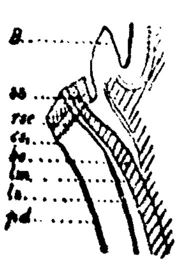

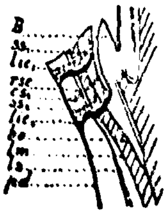

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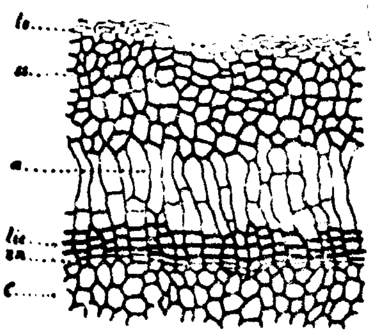

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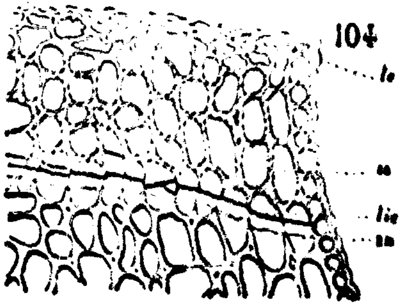

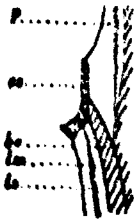

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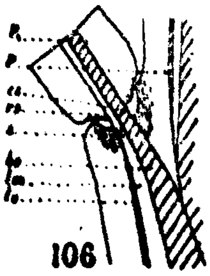

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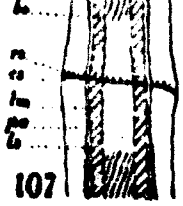

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