

# 1. THE COMPARATIVE ANATOMY AND PHYLOGENY OF THE CONIFERALES.

## PART 2. — THE ABIETINEAE.<sup>1</sup>

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### INTRODUCTION.

IN the first number of this series the writer (:03) has called attention to certain features of the anatomy of the genus *Sequoia*, which seemed to indicate for that genus an Abietineous origin. The results obtained in the case of *Sequoia* made it desirable that the Abietineae should be somewhat fully examined as a preliminary to the study of the other orders of the Coniferales. This procedure seems further advantageous, because the Abietineae are perhaps the most clearly defined and most accessible of existing Coniferous orders and are at the same time a geologically very ancient group.

The importance attachable to the anatomy of the Gymnosperms has recently been greatly increased by the discovery of the seeds of certain of the Cycadofilices. This alliance established by Potonie ('99, p. 160) on the basis of the morphology and anatomy of the vegetative organs alone, no longer ago than 1899, has recently received the fullest confirmation from the epoch-making discoveries of Oliver and Scott (:03) and Kidston (:03), which, as has been stated by Zeiller (:04), are destined to make a revolution in our conception of the nature of the Palaeozoic flora. By these discoveries, especially when taken together with older, similar ones in the case of the Calamites and Sigillarians, the taxonomic value of the anatomy of plants is placed at once on as secure a footing as that of animals since the time of Cuvier. The study of anatomy, which is so essential and which has recently yielded such important results in the case of fossil plants, has been much neglected in those now living, largely on account of the absence of proper perspective, which can alone be supplied by the knowledge of the older forms. In the case of the Angiosperms this perspective is still unfortunately lacking by reason of our entire ignorance of the nature and structure of their ancestry; but for the Gymnosperms the anatomical researches of the British, French, and German palaeobotanists have now reached a

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fullness which makes them of the greatest value in the interpretation of the phylogenetic relationships of the existing Gymnospermous groups. Extremely important results have been obtained in recent years by the anatomical method, in the case of the Ginkgoales and Cycadales; but the Coniferales can scarcely be considered to have been properly investigated in the light of recent additions to our knowledge of the structure of the Cycadofilices, Cordaitales, and other ancient and transitional groups. This statement is made because investigations of recent date on the Coniferales either do not concern themselves with a consideration of the fossils at all, or are devoted to some special theme, such as the structure of the wood, the anatomy of the leaf, etc. Modern work on the anatomy of plant fossils emphasizes the fact that all the organs and tissues should be examined, where successful comparisons are to be made. It will accordingly be the aim of the present investigation to include all the structural features of the Abietineae, so far as they seem to have any bearing on the phylogeny of the order.

#### PSEUDOTSUGA.

In a transverse section of a vigorous yearling shoot of *Pseudotsuga douglasii* Carr., one sees the comparatively thick fibrovascular ring surrounded by a thick cortex. The wood of this genus is characterized by the presence of resin canals of which there are generally present about three rows. Occasionally one finds shoots in which the resin ducts of the wood are quite absent. The pith is irregular in outline, on account of the occurrence of projections from its periphery corresponding to the outgoing leaf traces. These rays of medullary parenchyma become deeper and deeper as the leaf trace passes outwards from the medullary crown towards the cortex, and where the trace is about to leave the fibrovascular ring there is a radial stripe of parenchyma several cells broad extending entirely through the woody cylinder. This is the foliar gap. Very shortly after leaving the medullary crown, the leaf trace becomes divided into two by a radial row of parenchyma cells, which as the trace begins to approach the outside of the woody cylinder, becomes two and even three layers of cells wide. One or both of the leaf traces at this time may contain a resin canal, which disappears as soon as the trace begins to pass into the phloem. Figure 4, plate 1, shows the topography of the passage of the foliar trace out of the central cylinder and demonstrates that it is distinctly double. It is important to note this point because Bertrand ('74) states that *Pseudotsuga*, together with *Tsuga* and *Larix*, is characterized by a single undivided leaf trace. In figure 5, plate 1, the leaf trace is seen at some distance out in the cortex, and is obviously



even more strikingly double than when it is leaving the central cylinder. The foliar trace continues as geminate strands for a short distance into the base of the leaf; but soon the two fibrovascular bundles become more or less intimately fused. In a section at some height in the leaf, the trace loses all appearance of being a double strand. This is clearly shown in figure 3, plate 1, which is from a section taken at about the region of the lower third of the leaf of *Pseudotsuga douglasii* Carr. It will thus be seen that the leaf trace of this species becomes double at an early stage in its progress towards the leaf, and that its double nature only becomes obscured after having penetrated some distance into the lamina. The importance of this observation will be apparent at a later stage.

The root of *Pseudotsuga douglasii* is generally diarchous, although examples have been found in which there were as many as three clusters of primary xylem. The primary metaxylem contains no resin canal; but just outside each of the two clusters of protoxylem is a single duct. These features can be seen in figure 2, plate 1. The two first formed resin canals are lined with thin walled, glandular cells, such as occur in the resin ducts of the cortex in the Coniferales in general, and in the ligneous resin ducts of *Pinus*. The lining of the canals is further particularized by the fact that the cells composing it are quite unligified and stain a dark blue with haematoxylin. In this respect the tissue in question presents a marked contrast to that lining the later formed ducts of the secondary wood in the root and shoot of the species under discussion, which in most cases is thick walled and distinctly lignified. It not infrequently happens that the primary radial resin canals of *Pseudotsuga* communicate by radial anastomoses with the resin canals of the cortex. The walls of the radial connecting canals in this case are bounded by the same thin walled, resin secreting cells as are found in the ducts which they unite. These radial anastomoses are most frequent in the neighborhood of an outgoing rootlet, but are by no means confined to this position. In figure 2, plate 1, on the left, may be seen one of the radial canals in question. The plane of section does not include the cortical canal into which it opens. In the cortex of both root and shoot of *Pseudotsuga* are sclerotic cells; but these do not occur in the phloem as in *Tsuga* and *Abies*.

In figure 1, plate 1, is to be seen a section through a wounded portion of the wood in *Pseudotsuga*. On the left may be seen the margin of the layer of wound tissue, which is closing over the surface of the injured wood. By following this layer towards the right we reach numerous large resin canals along its inner border. These are traumatic resin ducts such as occur almost invariably in the injured wood of the Abietineae. They are characterized by their number, by the fact that they occur in close tangential rows, the ducts of which generally intercommunicate tangentially, and



by the nature of the cells lining their walls. They are apparently for the purpose of sterilizing the wound by pouring large quantities of resin over its surface. Their occurrence in close tangential rows with tangential intercommunication of the ducts is a source of mechanical weakness to the wood, which it is not surprising to find to some extent overcome by the nature of the cells lining the canals. The resiniparous canals in the case of traumatic resin ducts are lined by thick walled, resin secreting cells, which are able to accomplish their function of pouring out a resinous secretion by the presence of numerous simple pits.

In the wood of the cone of *Pseudotsuga douglasii* Carr., there is a single row of resin canals near the medulla. In longitudinal sections the tracheids of the wood in the female reproductive axis are without the spiral bands, which are a well known characteristic of those of the vegetative axis (Penhallow, '96). Although tracheids with tertiary spiral thickenings are absent in both the axis and the scales of the cone in this species, they occur in the leaf traces. This would seem to lead to the inference that their absence in the case of the female reproductive axis is rather due to the thickness of the walls of the tracheids in this organ than that the spiral thickenings in question are not a primitive feature of *Pseudotsuga*. This inference seems strengthened by the fact that the spiral markings are sometimes absent in the case of the thick walled, aestival tracheids of the vegetative axis. It does not follow, however, that the occurrence of spirally marked tracheids in the wood of *Pseudotsuga* is any indication of close affinity with the *Taxineae*, in which they also occur, since the same phenomenon is sometimes found in the hard pines and in *Larix* (Penhallow, :03).

#### LARIX.

A transverse section of the yearling stem of *Larix americana* Michx. presents very much the same appearance as one of *Pseudotsuga*. There is in this genus, however, an absence of the sclerenchymatous elements found in the pith and cortex of the last described genus. The leaf bases, too, are more crowded and more prominent and present a rounded contour. There is as a rule but a single layer of ligneous resin canals and this is present in the summer wood. The root of *Larix americana* somewhat resembles that of the genus described above, and has the same commissural radial canals connecting the resin ducts, subtending the two clusters of protoxylem, with those which occur in the so called secondary cortex. This feature is shown in figure 6, plate 1. The lining of the resin canals facing the angles of the primary wood is of the same thin walled, resiniparous cells, which have been described above for *Pseudotsuga*. The subsequently formed resin ducts of the wood of the root have this thin walled, glandular epithelium



more or less completely replaced by thick walled, resiniparous cells, which are at least partially lignified. There are, however, nearly always some of the more primitive, thin walled cells remaining. The radial canals connecting those opposite the primary wood with similar canals in the secondary cortex have their inner surface also lined with the thin walled type of gland cells. In the stem of *Larix*, as has been pointed out by Penhallow ('96, :03), the resin ducts of the wood are coated with thick walled, resiniparous cells, presenting in this respect a marked contrast to *Pinus*.

The leaf trace of *Larix* is described by Bertrand ('74) as resembling that of *Tsuga* and *Pseudotsuga* in remaining a simple undivided fibrovascular strand. An examination of thin sections through the yearling stem of *Larix americana* has shown that the foliar trace here is also double, as in *Pseudotsuga* described above. The trace sometimes shows indications of duplication even before it leaves the central cylinder of the axis, but generally does not become double until it has advanced some distance into the cortex, in its upward course into the leaf. Figure 7, plate 1, shows the condition of the leaf trace at about the level at which the resin canals of the mesophyll have made their appearance. As is well known (Strasburger, '71), the resin ducts of the fundamental tissues of the leaf in the Abietineae are not generally continuous with the similar canals of the cortex of the axis. At this height the leaf trace as seen in transverse section is obviously double, the tracheary strands being separated from each other by two or three rows of parenchyma cells. These two fibrovascular bundles become intimately fused in the base of the free portion of the leaf, and it is no longer possible to distinguish any signs of duplication.

#### PICEA.

In *Picea nigra* Link, a section of the yearling stem shows the presence of abundant sclerification in the pith. Sclerenchymatous strands are also present in the cortex, subtending the outgoing leaf traces. The woody cylinder normally contains but a single row of resin canals which are nearly midway between the beginning and the end of the annual ring. These canals differ somewhat from those of *Larix* in their lining, for their parietal glandular tissue is partially thick walled and partially made up of thin walled elements. The latter are always present to some degree and no doubt are responsible for the formation of the tyloses which occur in the canals of *Picea*, in contrast to those of *Larix*, where both tyloses and thin walled elements are for the most part absent. The leaf bases of *Picea* are sharp pointed instead of rounded in transverse section, as is the case in *Larix*. They are further particularized by the presence of two small resin canals, which in the mature stem end blindly upwardly, although they are inferiorly in communication with the much larger resin canals of the cortex of the axis. As Mayr



('84) has pointed out, *Picea* in contrast to the other Abietineous genera, has the resin canals of the leaves at first continuous with those of the stem, but the free communication between the two systems is cut off at an early date by the formation of absciss periderm. This continuity between the foliar and the axial systems of resin canals appears to have been the primitive condition for the Abietineae, but as has been indicated above, has become obsolete in most of the existing species.

Figure 8, plate 1, shows the effect of injury on the structure of the wood in *Picea nigra*. The sparse and small resin canals present in the normal wood are replaced by close tangential rows of resin ducts of much larger lumen, in the folds of traumatic wood, which in the course of time grow over the injured surface of the stem. The reaction which leads to the formation of the tangential rows of canals in the case of injury, is of course much more intense in the immediate vicinity of the wound, and fades away tangentially in the newly formed wood. The traumatic resin canals in question communicate tangentially and have doubtless the function of pouring out resin over the wounded portion of the stem. It is an interesting fact, that the formation of these tangential rows of traumatic resin canals in the Abietineae is most marked in those genera in which the resin canals are normally somewhat sparse or entirely absent. In *Pinus*, where the resin ducts of the wood are abundant in both the vertical and the horizontal planes, a marked reaction leading to the formation of tangential rows of traumatic resin ducts seldom or never occurs. In *Picea*, *Larix*, and *Pseudotsuga*, on the other hand, their formation is an almost invariable sequel to injury, and this is even more strikingly the case in *Abies*, *Tsuga*, *Cedrus*, and *Pseudolarix*, which are ordinarily described as entirely lacking ligneous resin ducts. In the genus at present under discussion, I have noticed a strong formation of traumatic resin canals, not only as the result of mechanical injury, but also as a sequel of the attacks of *Chermes abietis*, and of parasitic rust fungi producing witches' brooms.

In *Picea* the leaf trace is described by Bertrand ('74) as being a double one by the presence of a distinct median medullary ray. In *P. nigra* the foliar trace leaves the central cylinder of the axis as a single strand of very small size. As it reaches proximity to the base of the leaf it becomes distinctly double, as may be seen in figure 9, plate 2. In *P. engelmanni*, which was also examined in this connection, the trace is somewhat larger and the duplication correspondingly more marked. The root in *Picea* does not differ in any marked features from those of *Larix* and *Pseudotsuga*.

#### ABIES.

In *Abies balsamea* Mill., resin canals are normally quite absent in the wood of the shoot. This feature is illustrated by the central portion of figure 10, plate 1. In



the two last annual rings of the figure, dense tangential rows of resin canals can be clearly seen on either side of an injured part of the stem. Figure 11, plate 2, shows a portion of the traumatic wood on the left of figure 10 more highly magnified. In this case it is easy to make out that the resin canals are more or less strikingly in tangential communication with each other, and that they occur in the spring wood of each of the annual rings formed subsequently to the injury of the stem. The canals in question pour out a large amount of resinous secretion over the surface of the injured wood, and by their presence as a reaction to injury only afford a much more economical provision for antisepsis than the numerous resin canals which occur throughout the wood of *Pinus*. In the annual rings of the stem shown in figure 11, both in those containing resin canals and in those without resin canals, may be seen certain minute dark dots. These are especially noticeable, in spite of the low magnification, in the annual ring immediately preceding those which contain resin canals. These dots are the so called resin cells, which are frequently characteristic of those Coniferous woods which do not contain resin canals under normal conditions. The dark color which is a feature of the cells in question is due to the presence of a tanniniferous substance. In figure 12, plate 2, is seen a part of the woody tissue from the axis of a witches' broom of *Abies balsamea*. It is clear from this figure that resin canals of the tangentially crowded traumatic type are also present as the result of the attack of the fungus producing the witches' broom. This feature has been described by Anderson ('97) and other pathologists. It is to be further noted that the place of occurrence of the rows of traumatic resin ducts is in general the same in the species under consideration, viz., in the spring wood.

In figure 13, plate 2, is seen part of a section of an injured stem of *Abies magnifica* Murr. The area of the figure is all contained within the breadth of a single annual ring, yet there are four rows of traumatic resin canals. This is the largest number occurring within a single annual ring of wood which has come under my notice. Generally in the various species of *Abies* there is but a single row of such ducts in a year's growth. The position of the row of traumatic resin canals is usually constant in the same species, and they may lie either in the spring or summer wood or in an intermediate position.

Figure 14, plate 2, brings out an interesting peculiarity in the structure of the wood of *Abies magnifica*. In this species the resin canals which are normally absent in the wood of the vegetative axis are found to occur with great constancy in the woody axis of the cone. I have already referred to a similar phenomenon in the first memoir of this series devoted to the anatomy of *Sequoia*. In *S. gigantea* in all the numerous cones which have come under my notice from various sources, resin canals have always appeared in the axis of the female cone, although they are normally quite absent from the annual rings of the older parts of the stem and branches. I have had access to four



different examples of the large cones of *A. magnifica*, three of which were from entirely different sources. Rows of resin canals such as appear in figure 14, occurred in all of them. Special care was taken to observe whether the cone or its peduncle had suffered injury in any of these examples; but in all the cases examined both organs were quite normal in every way. Figure 15, plate 2, shows a part of another section of the same cone as that shown in figure 14, more highly magnified. The plane of section in this case is lower down in the cone, and the figure as a consequence, although under a greater magnification than the preceding one, shows the resin ducts of smaller size. The resin ducts become fewer and of less caliber as the base of the cone is reached, until finally in the peduncle, or even above the actual peduncle, they disappear altogether. If instead of progressing towards the base of the cone, one moves in the opposite direction, the resin ducts instead of becoming fewer and of smaller size, are found to have larger lumina and to become more numerous. The larger ducts of the upper part of the cone by reason of their greater size and close proximity tend to become fused with one another, as is clearly shown in figure 16, plate 2. The resin secreting cells which surround the resin ducts of the woody axis of the cone in the species under discussion are thick walled and are quite similar to those surrounding the resin passages in the wood of *Larix*. Thin walled, resiniparous cells are, however, occasionally found where a resin canal abuts directly on a medullary ray. Although a good deal of brown tanniniferous secretion is found in the medullary rays of the cone, little or none appears in the parenchymatous cells surrounding the resin ducts.

In the memoir on *Sequoia* reference is made to the fact that resin canals occur in the *first* annual ring only of vigorous shoots, in the case of trees which have already produced female cones. Interestingly enough, the same state of affairs has been found by the writer in the case of the present species. Figure 17, plate 3, reproduces the two first annual rings and part of the third in a cone-bearing branch of *A. magnifica* from the collection at the Arnold arboretum of Harvard university. I am indebted to Mr. George S. Shaw and Prof. Charles S. Sargent for the opportunity of examining authentic material of the present and other species studied in connection with the present work. The magnification is just sufficient to show the presence of resin ducts which are entirely confined to the first annual ring of the four year old shoot in question. There was no evidence of any injury to the branch, so the presence of the ducts must be regarded as a perfectly normal feature, especially in view of other similar observations shortly to be recorded. In the stouter lateral branches of the shoot in question there was in some instances a similar occurrence of ducts in the first annual ring; but in the more delicate twigs these were entirely absent, thus duplicating the similar phenomenon found in *S. gigantea*. Figure 18, plate 3, shows the structure of the first and second annual rings



in a two year old branchlet from a cone-bearing branch of a different specimen of *A. magnifica*. Resin canals are clearly present in the first annual ring and absent in the second. No injury to the tissues could be made out in the case of this branch any more than in the case shown in figure 17 of plate 3. In figure 19, plate 3, is shown a cross section of the internal region of the woody ring of a vigorous branch from a flourishing specimen of *A. magnifica*, between 8 and 10 meters high, growing in the Hunnewell pinetum at Wellesley, Mass. Resin ducts are present here as well as in the other cases. In less vigorous branches from the lower part of the tree the resin ducts do not appear. In figure 20, plate 3, a portion of a section from the same branch as that appearing in figure 19 is represented more highly magnified to show the nature of the resin ducts and of the cells forming their walls. It will be seen that the ducts under consideration are quite close to the primary wood. They are obviously surrounded by the same thick walled, resiniparous cells as occur normally in all the annual rings of *Larix*. The magnification is sufficient to show the presence of nuclei in four or five of the parietal cells of the ducts. The nuclei present in the remaining cells have been missed by the plane of section. To summarize, resin canals surrounded by thick walled, epithelial cells, such as are found about the ducts in the annual rings of *Larix*, occur in the first annual ring only of vigorous branches from vigorous trees of *Abies magnifica*.

In longitudinal section the pith of branches of *A. magnifica* presents a curious appearance, which is shown in figure 21, plate 3. The medulla is crossed by diaphragms consisting of sclerotic tissue, and alternating with these are segments of soft parenchyma, which tend to break down, thus producing a fistular medulla, such as occurred in many of the Cordaites. Sir J. William Dawson ('88) was the first one, so far as I am aware, to call attention to this feature in the genus *Abies*. It is referred to here because it appears to have a certain significance in connection with other facts to be described and discussed at a later stage. Noticed by Dawson first in the case of *A. balsamea*, it seems to be thoroughly characteristic of the genus, but occurs also in the curious *Cedrus*-like species, sometimes united under the subgeneric name *Keteleeria*.

In figure 22, plate 3, is seen a transverse section of a root of *Abies nobilis*, a species somewhat closely allied to *A. magnifica*. The root of the latter species differs from it only in unimportant details. The most striking feature of this root is the presence of a resin canal in the center of the primary wood. This peculiarity has been noted by De Bary ('84) as being common to the genera *Cedrus* and *Abies*. To these Strasburger ('91) adds the so called Chinese larch, *Pseudolarix*. The central resin canal in the case under discussion is surrounded by several layers of delicate parenchyma cells, the innermost of which functions as the resiniferous epithelium. There are normally no resin canals present in the secondary wood of the root of *Abies*, and the examination of a consider-



able number of roots of different species of the genus from the Arnold arboretum of Harvard university and from the Hunnewell pinetum at Wellesley, Mass., has revealed no exceptions to this rule. The cells of the phloem in the root of *Abies* are sometimes very small. As an example of this feature *A. magnifica* may be cited. Sclerotic nests of cells are somewhat constantly present in the so called secondary cortex of the root in *Abies*, and may clearly be seen in figure 22. Resin ducts occur occasionally in the same situation, but there is never any communication between these and that which is present in the first annual ring of the wood.

In figure 24, plate 3, is shown a transverse section through the woody axis of the cone of *Abies apollinis*. This is the only species of the Old World in which resin canals have been found in the wood of the reproductive axis. Two cones, which as far as could be learned were from different sources, showed this peculiarity. In the one figured there are two rows of resin ducts present extending completely round the cone, although somewhat better developed on one side than on the other. Figure 25, plate 4, shows a portion of a similar section more highly magnified. The resin canals in this case do not become very large towards the top of the cone, as in *A. magnifica*, but resemble those of the former species in disappearing entirely at its base. The cells which surround the resin canals are characterized by the presence of a small amount of tanniniferous material in the form of minute granules, but they contain much less of it than do the cells of the medullary rays. *A. apollinis* differs from *A. magnifica* in that the resin ducts of the wood of the stem are confined to the axis of the cone, and do not appear in the first annual ring even of vigorous vegetative branches. The only other species of *Abies* in which resin canals have been found in the cone is *A. grandis*, as has been described in the first memoir. Here, however, the occurrence of the resin passages appears to be sporadic, for they have only been observed in a single specimen and are absent in four others. In *A. balsamea*, *A. fraseri*, *A. concolor*, *A. amabilis*, *A. nobilis*, *A. bracteata*, *A. veitchii*, and *A. cephalonica* no resin canals were found in the woody axis of the female cone. *A. nobilis* was erroneously described in the first memoir as possessing resin ducts in the wood of the female cone. The cone in which these structures were found turned out to be incorrectly diagnosed, and was really *A. magnifica*. *Keteleeria* in its anatomy obviously belongs with *Abies* although it has the habit of *Cedrus*; the wood of both vegetative and reproductive axes is entirely without resin canals.

The leaf trace of *Abies* is often double, even in the lamina, and where a geminate fibrovascular strand cannot be distinguished in the blade of the leaf, it can usually be made out in the part of the trace which runs in the cortex. This, for example, is the case in *Abies magnifica*, where the foliar trace does not give clear evidence of being a double strand in the free flattened portion of the leaf. By following the trace down into



the cortex of the axis its double character can generally be clearly distinguished. Bertrand ('74) describes a double trace as characteristic of the genus *Abies* in general, and to this statement I can subscribe. In figure 23, plate 3, is represented a foliar trace of *A. magnifica* in transverse section at a height of two millimeters in the free part of the leaf. The striking feature of this figure is the fact that the transfusion tissue, connected with the bundle of the leaf in this as in most other Conifers, is unusually abundant, and instead of forming a scattered reticulum about the fibrovascular strand, interspersed with living parenchyma cells as is the rule, constitutes a dense and continuous ring of tracheidal tissue, completely surrounding the phloem. There is a tendency for it to become interrupted opposite the cambium on either side of the bundle by parenchyma cells. The condition of the transfusion tissue found in this case is to be compared with that recently described by Miss Stopes (:03) in the leaf of a *Cordaite*, probably the *Cordaites principalis* of Renault. In his description of the bundles of this leaf, Renault interprets a layer of tracheary tissue outside the characteristic centripetal wood, found so commonly in the leaves of the more ancient Gymnosperms, as centrifugal so called phanerogamous wood, similar to that occurring, for example, in the bundles of the petiole of the Cycads. Miss Stopes has pointed out that this so called centrifugal wood is separated from the centripetal xylem by a layer of irregularly disposed, thin walled tissue comparable in every way to primary phloem. Moreover the tracheary tissue in question is attached to the flanks of the centripetal wood, and its elements, arranged in the form of a double sheath, correspond to the transfusion tissue of the Conifers and other Gymnosperms.

In this connection Miss Stopes calls attention to the researches of Worsdell on transfusion tissue in the Gymnosperms. Worsdell ('97) reaches the conclusion that the transfusion tissue, "which occurs almost universally in the leaves of Gymnospermous plants as an auxiliary conducting system, has been phylogenetically derived from the centripetally formed xylem of the vascular bundle." In the example in figure 23, plate 3, the transfusion tissue extends well round towards the back of the flanks of the bundle, and there are even some elements formed in a centripetal direction. Miss Stopes draws the conclusion that the sheath described by her in *Cordaites principalis* is not centrifugal wood, but "a primitive stage in the development of transfusion tissue from centripetal xylem." The condition of affairs shown in our figure 23 seems to be strong evidence for the truth of this hypothesis, and it supplies a transition from the condition ordinarily found in the Conifers to that sometimes found in *Cordaites* as described by Miss Stopes. At a higher level in the leaf the continuity of the transfusion tissue on the outside of the phloem is generally lost, and we have resulting a condition in which there are merely massive wings of transfusion tissue on the flanks of the bundle, a state of affairs which is permanently present in *Sequoia*, *Cunninghamia*, etc. A good figure of this arrangement of the



transfusion tissue in *Cunninghamia* appears in De Bary's textbook ('84). There is another possible fate for the transfusional sheath, however. Instead of becoming interrupted opposite the phloem, it may only suffer a sort of general disintegration by the intrusion of parenchyma cells into its mass. This condition is exemplified by *Pinus* as described by Strasburger ('91, p. 133). The interesting arrangement of the transfusion tissue represented in figure 23, plate 3, is not confined to *A. magnifica*, but also occurs in a less marked degree in the allied species, *A. nobilis* and *A. bracteata*. In these species, too, the sheath tends to become discontinuous in the upper part of the lamina of the leaf. This is especially true of *A. bracteata*.

#### PSEUDOLARIX.

Although this genus, in spite of its deciduous cone scales, is generally put in proximity with *Larix* on account of its deciduous foliage, its anatomy as will be shown in the sequel makes it desirable to place it with *Abies*.<sup>1</sup> Figure 26, plate 4, is of a nine year old branch of *Pseudolarix kaempferi*. In the first six annual rings the wood closely resembles that of *Abies*, as shown in our figure 10, plate 2. In the seventh year of growth the stem suffered injury and as a result there is a great hypertrophy of the wood in the region of the wound, accompanied by a corresponding reduction in the thickness in the region of the annual rings, which is on the opposite side of the stem. In the first annual ring formed after injury there are tangential rows of resin canals running backward from the wound on either side. In figure 27, plate 4, some of these canals from the right hand side of the foregoing figure are represented under a higher magnification. The canals in this case are surrounded by cells containing more or less starch. Similar starch-bearing cells occur normally as a single row on the face of the aestival wood of each annual ring. The cortex and phloem of *Pseudolarix* are characterized by the presence of numerous mucilage cells, which become very large externally. In figures 26 and 27 they are emptied of their mucilaginous contents, which are very soluble in the aqueous stains most suitable for differentiating sections for photomicrography, the method of illustration used throughout this article. There are no resin canals present in the cortex of the vegetative axes of *Pseudolarix*. They do not appear even in the cortical tissues of the seedling. As has been shown above, they are equally absent in the ligneous tissues. There is this difference between the wood and the cortex in regard to the absence of resin ducts, *viz.*, that they may be produced in the wood as the result of injury, whereas they never occur in the tissues of the cortex under this condition. Not even in the most vigorous vege-

<sup>1</sup> Since the above was written I have had the opportunity of examining male cones of *Pseudolarix*. The pollen has air sacs like that of *Abies* and *Cedrus*, and in this feature presents a marked contrast to *Larix*.



tative shoots of the genus under consideration have I ever found resin ducts in the first annual woody ring, such as occur in *Abies magnifica* as described above, and in *Sequoia gigantea* described in the former memoir.

The root of *Pseudolarix* closely resembles that of *Abies*, for it has the same central resin canal in the primary wood and numerous mucilage cells in the cortex as well. The sclerotic nests which are characteristic of the cortical tissues of *Abies* are absent in the present genus. Figure 28, plate 4, sufficiently illustrates the truth of the statements made above. The dark cells appearing in the cortex contain tannin, while the large empty ones are those which in life contain mucilage. In figure 29, plate 4, a part of another root is represented. In this instance the section was treated with chrome alum, in order to render the mucilage insoluble in the aqueous dyes employed in staining. In one of the mucilage cells on the extreme right of the figure the contents, although rendered insoluble by the use of chrome alum, have come out bodily, and are lying over some of the other cells. The central resin canal, which is always present in the root of *Pseudolarix*, is surrounded by parenchymatous cells with thin walls of unmodified cellulose, and thus closely resembles that of *Abies*.

In figure 30, plate 4, appears a transverse section of the ligneous portion of an injured root from a seedling from *Pseudolarix*. The magnification is sufficient to show a semicircle of resin ducts running off from the margins of the wound. There is no corresponding formation of traumatic resin canals in the cortical tissues, which like those of the stem are normally entirely without resin ducts. I have had no opportunity of examining the reaction of the root in the mature plant of *Pseudolarix* when injured, but there seems no reasonable doubt that the result would be the same as in the stem of the seedling described above.

Figure 31, plate 4, shows the structure of a three year old branch of *Pseudolarix* as seen in transverse section. The material in this case came from a large tree growing in the Hunnewell pinetum at Wellesley, Mass., which has produced cones abundantly for a number of years. From the seed of this tree a number of seedlings have been grown by Mr. Jackson Dawson at the Arnold arboretum of Harvard university, so that there can be no doubt as to its vigor. There are no resin canals present, either in the cortex or in the wood. The empty spaces seen in the former tissue are the mucilage cells referred to above. In figure 32, plate 4, is a transverse section through the bracteolate portion of the peduncle of a female cone of the species under consideration. Resin canals are equally absent in both wood and cortex. The mucilage cells of the cortex in this case are much fewer in number than they are in the vegetative axis, and in the higher portion of the peduncle they disappear entirely.



In figure 33, plate 5, is shown part of a transverse section of the axis of the female cone in *Pseudolarix*. On the lower side of the figure may be seen a few small bundles belonging to the fibrovascular ring of the cone axis. On the inner side of these is a dense mass of sclerenchymatous tissue, which is the only part of the cone left hanging to the tree after the very deciduous ovuliferous scales have fallen away, carrying with them piecemeal the bundles of the axis to which their own fibrovascular supply is attached. Outside the ring of fibrovascular bundles, the cortical tissues of the reproductive axis are for the most part made up of delicate parenchyma cells; but these are interspersed with a considerable number of short stone cells, which make the cutting of suitable sections of the axis a rather difficult matter. The most interesting features of the cortex of the cone, however, are the presence of resin canals similar to those occurring in the cortical tissues of all the organs of most of the *Abietineae*, and the absence of the mucilage cells, such as are found in the vegetative cortex of *Pseudolarix*. The resin canals in the present instance are quite large in size, and do not appear at once in the base of the cone proper. Further, they are of short length and do not intercommunicate with each other, a fact which makes the proper infiltrating of the axis with celloidin somewhat difficult. In figure 34, plate 5, is seen a section through the base of one of the ovuliferous scales and its subtending bract. The ovuliferous scale is very large and only a small part of it is shown on the upper side of the figure, while the bract is so small as to be entirely included. The sterile bract has not yet become free from the lower surface of its ovuliferous scale and does not show the presence of any resin canals. The magnification is not sufficient to show that the fibrovascular strand of the bract is double. In the tissues of the ovuliferous scale proper there are numerous quite typical resin canals, such as are characteristic of the cortical tissues of the other *Abietineae*. These canals are continuous with the similar canals already described in the case of the axis of the cone.

In figure 35, plate 5, is a section of the sterile bract at a point some distance above its separation from the face of the ovuliferous scale. The fibrovascular bundle has shrunk badly as the result of imperfect preservation in an insufficient amount of alcohol. The important point to note in the present figure is the presence of a pair of resin canals, one on each side of the gap in the tissues corresponding to the position of the fibrovascular bundle.

Figure 36, plate 5, represents a cross section of one of the rather slender leaves of *Pseudolarix* under a considerable degree of magnification. The histological elements present are very small so it is not easy to make out that there are present five resin canals on the margin of the mesophyll and over against the hypodermis, which surrounds the leaf underneath the epidermis. Of these canals three are on the upper surface, one of which is median and two lateral; the remaining two canals are placed laterally on the



lower border of the leaf. It will thus be seen that resin ducts are present in the cortical tissues of the leaf in *Pseudolarix*, as well as in the female reproductive axis, although they are quite absent from the cortex of the stem. From the fact that there are two resin canals only present in the leaves (*i. e.*, sterile bracts) of the female reproductive axis, it may perhaps be inferred that two is the primitive number for *Pseudolarix*. It should be stated at this point that the two resin canals of the sterile bracts end blindly below, just as do those of the ordinary vegetative leaves, in spite of the fact that the axis to which they are conjoined, unlike the vegetative, possesses cortical resin ducts.

It will be seen from the foregoing paragraphs that resin ducts are present in the wood of *Pseudolarix* under two conditions, *viz.*, normally in the primary wood of the root and as the result of injury in the secondary wood of both root and shoot. In the cortical tissues they are normally present in the reproductive axis, the ovuliferous scales, the sterile bracts, and the ordinary vegetative leaves. They do not occur in the vegetative branches nor the root even in response to injury.

It may be noted by looking a little closely at the fibrovascular bundle of the leaf of *Pseudolarix*, reproduced in our figure 36, plate 5, that the leaf trace is double, being divided into two by a parenchymatous strand passing through the xylem. As in the genera already described, the leaf trace in the genus under consideration is very distinctly double in the outer cortex of the axis, although it departs from the central cylinder as a single strand as in *Picea*.

#### CEDRUS.

In the case of this genus we shall first examine *Cedrus atlantica*. The material studied came from a small tree of the variety *glauca* growing in the Hunnewell pinetum, at Wellesley. As is well known, those fossil woods which are without resin cells or resin ducts, which do not possess spirally marked tracheids, and have their bordered pits opposite and not alternating in the same tracheid, are united in the structural genus *Cedroxylon*. The characters just enumerated are found in the wood of *Cedrus atlantica*. Although resin canals are normally absent in the wood of this species, they occur frequently as a result of injury under the same conditions as in the genera previously described. Figure 37, plate 5, shows the structure of the wood on the margin of a wound in the species being considered. Resin ducts of the usual type form a continuous row, to the right of the area of injury. The cells surrounding the canals in this case are thick walled and partially lignified as in the traumatic resin canals of some of the other genera described above. They are enabled to pour out their secretion by the presence of numerous pits. In figure 38, plate 5, is seen a transverse section of a wounded root of *Cedrus*



*atlantica*. Running in a circular fashion through the wood is a tangential row of traumatic resin canals. It is an interesting fact that in *Cedrus* the lining of the traumatic resin canals of the injured root is different from that found in the stem under the same conditions. Instead of the glandular cells in this case being thick walled and lignified as they are in the stem, they are thin walled and of pure cellulose, and in fact strongly resemble in their characteristics the resiniparous lining of the normal resin canals of the wood in *Pinus*. Figure 39, plate 5, sufficiently illustrates the structure of the traumatic resin ducts of the wood of the root in *Cedrus atlantica*. It will be seen in this highly magnified representation of the canals, that they are lined with thin walled cells, containing protoplasm and a nucleus. No resin canals are formed as a result of injury to the cortical tissues of either the stem or the root in *C. atlantica*. Before leaving the discussion of this species, reference must be made to an interesting phenomenon, which occasionally is present in wounded roots. Ordinarily only vertical resin canals are produced as the result of injury to the tissues of the wood in *Cedrus atlantica*; but in one case which has come under my notice horizontal canals were present as well. These started from the vertical canals and ran for a short distance radially outward, and then ended blindly. Like the vertical resin ducts of the root they were lined with thin walled, glandular epithelium and not with thick, lignified, resiniparous cells such as are found in the stem. I have not found horizontal resin canals in the stem of *C. atlantica*; but this is probably to be explained by the fact that my material was limited rather than to their being non-existent, for I have observed such horizontal canals frequently in material of *Cedrus deodara*, to be described below.

In figure 40, plate 5, is seen a part of a transverse section of the wood of *Cedrus deodara*. Crossing the lowest annual ring in the figure and in the summer wood is to be seen a row of resin ducts, which we may compare with those occurring as the result of injury in *C. atlantica*. Although the piece of wood did not actually show the presence of an injury in this case, there appears to be little doubt that the tangential row of resin canals occurring here is due to a wound either above or below the region from which the block of wood was cut. This appears extremely probable, since traumatic resin canals occur far above and below the actual spot of injury, as has come under my observation many times in American genera of the Abietineae, and in *Sequoia*, in which, as has been shown in the first memoir, similar conditions occur. It is further to be noted that the resin ducts in *C. deodara* occur in the summer wood, in contrast to *C. atlantica*, where they are found in the spring wood. The two species differ from each other in this respect in the same way as do *Sequoia sempervirens* and *S. gigantea*. It is worth while to call attention to the different position of the traumatic resin ducts of the two species of *Cedrus* under discussion as it furnishes a means of distinguishing their woods. Similar differ-



ences in the place of formation of the traumatic resin canals occur, as has been pointed out above in the case of different species of *Abies*. Unfortunately I have not had access to material of the wood of *C. libani*. The only specimens available were seedlings of the species growing in the nursery of the Arnold arboretum, of Harvard university. None of these showed injury, as they had been grown with great care. As a consequence they were useless for my purpose.

Another striking feature of figure 40 is the presence of a single horizontal resin duct passing radially outward from the row of tangential ducts. In figure 41, plate 6, is seen another example of a horizontal resin canal from the same material. The horizontal ducts in the two figures just described ended blindly and did not communicate externally with other similar ducts running in the vertical plane. Often, however, when two rows of traumatic vertical canals occur near each other in the wood, horizontal ducts extend from the one series to the other. Such an instance is clearly shown in radial section in our figure 42. Very often these radial ducts conjoining different tangential rows of vertical ducts, are very much larger in caliber than are the vertical ducts. This feature appears clearly in figures 42 and 43, plate 6. In figure 43, the horizontal canal extends beyond the second series of vertical ducts only to end at a short distance to the outside of it. It should here be stated that the horizontal ducts, so far as my observations go, always start with a series of vertical ducts and run radially outwards, ending blindly or joining with a more exterior series of vertical canals. They never pass inward from a vertical series of resin ducts, which is another argument for their being entirely a traumatic phenomenon. Figure 44, plate 6, is a tangential section of the wood of *Cedrus deodara* in a plane outside the vertical row of resin canals shown on the left of figure 43. It will be observed that in addition to the small linear rays, which are normally present in the genus *Cedrus*, there is a number of large, so called fusiform rays. Some of these enclose a resin canal, while others do not. The smaller fusiform rays are cross sections of resin canals which have ended blindly, while those which are of larger size contain obvious resin ducts, which are becoming narrower of lumen, but which have not yet been occluded.

Figure 45, plate 6, shows part of the transverse section of the axis of a cone of *Cedrus atlantica*. In the row of bundles which occurs on the upper side of the figure there are no resin canals in the woody tissues. The cavities, appearing on the outer sides of the wood bundles, indicate the position of the collapsed phloem, the section being made in this instance from dry material. Resin canals occur in the cortex only of the female cone of *C. atlantica*. Cones of *C. libani* and *C. deodara* were examined with similar results. In no case have I found resin ducts in the woody tissues of the cone in the genus *Cedrus*.<sup>1</sup>

<sup>1</sup> Radais ('94) has, however, described resin canals in the first year's growth of the cone of *Cedrus deodara*.



In figure 46, plate 6, is a cross section of the root of *Cedrus atlantica*. The center of the primary wood is occupied by a resin canal of considerable size, which is surrounded, as in *Pseudolarix* and *Abies*, by thin walled cells of the secretory parenchyma. The walls of the gland cells in *Cedrus* are of pure cellulose. The presence of a median resin canal in the root of this genus has already been described by De Bary ('84). The secondary wood of the root in the various species of *Cedrus* contains no resin ducts except in the case of injury. There are no sclerifications either in the bast or in the cortex, and mucilage cells are absent as well. In the smaller roots which have been mainly examined there were no cortical resin canals, although these are abundant in the stem.

The leaf trace of *Cedrus* is described by Bertrand ('74) as showing some evidence of duplication by the presence of a very distinct median medullary ray. In the cortical course of the leaf trace it is obviously double, as in the case of the other Abietineous genera described above.

This condition is shown in figure 47, plate 6, which represents the foliar trace of *Cedrus atlantica* as it is passing through the cortical tissues on its way to the leaf. A similar state of affairs has been made out in the leaves of seedlings of *Cedrus libani*. It will thus be seen that in its outgoing leaf trace *Cedrus* is no exception to the condition of affairs described above for the other Abietineae. Although the foliar trace in this genus is geminate in the middle and outer cortex, it nevertheless leaves the central cylinder of the axis as a single strand.

#### TSUGA.

In figure 48, plate 6, is shown a transverse section of an injured stem of *Tsuga canadensis*. There are four normal rings of wood present and part of another. The injury took place obviously in the early summer of the fifth year of growth of the branch represented in our figure. From the mode of formation of the traumatic wood it is clear that the injury must have been very severe, for the first ring of woody tissue formed subsequently to this event extends only half way around the stem. Although the magnification is not great, it is obvious that resin canals are present in the usual tangential row, which is characteristic of the traumatic canals in the Abietineae in general. The resin ducts are situated in the early formed part of the traumatic wood. The usual position of the resin ducts in the injured wood of *T. canadensis* is in the later formed portion of the spring wood. This is clearly seen in the case of large wounds in thick stems, where a number of years is necessary for the closing over of the exposed surface by



traumatic wood. Under these circumstances tangential rows of resin canals are formed in the spring wood of successive but generally not consecutive annual rings. Although a good deal of material has been examined from various sources and of wide geographical distribution, no examples of horizontal resin canals have been found such as are present in *Cedrus*, described above. The resiniparous cells lining the interior of the traumatic resin ducts in *Tsuga* are thick walled and much pitted. They frequently contain dark brown tanniniferous globules or masses, similar to those found in the resin cells of the normal wood of *Tsuga*. Traumatic resin canals of a similar nature have also been found in *Tsuga mertensiana*. In this species they are entirely confined to the aestival wood. It is thus possible to distinguish the two species by the reaction of their wood to injury.

In figure 49, plate 7, appears a transverse section of a yearling stem of *Tsuga canadensis*. Although the branch is a vigorous one there is no evidence of the presence of resin ducts. Even in the most flourishing branches of *T. canadensis*, bearing female cones, there are no resin canals present in the first year's growth, such as are found in similar shoots of *Abies magnifica*. Another feature of *Tsuga* shown in the figure is the entire absence of cortical resin canals. This condition is likewise present in *T. mertensiana*, which resembles *T. canadensis* in the structure of its woody tissues. The cortex of the two species mentioned is also free from the mucilage cells which are such a striking feature of this tissue in *Abies* and *Pseudolarix*.

In figure 50, plate 7, is shown part of a transverse section of the cone of *Tsuga mertensiana*. Although there are still no resin ducts in the wood of the large cone of this species, they are obviously present in the cortex. On the right of the figure two very large ducts are about to pass off into the fructiferous scale. Figure 51, plate 7, shows a similar view of a transverse section of the cone axis of *T. canadensis*. In this case, too, cortical resin canals are present although there are no ligneous ones. On the right and left of the figure, ducts are to be seen passing out into the two fructiferous scales which are included in the plane of section. It will be seen that *Tsuga* resembles *Pseudolarix* in the distribution of cortical resin canals in the vegetative and female reproductive axis, for as in the latter genus, they are present in the reproductive axis and in the fructiferous scales, but are entirely absent from the cortex of the vegetative stem. As is well known, there is a single median resin canal present in the mesophyll of the vegetative leaf of *Tsuga*.

In figure 52, plate 7, is represented a transverse section of the root of *Tsuga mertensiana*. The magnification is just sufficient to show the presence of a median resin duct in the primary wood. There are no resin canals present either in the



secondary wood or in the secondary cortex which appear in the figure. Figure 52 shows the structure of a three year old root of *Tsuga canadensis*. There is the same median resin duct as in the preceding figure, but no resin canals appear in the secondary wood, the phloem, or the cortex. In figure 54, plate 7, is shown a section of a wounded root of *T. canadensis*. There is a row of resin canals present in the traumatic wood formed subsequently to the receiving of the injury. The cells surrounding these canals are of the thick walled type, and they often contain considerable tanniniferous substance. Figure 55, plate 7, reproduces the structure of the central portion of the primary wood and part of the secondary wood which lies about it. The parenchyma separating the primary from the secondary wood contains a large amount of tannin, but the cells surrounding the resin canal in the center of the primary wood are obviously free from this substance. The resiniparous lining of the median resin canal of *Tsuga* is thicker walled than in *Pseudolarix*, *Abies*, and *Cedrus*, but its cells are nevertheless quite typical resin-secreting elements. In figure 56, plate 7, is shown the passage of a leaf trace into the leaf in *Tsuga mertensiana*. The trace is plainly double in this instance, as in the other Abietineae described in this investigation. Bertrand ('74) cites *Tsuga* as a genus possessing a single leaf trace. If the exit of the trace from the central cylinder be studied in this genus, it becomes evident that the fibrovascular strand is clearly duplicate even before it leaves the wood of the axis, and persists as an obviously geminate strand up into the base of the leaf proper. *Tsuga canadensis* was examined with the same result, although here the size of the strands of the double trace is somewhat smaller. With the description of the leaf trace in *Tsuga*, the consideration of the recognized genera of the Abietineae, with the exception of *Pinus*, is completed. In the following paragraphs the bearing of the observed facts on the phylogeny of the order will be discussed.

#### CONCLUSIONS.

Having examined from a comparative standpoint the general features of the anatomy of the Abietineae, we are now in a position to discuss the significance of the facts described, in connection with the affinities and phylogeny of the order. The discussion may conveniently be divided under three heads: (1) The bearing of anatomy in the broadest sense on the interrelationships of the various genera of the Abietineae; (2) The relationship of the Abietineae to the other groups of the Coniferales; (3) The affinity of the Abietineae with other groups of Gymnosperms, living and extinct. These will be considered in the order in which they have been mentioned.

*The interrelationships of the Abietineae.*—In the foregoing paragraphs it has been



noted that certain genera of the Abietineae were characterized by the abundant occurrence of resin canals in the secondary wood of their vegetative and reproductive axes and in the secondary wood of the root as well. In these genera resin canals are also abundant in the cortical tissues of all the organs. They are further characterized by their persistent cone scales.

In contrast to these are a number of genera in which the resin canals, so abundant in the forms just described, are almost entirely absent in the secondary woody tissues of the vegetative and reproductive axes. Where they do occur in the secondary wood of the stem organs, they are confined to the female reproductive axis, and to the *first* annual ring of vigorous branches of sexually mature trees. These genera are further particularized by the fact that in the woody tissues of the root, resin canals are confined to the primary wood, but are never absent from this position. In the cortical tissues of some of the genera included in this group, resin canals are abundantly present, but in others they occur only in the female reproductive axis and its appendages, and in the mesophyll of the leaves. Although resin ducts are normally absent in the secondary wood of the vegetative axial organs of the genera under discussion, their formation may be brought about in dense tangential rows by the attacks of fungi, or by mechanical injury. Finally the genera included here are with one exception characterized by deciduous cone scales.

The genera to be included in the first group are *Pinus*, *Pseudotsuga*, *Larix*, and *Picea*. The second group contains the genera *Abies*, *Pseudolarix*, *Cedrus*, and *Tsuga*. It seems advisable to include the first four genera in a special subfamily, the Pineae, and the last four in another special subfamily, the Abietae. These two series are so distinct in both their reproductive and anatomical characters, that it will conduce to a clear understanding of their phylogenetic relationships to keep them separate under the designations which have been suggested above.

Having separated the genera of the Abietineae into two distinct groups we may now go on to inquire how these two groups are related to each other and which of them is the more primitive. Further, after having as far as possible from the data here made available, settled their general relationship, we may advantageously pass on to the consideration of the affinities of the several genera which they include.

As a preliminary to the discussion of the relative antiquity of the Pineae and Abietae as here defined, it will be convenient to recall the anatomical differences between the two subfamilies. The Pineae are characterized by the presence of resin ducts in the woody and cortical tissues of their stems and roots. There are peripheral resin ducts in the primary wood of the root and similar ducts are in some cases found in the primary wood of the stem. The integument of the ovule is relatively thin and the scales of the cone are not deciduous. In the Abietae on the other hand, resin canals are



entirely absent in the woody tissues of the stem. The only exception to this rule is their occasional occurrence in the wood of the reproductive axis (species of *Abies*) and in the first annual ring of vigorous branches in mature trees (species of *Abies*). Resin ducts occur normally and without exception in this group in the center of the primary wood of the root. Resin canals are also present in the cortex but in the genera *Tsuga* and *Pseudolarix* the cortical canals are confined to the reproductive organs and to the leaves. In the *Abietae* the integument of the ovule is relatively thick, and the cone scales are usually deciduous.

As a further preliminary to the discussion of the phylogeny of the *Abietineae* attention must be called to certain principles or canons of comparative anatomy, derived from the study of living and fossil plants, which are of such recent origin that they have scarcely as yet been definitely formulated. One of the most important of these canons is, that ancestral structures are apt to linger on in the reproductive axes after they have disappeared from the vegetative organs. Solms-Laubach ('90) first called attention to this principle in the matter of the arrangement of the bundles in the cones of the Cycads, which is much simpler in the reproductive axis than in the vegetative stem, and according to his view is archaic. The most important contribution to this generalization, however, has been made by Scott ('97). He pointed out that in certain Cycads there are present, in the axis of the cone, mesarch bundles comparable to those found in the vegetative axes of certain of the fossil and ancestral *Cycadofilices*. He draws the inference that the mesarch type of bundle is primitive for the Cycads and has lingered on in certain instances as an anatomical feature of the male and female cones. The present writer ('99) has directed attention to the fact that the course of the fibrovascular bundles in the cones of the more modern *Calamites* is the same as that found in both vegetative and reproductive axes of the more ancient *Calamites* included in the genus *Archaeocalamites*; for in the latter there is no alternation of the course of the bundles at the nodes, a feature retained in the cones of the later *Calamites* and to some extent even in the modern *Equisetum*. In the younger stages of the development of the fibrovascular bundles of the cone in *Equisetum* there is present a cambium, another point of resemblance to the *Calamites*, ancient and less ancient, which were characterized by the presence of very marked secondary woody growth. In this connection it may be pointed out that Cushman (:03) has noted the resemblance of the leaves occurring on the reproductive axis of certain higher plants to those first appearing in the seedlings. Jackson ('99) had previously shown that the nepionic or earlier leaves of phaenogamous seedlings in many cases present remarkable resemblance to the leaves of allied fossil species. These illustrations will serve to indicate that there is a strong tendency towards the retention of ancestral characteristics in the reproductive axes of vascular plants.



Persistent as ancestral characters are in the reproductive axis, they are much more markedly so in the foliar organs. In the case of the Cycads, the fibrovascular bundles of the leaves are of the old quasi-cryptogamic mesarch type found in the medullary crown of the vegetative stem of *Lyginodendron* and others of the transitional Gymnosperms. We thus find living on in the leaf, a type of bundle which in the Cycads has long disappeared in the vegetative stem and occurs only in rare instances even in the more conservative reproductive axis (Scott, '97). A similar feature is presented by the leaf bundles of *Lyginodendreae* (Williamson and Scott, '95) and the *Osmundaceae* (Faull, :01; Jeffrey, :02), for in these groups the concentric Filicinean type of fibrovascular strand, which has almost disappeared in the fibrovascular zone of the stem, persists, often in full vigor, in the leaves. It has further been shown by Jackson ('99) that the outward form of the earlier or nepionic leaves of many Angiospermous and Coniferous seedlings presents striking resemblances to the adult leaves of extinct fossil species. Numerous other examples and illustrations of the same principle might be cited, but the foregoing have been chosen because they are particularly convincing on account of their confirmation by fossil data.

Lastly, in this connection we come to the ancestral features presented by the seedling. It is a recognized principle in the embryology of animals that ancestral features are apt to persist in the earlier stages even where they have quite disappeared in the adult. As a striking illustration of this principle may be cited the fact that gill slits are found in the embryos of all the great groups of the Vertebrata, although gills have long disappeared in the adult of most of the classes of the phylum. In the case of plants, as has been pointed out by Scott ('96), this feature is much less marked, but striking examples of recapitulation in the case of seedlings have been described by Strasburger ('72), Goebel ('89, date of part), Jackson, and others. The Cupressineae present particularly good illustrations of this principle, since in them the older stem has undergone very marked xerophytic modifications in the way of flattened, appressed leaves, etc. These extreme xerophytic features are absent as a rule in the seedling, where a somewhat Taxodineous type of foliage is often found. The more ancestral type of foliage may further be discovered in the relatively more vigorous main axes, where there is often present a larger and less appressed type of leaf. In this connection may be mentioned the reversion to ancestral conditions of internal structure, which sometimes occurs in the first annual ring of vigorous branches. The writer has pointed out in the first memoir of this series (Jeffrey, :03) that in the more vigorous ramifications of the cone-bearing shoots of *Sequoia gigantea* there occur, in the first annual ring only, resin canals such as are found as an unfailing structural feature of the wood in



the female cone. This feature is the more remarkable since resin canals are absent ordinarily in the woody tissues of the Sequoias and are replaced by resin cells of the usual Cupressineous type. This characteristic of the first annual ring of vigorous branches of mature trees of *Sequoia gigantea* must apparently be interpreted as ancestral, since it is paralleled by the presence of a similar feature in the reproductive axis.<sup>1</sup> The condition of reduction from a more luxuriant ancestry also explains why the resin canals in question are not found in the seedling in the first annual ring. Apparently there must be a considerable accumulation of nutritive capital before the species under discussion is able to reproduce the ancestral conditions even in the first annual ring. It may be set down then as a rule, which in the future will doubtless receive numerous exemplifications, that in forms which have clearly suffered vegetative reduction the reappearance of ancestral conditions may be delayed to the first annual ring of the more vigorous shoots of the adult.

A further general principle of comparative anatomy, which is beginning to be established, is that ancestral conditions may be recalled by appropriate experimental conditions. Where there has been reduction from a more luxuriant ancestral type, experimental conditions, which bring about a greater determination of nutrition to the parts in question are apt to cause a reversion to the ancestral structure. It has been shown by Jackson ('99) that this is often true of the external form. In the case of Sequoia, as I have pointed out in the first memoir of this series (Jeffrey, :03), injuries to the phloem and the cambium, which bring about a damming up of the products of assimilation in the region of the injury, cause a hypertrophy of the woody tissues. In this hypertrophied wood more or less typical resin canals occur, similar to those found in the first annual ring of certain branches and invariably in the woody tissues of the female cone of *S. gigantea*. It is apparent that experimental morphology is likely in the near future, to receive from botanists the same attention that it has already begun to enjoy in the hands of the zoologists.

*The phylogeny of the Abietineae.*—The enunciation of general principles briefly attempted in the foregoing paragraphs will serve a useful purpose in the discussion of the phylogenetic relationships of the Pineae and Abietae. In the latter group, it has been noted in the descriptive part of the present memoir that resin canals are generally absent from the woody tissues of the root and shoot. Exceptions to this statement occur in the following cases. In the genus *Abies*, resin ducts have been found in the wood of the cones of *A. grandis*, *A. magnifica*, and *A. apollinis*. In *A. magnifica* (as in *Sequoia gigantea*) these are also in the first annual ring only of vigorous vegetative branches of mature trees. Resin ducts also are found invariably in the primary wood

<sup>1</sup> Radais ('94) has also noticed this feature of the cone in *S. gigantea*.



of the first annual ring of the root. The resin canals present under the conditions described above are perfectly normal, and are surrounded by a continuous jacket of resiniparous epithelium. A further mode of occurrence of resin canals in *Abies* is that seen in the case of injury to the bast and cambium, either from mechanical causes, or by the attack of parasitic fungi. The resin canals formed under these conditions are generally confined to the wood, and occur as tangential rows of so called "imperfect canals," which are in full communication with each other tangentially, and thus serve to pour resin over the surface of the wound. The resiniparous epithelium in this case is ordinarily thick walled and as a consequence conspicuously pitted. The thickening of the wall seems to be merely a mechanical device, as all parenchyma of the wood is more or less characterized by this feature in the vicinity of a wound. Further, the resiniparous cells surrounding the traumatic resin ducts under consideration are apt to partake of the general features of the parenchyma normally occurring in the wood and the medullary rays. They may often as a consequence contain the globules of tanniferous material, which are so constant a characteristic of the so called resin cells in *Abies* and other genera of the Abietae as limited above. In the remaining genera, *Cedrus*, *Pseudolarix*, and *Tsuga*, the normal occurrence of ligneous resin canals is confined to the first annual ring of the root. Traumatic resin ducts are found in the last mentioned genera as a feature of the wood in the case of injury just as in *Abies*. It is of importance to note, that in *Cedrus*, traumatic resin canals may occur both in the horizontal and in the vertical planes, with correlation between the two systems. Only vertical ducts have been made out in the other genera of the Abietae.

Before going on to discuss the significance of the structural features of the wood summarized in the foregoing paragraph we may turn our attention to the distribution of cortical resin canals in the Abietae. In *Abies* and *Cedrus*, resin canals occur abundantly in the cortex of both vegetative and reproductive axes and in the mesophyll of the leaf as well. In *Pseudolarix* and *Tsuga* on the other hand, the resin canals of the cortex are strictly confined to the female reproductive axis together with its appendages and to the mesophyll of the leaves. Cortical resin ducts cannot be produced as the result of injury.

The distribution of the resin canals in the wood and cortex of the Abietae is such that if the validity of the general principles enunciated above be admitted, we must regard them as having come from ancestors having resin canals throughout their wood and cortex, as is the case with the genera included in this memoir in the subfamily Pineae. The resin canals in the Abietae have almost entirely disappeared in the woody tissues, only retaining their place in an isolated fashion in such conservative regions as the wood of the female cone and the first annual ring of the root and shoot. They further show their vestigial character in the phenomena of injury. In the cortical tissues there



is a close parallelism of distribution, for in *Tsuga* and *Pseudolarix*, in which cortical resin passages are largely obsolete, they persist in the ancestral situations presented by the cortex of the female cone and its appendages, and the mesophyll of the leaf. If the general principles of comparative anatomy enunciated at the beginning of this discussion are correctly formulated the Abietae have come from a stock characterized by the presence in both fundamental and fibrovascular tissues of resin ducts which form a continuous system of horizontal and vertical canals, such as are found in the living *Pineae*.

If we attempt to picture to ourselves the probable course of evolution which has led to the more or less complete loss of the resin canals in the Abietae (as defined above), it would appear to be as follows. The ancestral forms provided with a comprehensive and freely anastomosing system of resin canals in both cortical and ligneous tissues, were thus safeguarded against infection in case of injury, but at great cost both in the large supply of resinous secretion necessary to supply the needs of this extensive system, and in the large quantity expended in sterilizing a wound. On account of the reduced foliage of even the Abietineous Conifers, this was a very serious drain on the assimilatory apparatus. Gradually the more economical tendency arose of forming resin passages in the case of need only. In *Pinus* this tendency is scarcely observable, while in the other three genera of the *Pineae* it has become quite marked. In the Abietae it has passed beyond the stage even of a marked tendency and has become the rule, so that in this subfamily the original extensive and anastomosing system of resin canals has become reduced to isolated and uncommunicating ducts, quite useless as a rule from the protective standpoint and persisting as ancestral relics in the more conservative organs and parts of the plant. The place of this system is taken by the much less costly expedient of resin cells and by traumatic resin ducts which are formed in case of need only.

It should be pointed out here, although this matter is reserved for fuller discussion in connection with the study of the genus *Pinus* in a subsequent memoir, that this conclusion is supported by other anatomical considerations. A characteristic feature of structure in the medullary rays of many of the Abietineae is the presence of marginal tracheidal cells, generally interpreted as favoring the radial movement of water in the wood and rendered necessary by the fact that the pits of the tracheids of the wood are mainly on the radial walls, thus providing for a tangential rather than a radial movement of water. These marginal tracheidal cells are well marked in the genera *Pinus*, *Picea*, *Larix*, and *Pseudotsuga*, but as has been recently noted by Strasburger are much less prominent in *Tsuga* and *Cedrus*, while as was long ago pointed out by De Bary, in *Abies* they are lacking except in a few species. My own observations in the case of *Pseudolarix* show them to be absent here, although I have not had access to sufficiently robust stems to be able to state positively that they are never present in this monotypic genus.



Penhallow (:03) assumes that the occurrence of these ray tracheids marks a high stage of evolution in the genera which are characterized by their presence. It should be remembered in this connection, as Strasburger ('72) has emphasized, that the Coniferales are a group which has undergone regressive metamorphosis and as a consequence structural features of high complexity are more apt to be characteristic of the ancestral forms than of those of more modern origin. Further, Penhallow (:03) himself has called attention to the fact of the sporadic occurrence of ray tracheids in the genera *Juniperus* (*J. communis*, var. *alpina*) and *Cupressus* (*C. thyoides* and *nootkatensis*) among the Cupressineae. Their presence here is to be interpreted rather as vestigial than rudimentary especially in view of the peculiarities of the seedlings in this group, which seem to show clearly that it is a reduced order of the Coniferales. Furthermore, the occurrence of ray tracheids is in itself by no means an indication that the Abietineae are a modern order, for the same feature was present in that very ancient family, the Lepidodendraceae, which, as has been pointed out by Corda (Williamson, '81, p. 294) and Scott (:00), was characterized by the presence of scalariform tracheids in the medullary rays.

We may now pass on to consider the closer affinities of the several genera of the Abietineae. As has been pointed out above they fall naturally into two series as a result of the consideration both of their anatomy and of their reproductive organs. The genus *Pinus* appears to stand by itself among the Pineae, for its fascicled leaves and altogether unique cones, as well as its great geological age, separate it clearly from the other three genera. *Picea* and *Pseudotsuga* seem to be rather close to one another, but *Larix* cannot be regarded as far removed. The genus *Abies* includes perhaps the greatest number of primitive features among the Abietae. Closely allied to it is *Pseudolarix*, not only in its anatomical structure and its rapidly deciduous cone scales but also in its thickly integumented seeds. The deciduous foliage of *Pseudolarix* is by no means sufficient to unite it with *Larix*, as is generally assumed by the taxonomist, for *Cedrus*, which has always been regarded as possessing close affinities with *Abies*, is also occasionally deciduous, as has been pointed out by Carrière and Kent (:00). *Abies* and *Pseudolarix* closely resemble each other in the possession of very characteristic mucilage cells, which are quite absent in *Cedrus* and *Tsuga*. *Cedrus* is generally conceded to be allied to *Abies*, to which, as has been shown above, it presents a very close resemblance in the details of its anatomy, the structure of its seeds, and the deciduousness of its cone scales. It differs from *Abies* and *Pseudolarix* in the absence of mucilage cells. Of the four genera of the Abietae, *Tsuga* shows the least affinity with the others. Its cone scales are not deciduous and its seeds are not relatively as thick walled as those of the three first mentioned genera. Further, in the single resin canal of the leaf, it resembles many of the Cupressineae.



*Relationship of the Abietineae to other Coniferous orders.*—It is perhaps the prevailing tendency at the present time to regard the Abietineae as the most modern of the Coniferous orders. This view does not appear to be supported, however, by the recent results of palaeontological research, or by those of anatomy and general morphology. It has been recently shown by Zeiller (:04) that *Pinus*, which is often regarded as a very modern representative of the Conifers, was already present in the Jurassic in the two sections representative of the hard (*Pinaster*) and the soft (*Strobus*) pines. By this discovery the genus appears as a very ancient one, for if its two distinctive sections were already well marked as early as the Jurassic period, its primitive history must lie far in the geological past, extending perhaps to the Permian, for Penhallow (:00) has described a *Pityoxylon* of this age.

In discussing the relationship of the Abietineae to the other Coniferous orders, it will be convenient at the present time to confine our attention to the Cupressineae, in the larger sense, for these have already been touched on in the first memoir. As has been pointed out by Zeiller (:00), the Cupressineae are relatively modern in their appearance in the geological strata, and it may accordingly be suggested as probable that they are less primitive than the Abietineae. Anatomically the wood of the Cupressineae is characterized by the absence of resin canals, except in certain sporadic instances, and the place of these is taken by resin cells. By a course of reasoning similar to that adopted in the present memoir, the writer has reached the conclusion that the resin ducts described by him in the first annual ring of branches and in the wood of the cone-axis and scales of *Sequoia* are an ancestral feature. This conclusion was fortified by the occurrence of resin canals in this genus as the result of injury, and presumably as a reversion to the ancestral condition of the wood. The inference was drawn in the first memoir that the presence of what were apparently vestigial resin canals in *Sequoia* pointed to the derivation of that genus from a stock characterized by the presence of ligneous resin canals. The attempt has been made in the present memoir to show that this condition of the wood is not only characteristic of the Abietineae, but is also a very old one for this order. On the basis of wood structure alone it would appear that the Abietineae are older than the Cupressineae. It is obviously undesirable to interpret affinities from the structure of the wood alone, useful as this has proved in tracing affinities in the case of fossils, where no other evidence has been available.

The structure of the female cone is universally admitted to be of great importance in arriving at the relationship of the various orders of the Coniferales. There are several morphological interpretations of the female cone, the best established of which explains it as a main axis bearing a number of flattened and reduced ovuliferous shoots, each borne in the most primitive condition, in the axil of a bract. In the



less primitive types of female cone the bract and flattened axis become more or less completely fused with each other, so that in many cases it is only possible to distinguish them by their still separate fibrovascular supply. This view has received strong confirmation. As is well known, in the genus *Sciadopitys* the apparent vegetative leaves are really two fused leaves belonging to an abortive branch and are axillary to a scale-like bract. This interpretation is generally accepted in the case of the genus under discussion, and as has recently been pointed out with great aptness by Coulter (:01) is a clear case of parallel reduction in a vegetative shoot corresponding to that hypothetically found in the case of the ovule-bearing scales of the Coniferous cone. This parallel drawn by Professor Coulter receives the strongest confirmation from proliferous female cones of *Sciadopitys*, in which the ovuliferous scales are actually replaced by green double needles, such as are found on the vegetative axes of the same species (for a good original figure of one of these interesting proliferous cones, see Veitch's *Manual of the Coniferae*, 1900, p. 54). A shoot organ has appeared so often and in so many different genera of the Coniferales in place of the ovuliferous scale, that we may safely regard the two structures as homologous. If it be admitted that the ovuliferous scale is the representative of a reduced shoot occurring in the axil of a bract-like leaf, it follows, other things being equal, that the group which most nearly realizes the ancestral condition will be the most primitive, and those in which the bract and ovuliferous scale are wholly or partially fused must be more modern and specialized. On this basis we are compelled to regard the Abietineae, in which the bract is without exception quite free from the ovuliferous scale, as more primitive than the Cupressineae (in the large sense) in which the bract and ovuliferous scale are always intimately fused together.

But it is not in the structure of the female cone alone that the Abietineae appear to show themselves more primitive than the Cupressineae. The prothallium found in the ovule of this order is throughout characterized by the thick megaspore coat which surrounds it. This is a feature which the Abietineae possess in common with the Cycads and the fossil Gymnosperms. The thick coat surrounding the megaspore in the Cycads has been described by Warming and more recently by Lang. The figures of Williamson, Scott, and Oliver sufficiently establish the presence of a similar thick megaspore coat in several fossil Gymnosperms. In the Cupressineae, the Taxineae, the Gnetales, etc., the coat surrounding the megaspore is thin or obsolete. The Abietineae thus present in the structure of their megaspore coat a very significant feature of resemblance to the older Gymnosperms.

The structure of the male gametophyte in the Abietineae is also indicative of their being more primitive and less reduced than the Cupressineae. In the first



order two or three prothallial cells are formed within the germinating pollen grain previous to anthesis, as has been shown by Strasburger and others in the case of *Larix*, *Pinus*, *Tsuga*, etc. In the Cupressineae, using the term in the broader sense to include such forms as *Sequoia* and *Taxodium* as well as *Thuja*, *Cupressus*, and *Juniperus*, this is not the case as only the stalk and antheridial cells and the tube nucleus make their appearance in the germinating microspore. It may be urged that the winged pollen, found in *Pinus*, *Abies*, *Cedrus*, *Picea*, etc., is to be regarded as a mark of high specialization and as a consequence an indication of a modern origin for the group under discussion. This is by no means necessarily the case, for examples of winged microspores are known to have existed among the *Lepidodendrids* (Scott, '98), and there are no cases of winged pollen grains among anemophilous Angiosperms, which may be taken as the most modern type of wind-fertilized vascular plants. It seems probable that the air sacs are for the purpose of reducing the specific gravity of the ancestrally heavy and multicellular type of pollen grain found in the Abietineae.

Perhaps the most important indication of the primitive nature of the Abietineae is supplied by the study of their leaf trace. It is now a well established general principle that ancestral features are apt to persist for a long time in the vegetative leaves of the vascular plants. This principle is, for example, very well illustrated by the case of the Cycads, referred to in an earlier paragraph. Attention has been called in the descriptive part of this memoir to the fact that no matter what may be the character of the foliar strand in the lamina of the leaf in the Abietineae, it is always a double strand in the cortex. A double leaf trace was characteristic of *Lyginodendron*, *Poroxyton*, *Calamopityx*, the *Cordaitea*, and others of the fossil and transitional Gymnosperms. It is also exemplified in the foliar trace of *Ginkgo* and in the double strand, which often passes off to the sporophylls in the Cycads. Scott (:00) has called attention to this feature of the older Gymnosperms and suggests that it may have a taxonomic value. In view of the facts described in this memoir for the Abietineae, the double trace appears to have a peculiar significance, especially when it is recalled that the Cupressineae have but a single foliar strand (Bertrand, '74). The topography of the double foliar trace in the Abietineae is such that we may regard the single leaf trace, which is found in what we believe to be the less ancient orders of the Coniferales, *i. e.*, the Cupressineae, *Taxineae*, etc., as originating by the progressive reduction in size of the leaves. The process is centripetal, that is, it progresses from the apex of the leaf downwards into the cortex of the stem, so that starting with a single bundle in the foliar apex we arrive sooner or later at the primitive double bundle. The separation may take place high up in the lamina of the leaf, as has been pointed out by Strasburger ('91) in the case of *Pinus*. Further, in very small leaves of the Abietineae, as has been noticed



by Thomas ('66), there may be but a single strand throughout. This author is of the opinion that the single bundle is more primitive, and cites Ginkgo as an example in which the increased development of the leaf leads to the appearance of a double foliar trace. With our present knowledge of the more ancient and especially of the fossil Gymnosperms, this interpretation cannot be accepted, for we have now every reason to believe that the ancestors of the Coniferales had much larger foliar organs, much more richly supplied with strands of fibrovascular tissue, than their descendants. The progression is consequently in the opposite direction, *i. e.*, the more modern Gymnosperms have suffered reduction both in leaf surface and in the fibrovascular tissue constituting the leaf traces. The simplification of the leaf traces into a single strand has apparently been from above downwards. In further support of this view may be cited the observation made by Scott ('97) in the case of the reduced strands occurring in the peduncular portion of the cone in certain species of Cycads. Here paired strands coming off from the central cylinder of the cone, run a greater or less distance upward into the cortex and then become fused together. Dr. Scott considers it probable that these double strands represent abortive leaves. It is interesting in connection with the present argument that there should be the same fusion of originally separate leaf traces at the apex in the case of reduction.

Other indications of primitive affinity, less important it is true, because less wide spread and constant, are the occurrence of a chambered pith in *Abies* and in certain species of *Pinus*, and in the case of the leaf trace of the former genus, the complete enclosure of the phloem of the laminar bundle of the leaf in certain instances, by a cordon of transfusion tissue. The first of these features was very prevalent in the *Cordaites* although not universally present (Scott, :02), while the second has also been recently described in a *Cordaitean* leaf (Stopes, :03).

If the arguments advanced in the foregoing paragraphs are sound, we may assume, because they present many features of structure which unite them both with the older Gymnosperms on the one hand, and by an obvious process of reduction, with the Cupressineae, etc., on the other hand, that the Abietineae are a very ancient family or order of the Coniferales. This conclusion is favored by what is known at the present time of their geological occurrence, and will probably receive fuller confirmation from this source when the geological record is more complete than it is at the present time.

*The affinity of the Abietineae with other cohorts of Gymnosperms.*—The discussion of the relationship of the Abietineae with other great groups of Gymnosperms has been largely anticipated in the paragraphs of the last section. Both Coulter and Chamberlain (:01) and Scott (:00) among recent writers on the subject of the phylogeny of the Gymnosperms have derived the Coniferales as a whole from a *Cordaitean* stock or plexus.



The results of the present investigation seem only to add confirmation to this view. Although the reproductive apparatus of the Cordaites, as far as we are at present acquainted with it, was somewhat different in its organization from that of the Coniferales, still as Dr. Scott (:00) has pointed out in the case of the female axis, it is not difficult to trace homologies with that of the latter group, if we regard the ovuliferous apparatus in the Conifers as consisting of a reduced and modified axillary shoot. The anatomical study of the vegetative organs of the Coniferales, as represented in the present instance by the Abietineae, serves strongly to confirm the relationship of the two groups. It seems quite impossible to refer the Coniferales any longer to a Lycopodiaceous ancestry, although their superficial features seem somewhat to favor such a derivation. It has been pointed out by the writer (:02) that the mode of exit of the leaf trace from the central cylinder, even in those Conifers which have their foliage most reduced, is distinctly Filicinean, and of a type which is never found in the Lycopods or their allies. The present research increases the difficulty of the Lycopodiaceous phylogeny, by making clear that the foliar fibrovascular supply in the case of the Abietineae is of the same double type as that which is primitive for the Lyginodendreae, the Cordaitales, the Cycadales, the Ginkgoales, and many Filicales.

#### SUMMARY.

1. The Abietineae are divisible, on the evidence supplied by a study of their vegetative and reproductive organs, into two very distinct subfamilies, *viz.*, the Pineae and the Abietae.

2. The Pineae are characterized by the invariable presence of resin canals, forming an anastomosing system in the secondary wood and cortex of root and shoot. Resin canals are present in the outer margin of the primary wood of the root. The scales of the female cone are not deciduous. *Pinus*, *Picea*, *Larix*, *Pseudotsuga*.

3. The Abietae ordinarily do not possess resin canals in the secondary wood of root and shoot. Resin canals, however, are sometimes found in the wood of the female reproductive axis, and in the first annual ring of vigorous shoots of sexually mature trees. Resin canals occur in the secondary wood in tangential rows, as a result of injury. Resin canals are invariably found in the center of the primary wood of the root. The scales of the female cone are generally deciduous. *Abies*, *Pseudolarix*, *Cedrus*, *Tsuga*.

4. The evidence derived from anatomy and experimental morphology goes to show that the presence of resin ducts in the woody tissues and in the cortex of the Abietineae is primitive for the group. The resin canals persist longest in the reproductive axis, the leaf, and the *first* annual ring of root and shoot. In the more specialized genera the resin canals of the wood are replaced by resin cells, but in the latter condition



of the wood, resin canals may always be recalled as a result of injury. The disappearance of resin canals and their replacement by resin cells is probably for the sake of economy of carbo-hydrate material. In *Pseudolarix* and *Tsuga* even the cortical resin canals disappear from all organs except the female reproductive axis, together with its appendages, and the vegetative leaf.

5. The Abietineae are an older group than the Cupressineae, in the larger sense, and are either antecedent to these or from the same ancestry. This conclusion is reached from an anatomical and experimental morphological study of their organs, root, shoot, and leaf. It is confirmed by the examination of the female reproductive organs and of the pollen. It is further in conformity with palaeontological evidence.

6. The Abietineae are throughout characterized by the same double leaf trace which is a constant feature of the older Gymnosperms, the *Lyginodendreae*, the *Cordaitales*, the *Ginkgoales*, and the *Cycadales*. This feature serves to separate them from the *Cupressineae* in the larger sense, and to unite them with the *Cordaitales*, which they resemble in other important particulars, described in the body of the memoir.

7. The Abietineae must be regarded on comparative anatomical and morphological grounds as a very ancient order of the Coniferales, and may even be the oldest living representatives of this group.

In conclusion, I wish to express my obligation to Prof. G. L. Goodale for access to the specimens of wood in the economic collections of the Museum. I am indebted to my father for material collected during his summer vacation. My thanks are also due to Mr. George S. Shaw, former chairman of the visiting committee to the Museum, and through him to Prof. C. S. Sargent and Mr. Jackson Dawson of the Arnold arboretum of Harvard university, and to Mr. Walter Hunnewell, the present owner of the Hunnewell pinetum. But for the kindness of Mr. Shaw and those he has interested in my needs, this work could scarcely have been carried to a conclusion. A considerable amount of valuable material has reached me from the authorities of the Royal gardens, Kew, England, for which I likewise wish to offer my sincere thanks.



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## EXPLANATION OF PLATES.

(All the figures are from photomicrographs.)

## PLATE 1.

- Fig. 1. Transverse section through the margin of the traumatic wood in *Pseudotsuga taxifolia*.  $\times 20$ .  
Fig. 2. Transverse section of the root of *P. taxifolia*.  $\times 20$ .  
Fig. 3. Transverse section of the lower third of the leaf of *P. taxifolia*.  $\times 40$ .  
Fig. 4. Transverse section of a stem of *P. taxifolia*, showing the exit of the leaf trace from the central cylinder.  $\times 60$   
Fig. 5. Transverse section of the stem of *P. taxifolia*, showing the structure of the leaf trace in its passage through the cortex.  $\times 60$ .  
Fig. 6. Transverse section of the root of *Larix americana*, showing the communication of the resin ducts, opposite the groups of protoxylem, with the ducts of the cortex.  $\times 60$ .  
Fig. 7. Transverse section through the leaf base of *L. americana*, showing the double trace.  $\times 60$ .  
Fig. 8. Transverse section through part of a wounded stem of *Picea nigra*, showing the formation of traumatic resin canals.  $\times 10$ .

## PLATE 2.

- Fig. 9. Transverse section of the stem of *Picea nigra*, showing the double leaf trace.  $\times 60$ .  
Fig. 10. Transverse section of a wounded stem of *Abies balsamea*, showing the formation of traumatic resin canals along the margin of the wood.  $\times 8$ .  
Fig. 11. Part of the same more highly magnified to show the details of the resin canals.  $\times 30$ .  
Fig. 12. Traumatic wood of the base of a witches' broom of *A. balsamea*, showing the formation of resin canals.  $\times 30$ .  
Fig. 13. Section of the injured wood of the stem of *A. magnifica*, showing the formation of numerous rows of resin canals in the same annual ring.  $\times 60$ .  
Fig. 14. Transverse section through the upper part of the axis of the cone of *A. magnifica*, showing the presence of normal resin canals in this organ.  $\times 20$ .  
Fig. 15. Section through part of the lower region of the cone-axis of *A. magnifica*, showing the smaller size of the resin canals.  $\times 30$ .  
Fig. 16. Section through part of the same region as that shown in Fig. 14 more highly magnified to show the fusion of the resin canals.  $\times 40$ .

## PLATE 3.

- Fig. 17. Section through a vigorous branch in the reproductive region of *Abies magnifica*, showing the presence of normal resin canals in the first annual ring.  $\times 20$ .  
Fig. 18. Section through another specimen more highly magnified to show the normal occurrence of resin canals in the first annual ring.  $\times 20$ .  
Fig. 19. Section through a vigorous yearling branch of *A. magnifica*, showing the presence of normal resin canals.  $\times 20$ .  
Fig. 20. Transverse section of the inner portion of the last, highly magnified to show the structure of the resin canals.  $\times 180$ .  
Fig. 21. Longitudinal section of the pith of *A. magnifica*, showing the presence of sclerified diaphragms similar to those of the Cordaites.  $\times 25$ .



Fig. 22. Transverse section of a root of *A. nobilis*, showing the median resin duct of the primary wood.  $\times 15$ .

Fig. 23. Transverse section of the leaf trace of *A. magnifica*, showing the jacket of transfusion tissue surrounding the phloem.  $\times 150$ .

Fig. 24. Transverse section of the cone-axis of *A. appolinis* showing the presence of normal resin canals.  $\times 20$ .

## PLATE 4.

Fig. 25. Part of the last more highly magnified.  $\times 40$ .

Fig. 26. Section of a wounded branch of *Pseudolarix*.  $\times 8$ .

Fig. 27. Part of the same more highly magnified, to show the presence of traumatic resin ducts.  $\times 40$ .

Fig. 28. Section of the root of *Pseudolarix*, to show the median resin canal.  $\times 20$ .

Fig. 29. Part of another root more highly magnified.  $\times 30$ .

Fig. 30. A wounded root of *Pseudolarix*.  $\times 20$ .

Fig. 31. Transverse section of a branch of *Pseudolarix*.  $\times 15$ .

Fig. 32. Transverse section of the peduncle of a female cone of *Pseudolarix*.  $\times 20$ .

## PLATE 5.

Fig. 33. Section of a portion of the axis of the female cone of *Pseudolarix*, showing the presence of cortical resin canals.  $\times 30$ .

Fig. 34. Section through the base of the ovuliferous scale and the sterile bract of *Pseudolarix*.  $\times 25$ .

Fig. 35. Section through the sterile bract of the same.  $\times 40$ .

Fig. 36. Section through the foliage leaf of *Pseudolarix*.  $\times 40$ .

Fig. 37. Section through traumatic wood of *Cedrus atlantica*.  $\times 20$ .

Fig. 38. Section through the wounded root of the same.  $\times 20$ .

Fig. 39. Resin canals of the same more highly magnified.  $\times 180$ .

Fig. 40. Section through the wood of *C. deodara*, showing the presence of both horizontal and vertical resin canals.  $\times 20$ .

## PLATE 6.

Fig. 41. Another section more highly magnified.  $\times 70$ .

Fig. 42. Longitudinal section of wood of the same, showing horizontal and vertical resin canals.  $\times 15$ .

Fig. 43. Another of the same.  $\times 43$ .

Fig. 44. A tangential section of the same, showing resin canals of various degrees of development in transverse section.  $\times 20$ .

Fig. 45. Section of cone of *Cedrus atlantica*, to show absence of resin ducts in the wood.  $\times 30$ .

Fig. 46. Transverse section of the root of *C. atlantica*, to show median resin canal.  $\times 20$ .

Fig. 47. Transverse section of the double cortical leaf trace of *C. atlantica*.  $\times 120$ .

Fig. 48. Transverse section of wounded stem of *Tsuga canadensis*.  $\times 10$ .

## PLATE 7.

Fig. 49. Transverse section of a vigorous yearling stem of *Tsuga mertensiana*.  $\times 20$ .

Fig. 50. Transverse section through part of the cone of the same.  $\times 25$ .

Fig. 51. Transverse section of the axis of the cone, *T. canadensis*.  $\times 25$ .

Fig. 52. Transverse section of root of *T. mertensiana*.  $\times 20$ .

Fig. 53. Transverse section of root of *T. canadensis*.  $\times 30$ .

Fig. 54. Transverse section of part of a wounded root of *T. canadensis*.  $\times 30$ .

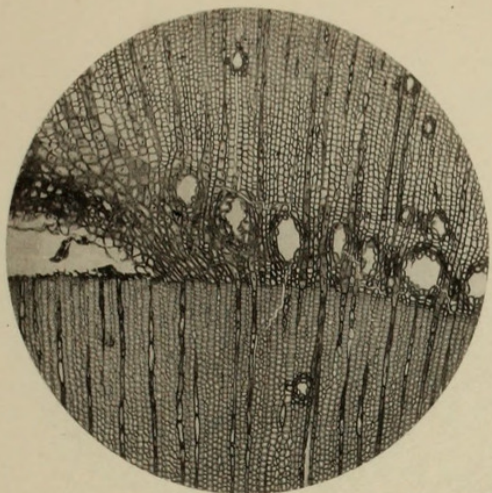
Fig. 55. Transverse section of center of root of the same.  $\times 180$ .

Fig. 56. Transverse section of stem of the same showing double leaf trace.  $\times 40$ .

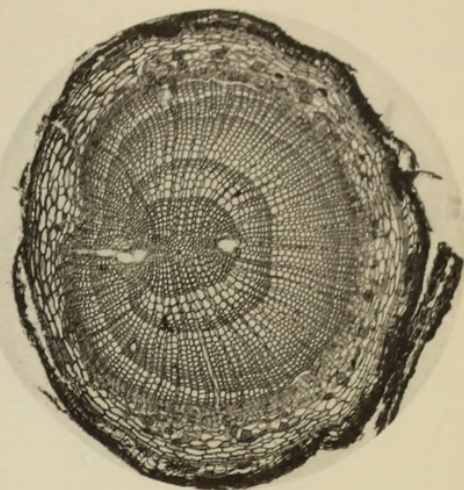




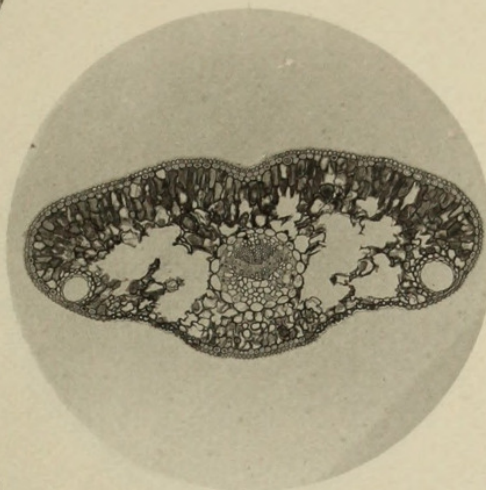




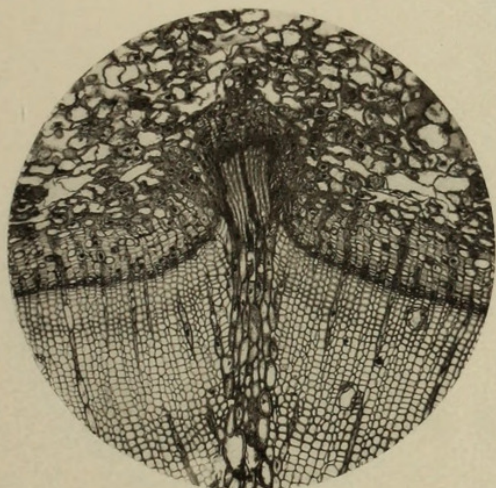
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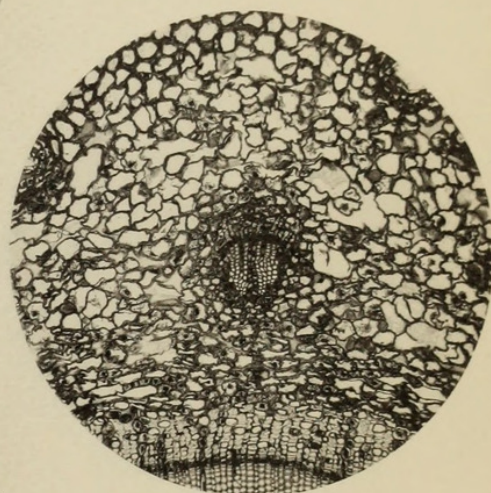
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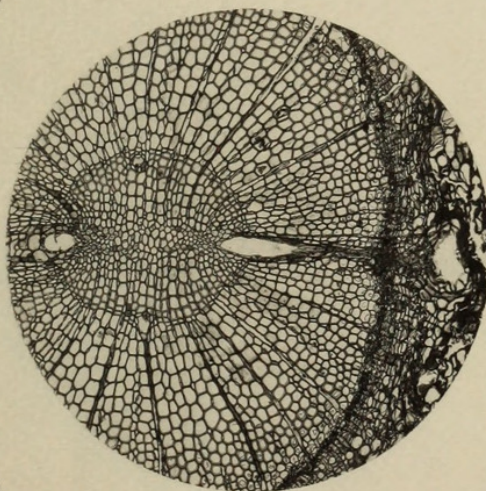
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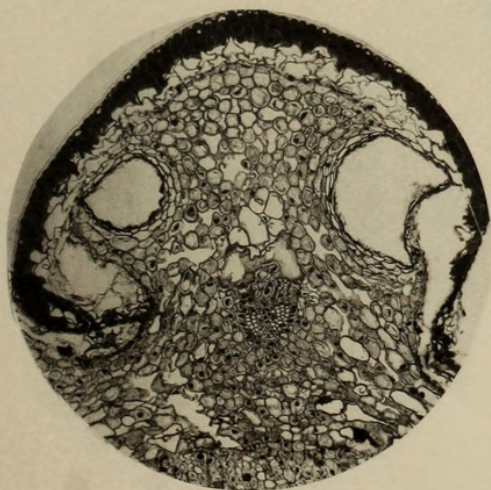
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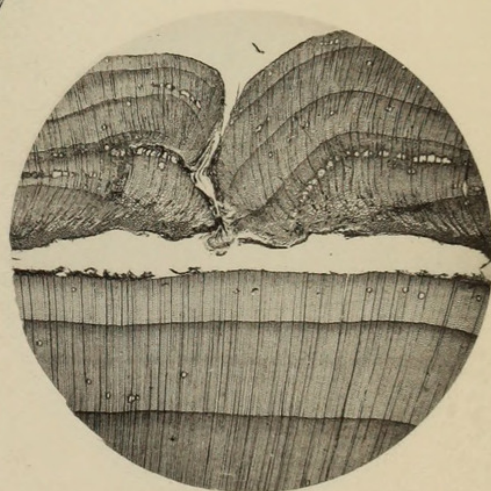
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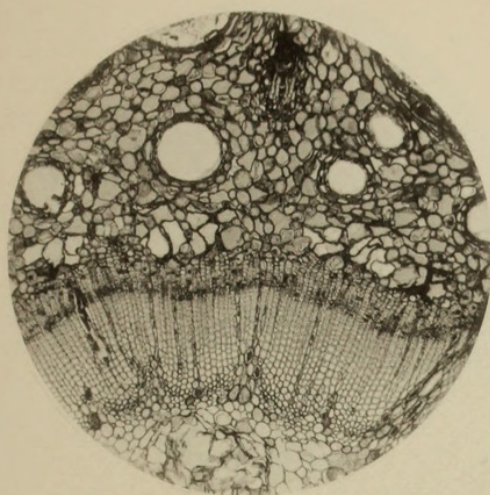


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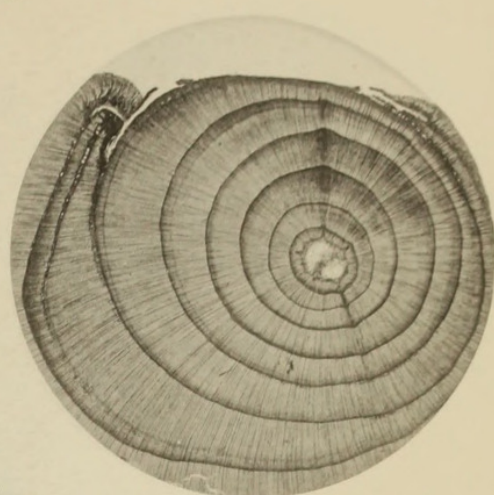




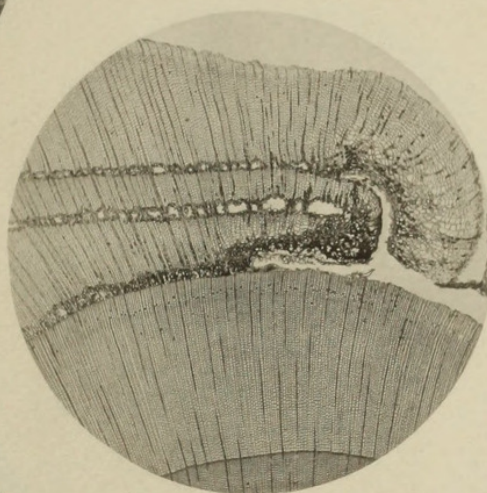




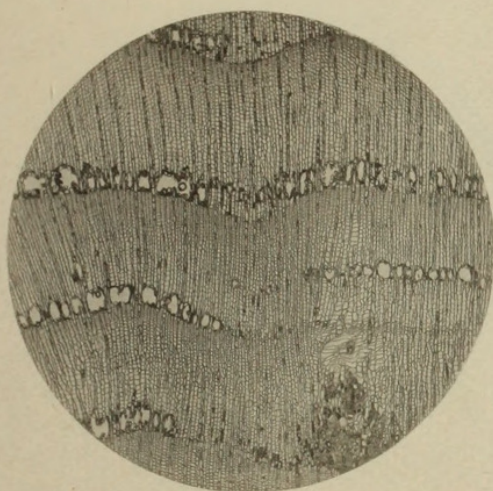
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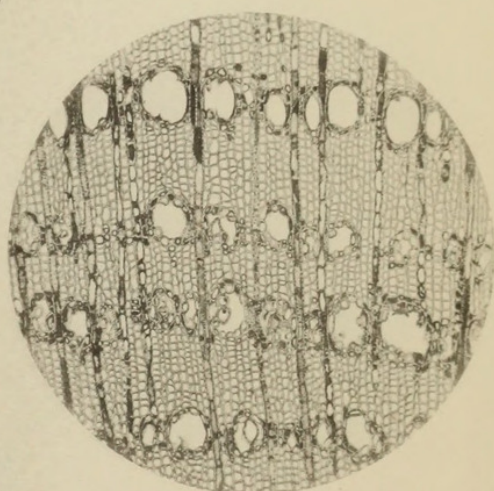
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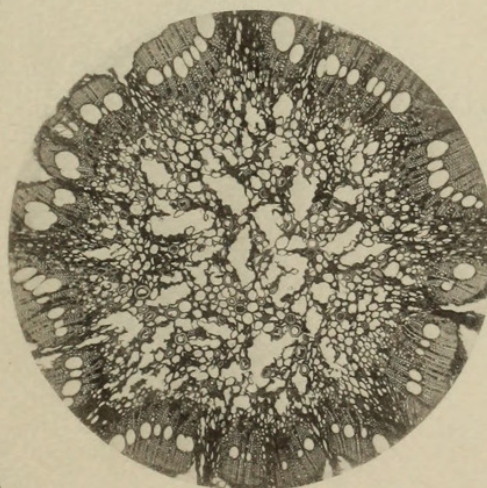
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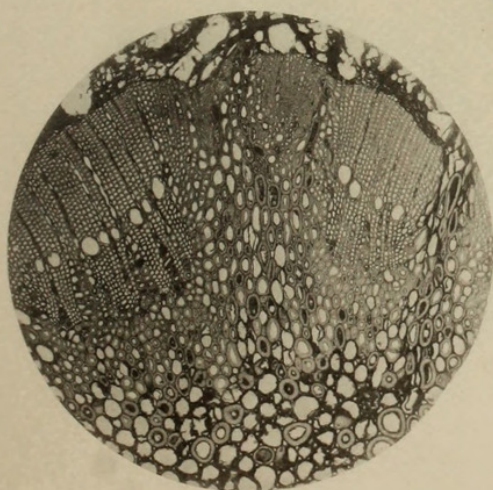
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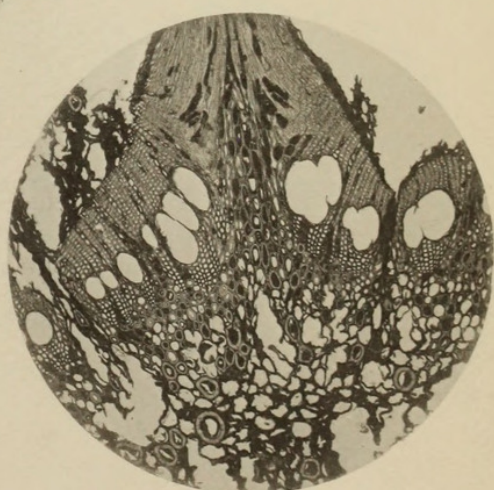
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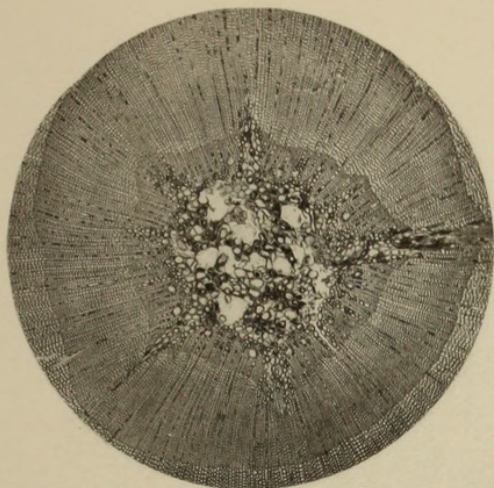


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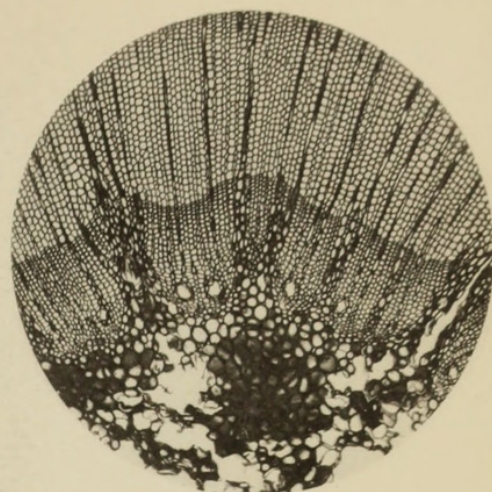




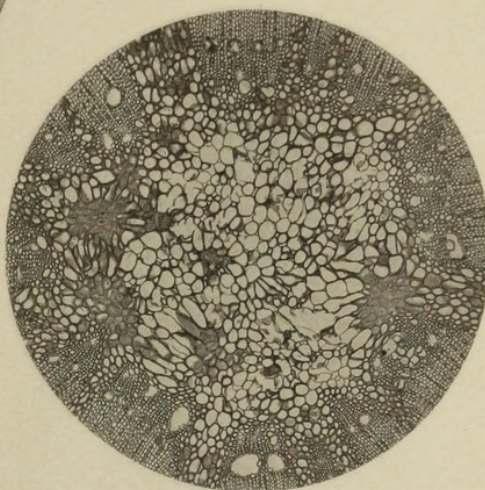




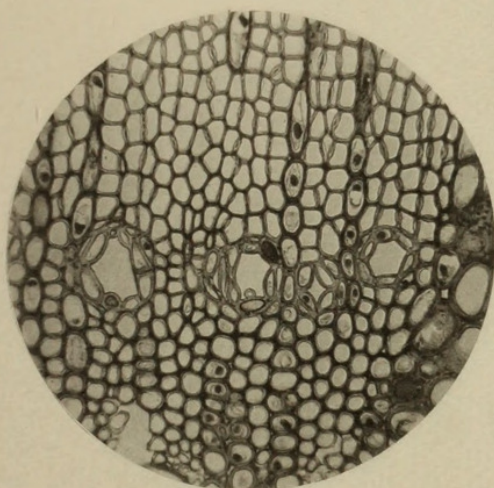
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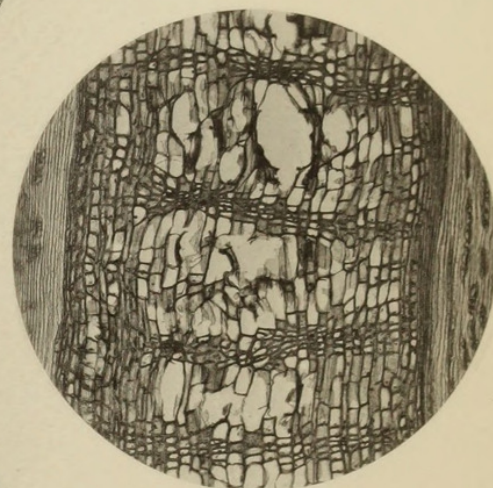
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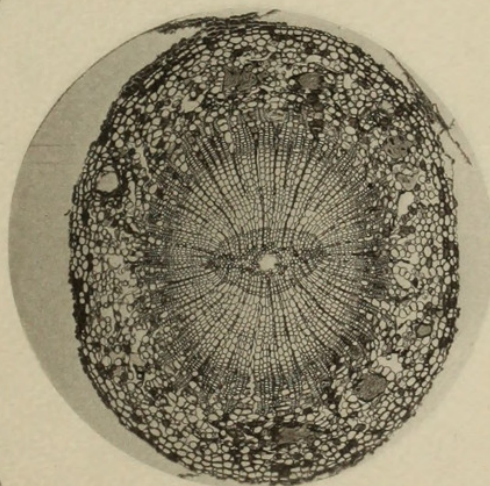
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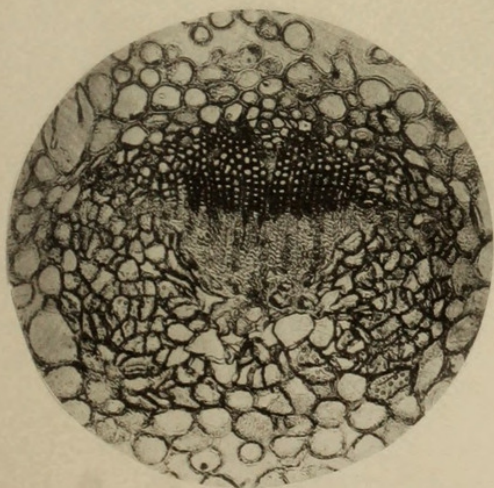
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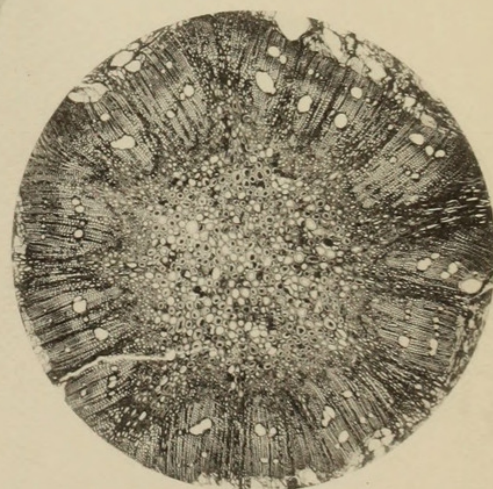
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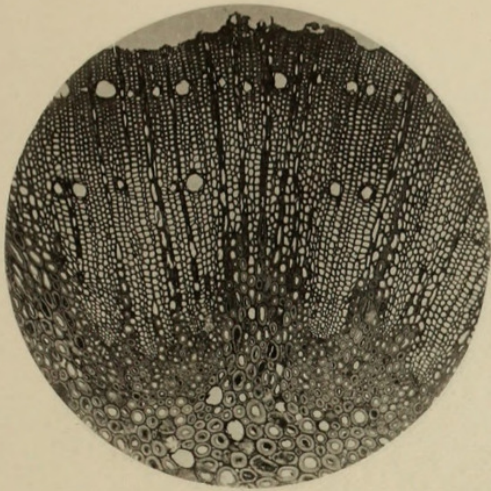


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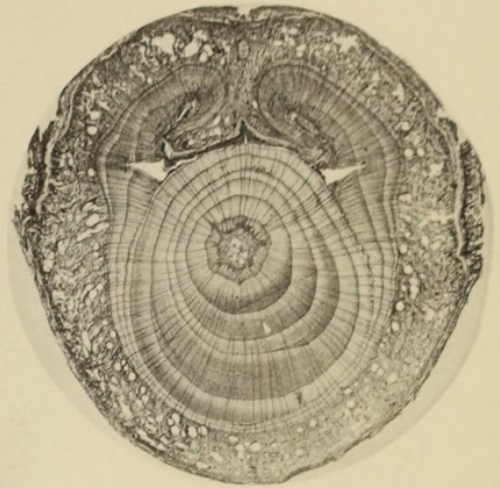




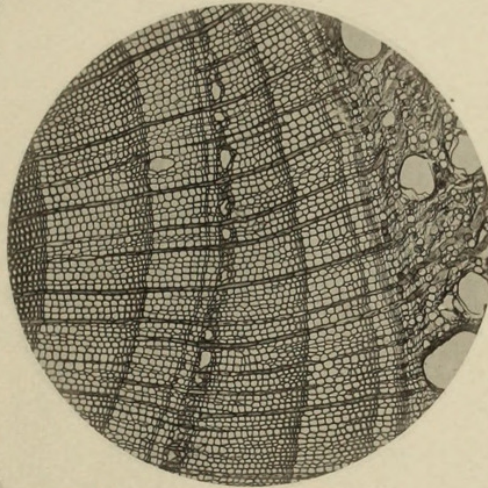




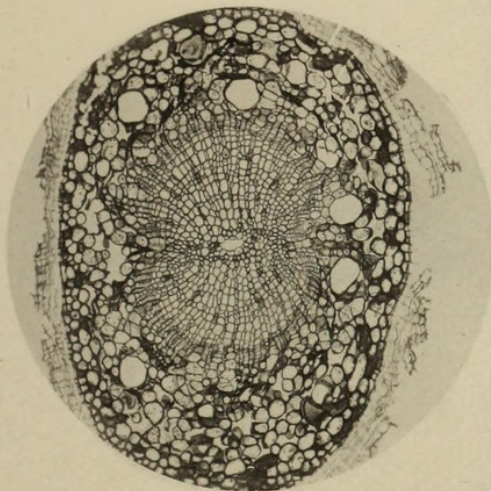
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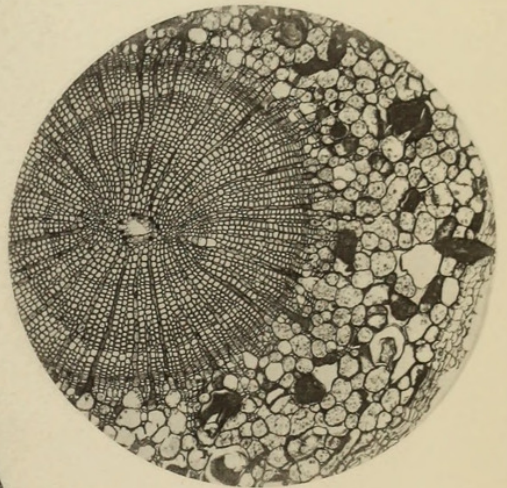
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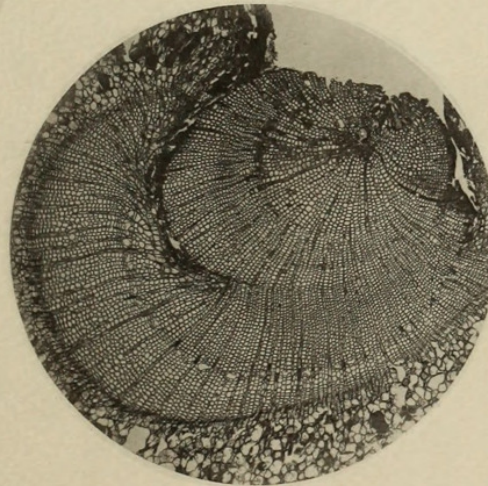
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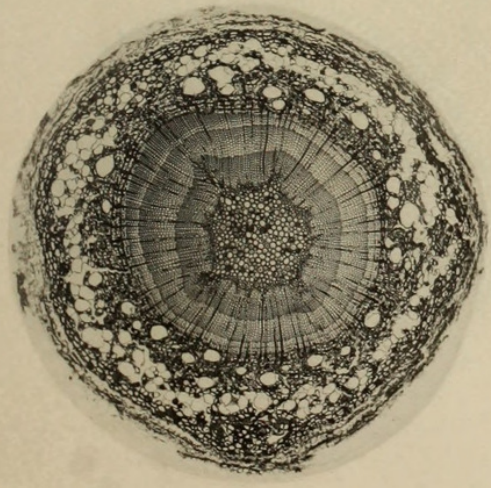
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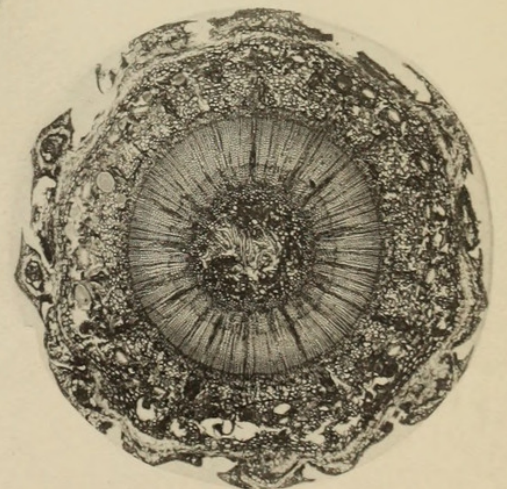
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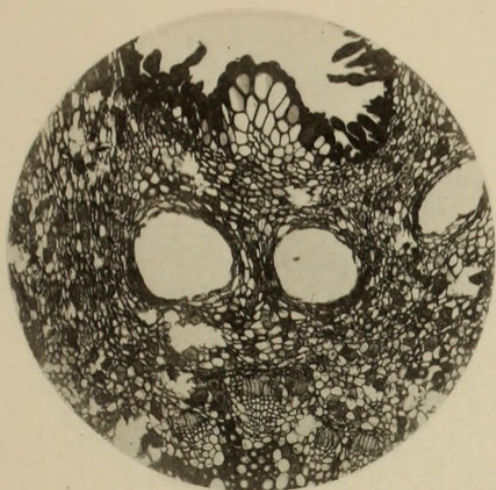


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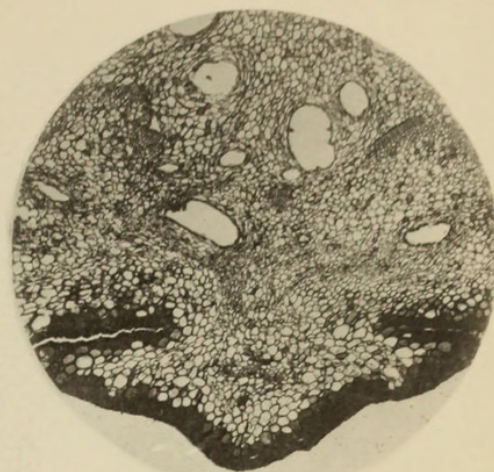




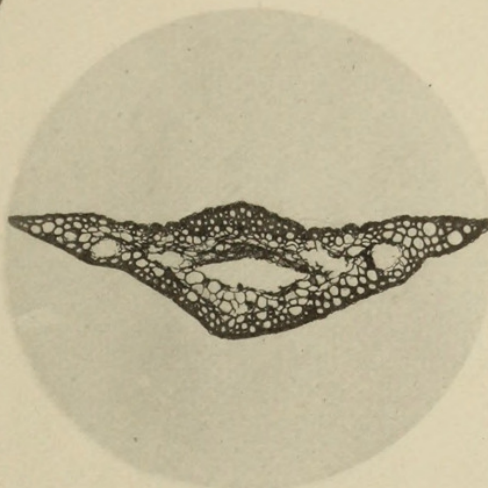




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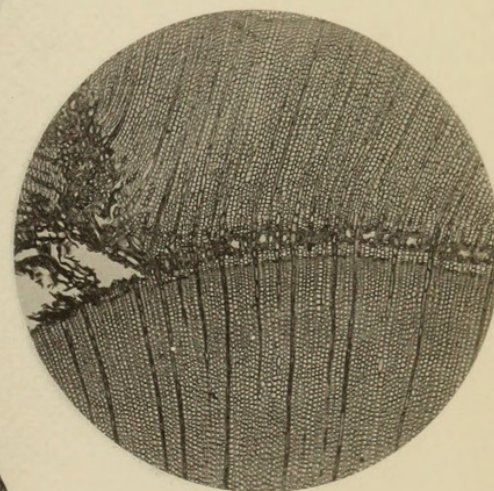
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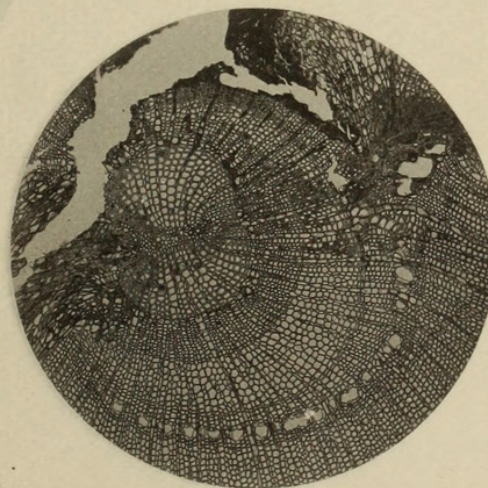
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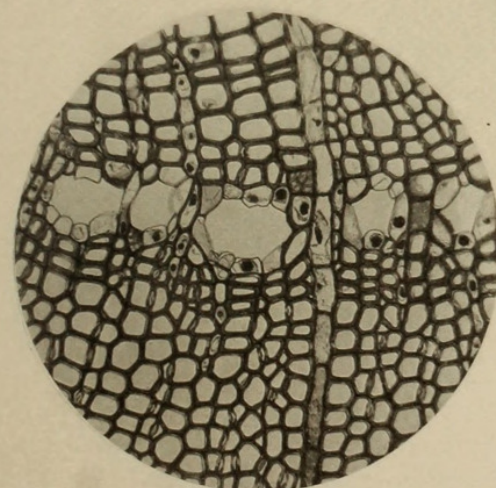
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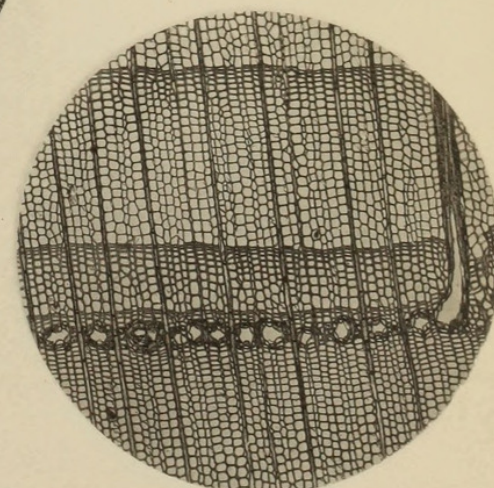
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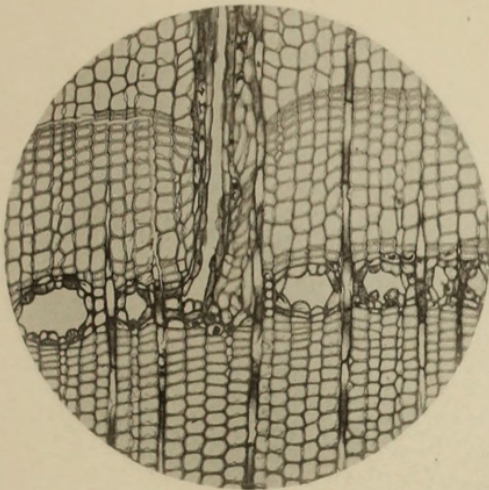


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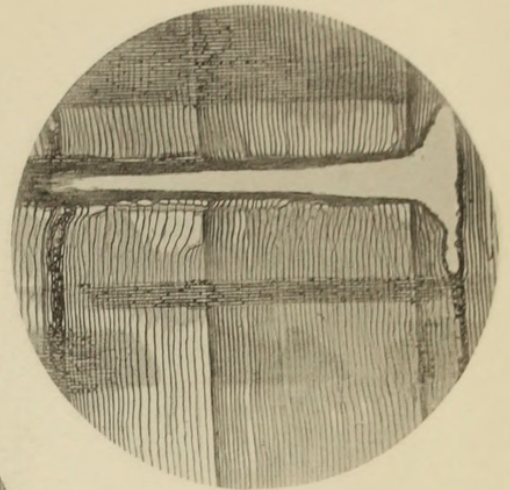




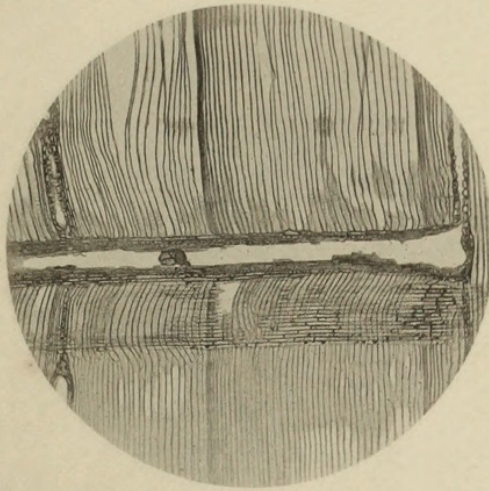




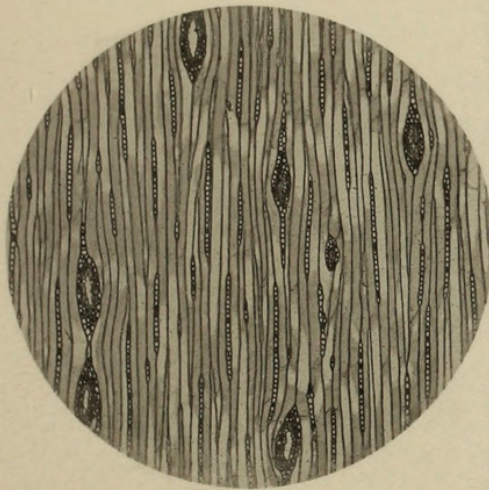
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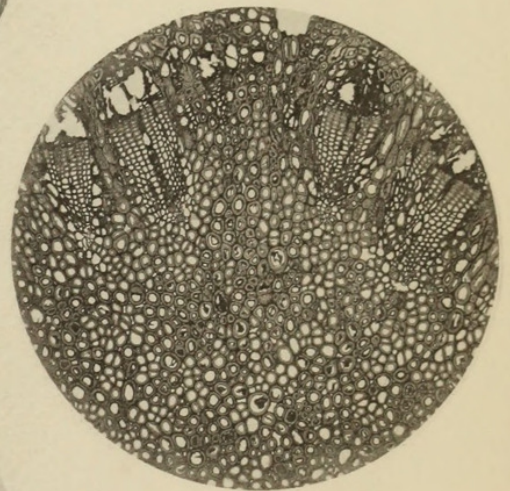
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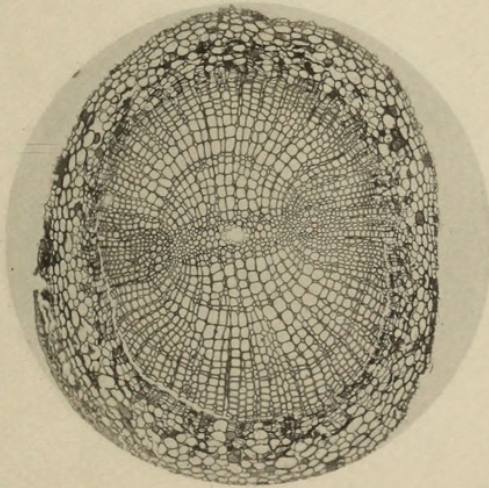
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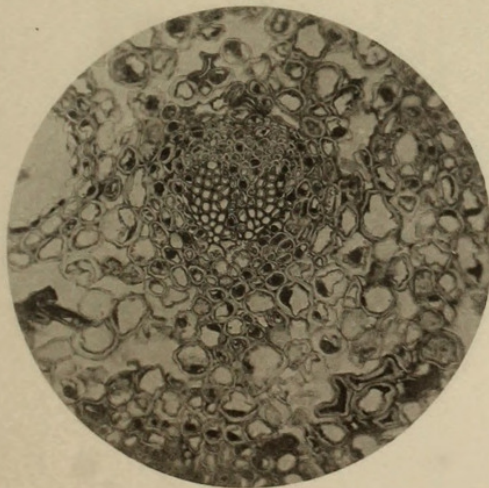
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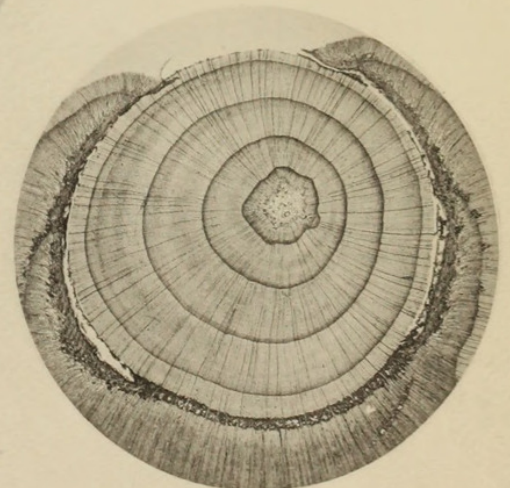
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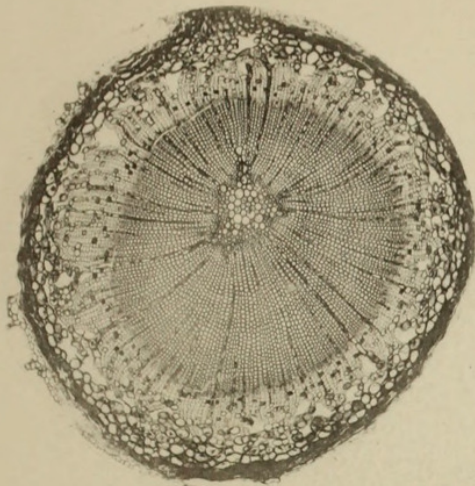


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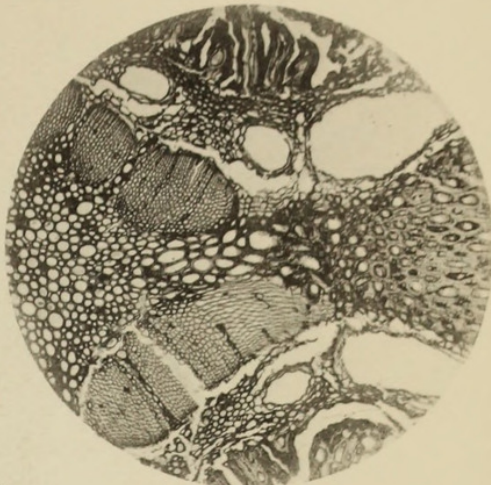




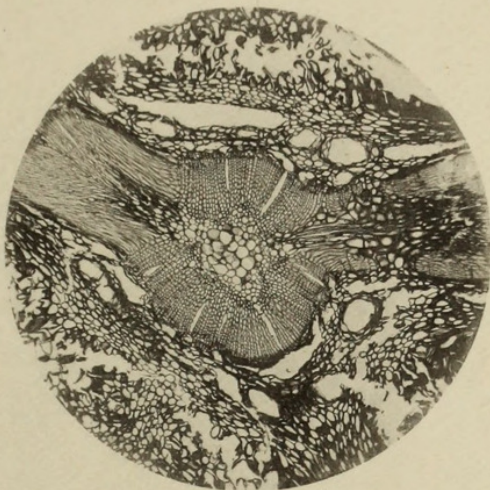




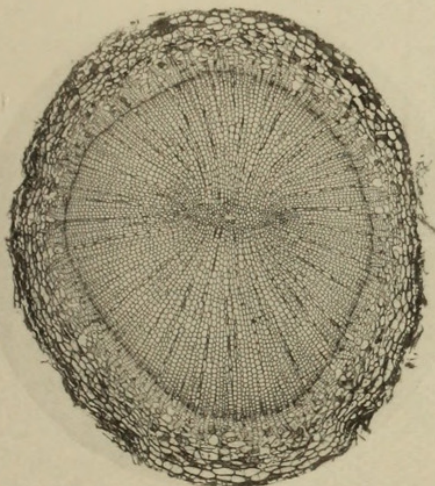
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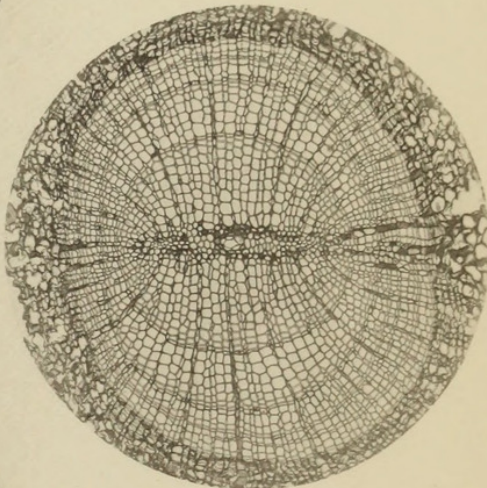
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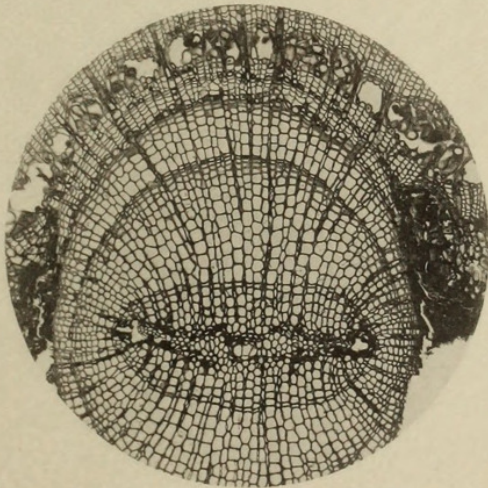
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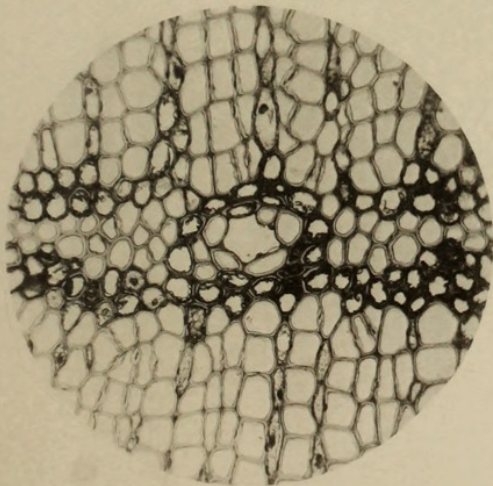
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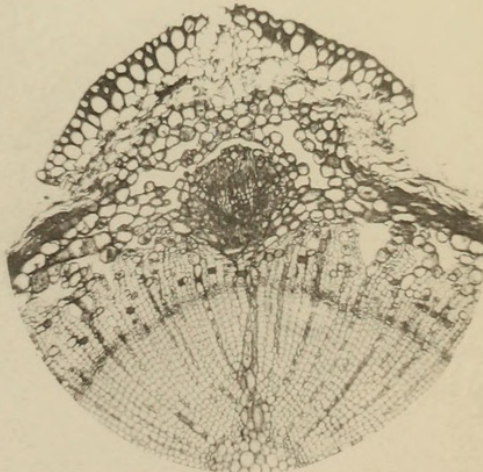
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