10. The Comparative Anatomy and Phylogeny of the Coniferales.

Part 1.—The Genus Sequoia.[1]

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Introduction.

In the present and following memoirs, it is my intention to describe certain features of the anatomy of the Coniferales which appear to be of interest. The actual state of our knowledge of the morphology and history of the group is not sufficient to justify much certainty as to its classification, and consequently additions from any standpoint are likely to be of value. The prevailing views as to the relationship of the various orders of the Coniferales are based almost entirely on reproductive characters, and valuable as these must always be, they constitute, nevertheless, but a single line of evidence. The study of the anatomy of the older groups of Gymnosperms has done so much to clear up the question of their affinities that it does not seem unreasonable to expect that a good deal should be learned from investigations carried out on the same lines in the case of the Coniferales, the prevailing Gymnosperms of the present day. It is to be anticipated that the results of such investigations will serve to correct and supplement the conclusions drawn from the study of the reproductive organs alone.

The existing Sequoias are chosen as the subject of the first memoir, both because of their interest as the sole survivors of a genus which once flourished in many species throughout the entire northern hemisphere, and because investigations, already somewhat extensive although as yet incomplete, make it apparent that the genus Sequoia presents a striking example of those rare and important forms which so infrequently persist as links of transition between distinct and different natural orders of the present day.

The Stem of *Sequoia gigantea*.

Figure 1, plate 68, illustrates the structure of the wood in *Sequoia gigantea* as it appears in a transverse section of the heart of an old stem. There are three annual rings represented in the figure. In contrast to *S. sempervirens*, to be described later, the

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autumnal tracheids form a very narrow zone in each annual ring of growth, and the wood consequently lacks the strength which is characteristic of the latter species. The radial rows of tracheids are interrupted at intervals, especially in the autumnal region, by the resin cells which are so constant a feature of the wood of the *Taxodineae* and *Cupressineae*. As has been pointed out by Penhallow (Generic characters of North American *Taxaceae* and *Coniferae*, Proc. and trans. roy. soc. Canada, 1896, series 2, vol. 2, p. 33), the resin ducts, found so frequently in the wood of the *Abietineae*, are absent in the mature ligneous cylinder of *S. gigantea*. Figure 2, plate 68, gives a general view of the central cylinder of a branch of a young tree from the arboretum of Leland Stanford university, California. The stem is a year old and shows as a consequence a single ring of wood. The resin cells of the wood are poorly developed as yet, although those of the phloem are very apparent in spite of the comparatively low magnification. The minute structure of the fibrovascular tissues cannot be made out.

Figure 3, plate 68, is of the central cylinder of a five year old branch of *S. gigantea* taken from a tree which had already produced cones and seeds. The autumnal wood is relatively much thicker than in the old stem shown in figure 1. The feature of special interest in this section is the presence of *resin ducts* in the inner region of the *first* annual ring. Figure 4, plate 68, shows the first annual ring and the resin ducts more highly magnified from another section, cut from a different twig of the same main branch. As the material came from the Gray herbarium of Harvard university and was consequently in a dried condition, the cells surrounding the resin ducts show no evidence of the presence of protoplasm and a nucleus; but the obviously resinous contents of the ducts in the dry condition, as well as the parenchymatous nature of the cells surrounding them, leave no doubt as to their identity. In the last mentioned figure, the cells enclosing the lumen of the resin canals appear darker as to their walls than the adjacent tracheids. This is due to the fact that they become stained very intensely with haematoxylin, and thus are more non-actinic than the surrounding tracheids, counter-stained less strongly with aqueous saffranin. The material presenting these peculiarities in the first annual ring was taken from specimens accompanied by unusually large cones, and labeled "J. G. Lemmon, California." In order to test whether the structures in question were not abnormalities, sections were made from two other lots of material from the Gray herbarium, marked "Bridges 331" and "Henry 1086," respectively. Figure 5, plate 68, shows the central portion of a transverse section from the material marked "Bridges 331." The resin ducts are obviously even better developed than they are in figure 3. Sections from the other lot of material also showed the presence of large and typical resin ducts in the *first* annual ring of the wood. The resin passages just described disappear in the upper part of the annual ring as it reaches what was originally the end of the yearly growth in length of the branch. In no case which has come under my observation did the resin ducts of the first year's growth in one annual segment of a branch become continuous with those in the next upper segment representing a subsequent year's growth in length. As a consequence the resin ducts of each first annual ring form a closed system and are confined entirely to their own segment of the branch. There are, further, no lateral anastomoses of the ducts in the same annual ring. In the weaker lateral twigs of the branches from the three lots of material mentioned above, resin ducts were generally found to be entirely absent. Through the kindness of Prof. C. V. Piper, I received formalose material of the branches of a young tree twenty years old, grown at Pullman, in the state of Washington. Not even the largest and most vigorous branches in this material showed any indication of the presence of resin ducts. Similar observations were made in the case of alcoholic specimens supplied to me by Dr. A. A. Lawson, of the Botanical department of Leland Stanford university. It may consequently be stated that so far as the present observations go, the presence of resin ducts in the first annual woody ring of *S. gigantea* is confined to the more vigorous branches of older trees which have already produced female cones, and that the phenomenon is normally absent in the smaller twigs of large trees as well as in the entire branch system of young trees.

The Reproductive Axis of *S. gigantea*.

In figure 6, plate 68, is seen the woody portion of the base of the female reproductive axis of *S. gigantea* in transverse section. In the first annual ring are numerous large resin ducts similar to those described above in the case of the more vigorous vegetative shoots of adult trees. The second annual ring is very broad and is quite free from resin passages. It is followed by a number of much narrower rings equally free from resin canals. The peduncular portion of the reproductive axis of *S. gigantea* continues to grow in thickness for some time after the seeds have been shed, and in this respect it resembles certain species of Pinus with persistent cones, and at the same time presents a marked contrast to *S. sempervirens*. Figure 7, plate 68, shows the center of the same section more highly magnified. The size and distribution of the resin ducts and of the resin cells also can be very well made out. Figure 8, plate 68, reproduces a cross section of a higher region of the same peduncle. The narrow annual ring containing the resin ducts seen in the last two figures, has disappeared, and the broad second ring of annual growth now abuts directly on the pith. In figure 9, plate 69, there is represented an intermediate region between those shown in figures 6, 7, and 8, of plate 68. Some of the resin canals in this section are very much enlarged. This appearance is due to the fact that the resin ducts end upwardly in resin pockets of considerable size. Figure 10, plate 69, illustrates the structure of the reproductive axis proper as seen in cross section at a height much above any of the foregoing. The resin ducts have reappeared in the wood close to the medulla, which in the present figure presents an elliptical outline due to the fact that two fructiferous scales of the cone derive their fibrovascular supply from the central cylinder of the axis in this region. The resin canals are particularly well developed around the bays corresponding to the departing traces of the fructiferous scales. The figure includes only part of the first annual ring of wood. In the reproductive axis of *S. gigantea* there are two annual rings of wood only, in the portion corresponding to the cone proper, and as a consequence growth does not continue after the second year when the seeds are ripe. The additional annual rings which are characteristic of the peduncle of the cone gradually die away in the transitional region between the peduncle and the axis proper. It is to be noted that there is no connection between the resin ducts of the peduncle and those of the proper axis of the cone, a condition quite similar to that described above for the successive longitudinal annual segments of the more vigorous vegetative branches of adult trees. I have not yet found any cone of *S. gigantea* in which the resin canals were absent from the first year's growth of the wood.

In figure 11, plate 69, is seen a transverse section through the woody portion of the base of a cone scale, including all of the first annual ring of growth and a narrow zone of the second. On the lower side of the first annual ring, resin ducts appear near the medulla. These form the direct continuation of the resin ducts of the axis shown in figure 10, plate 69. In figure 12, plate 69, is represented a section through a somewhat higher region of another fructiferous scale. In the center appears the medulla, above and below it is the wood of the fibrovascular system of the scale. The most interesting feature of this figure is the large number of resin canals present in the wood. Of these there are two series: the one composed of larger and less numerous ducts nearer the pith, and the other made up of smaller and more numerous ducts, farther out in the wood of the scale. Both series of ducts tend to become divided by radial partitions, and the two systems are not infrequently united by radial anastomoses as well, comparable to the radial canals running in the medullary rays of most of the *Abietineae*. The last two figures present extreme conditions in the modes of occurrence of resin canals in the wood of the fructiferous scales. Where the ducts are least abundant they are confined to the lower side of the scale as in figure 11, plate 69, and form a single series. They may also extend as a single series to the upper side of the scale. When the system of ducts is double, it may be double on the lower side of the scale only, or on one or other wing of the scale as well, or finally as in figure 12, plate 69, the double series may extend all around the medulla. Whenever a double system of ducts extends more or less completely around the wood of the scale, the series nearer the medulla is always complete, whatever may be the case with the more external series. The more complex arrangements of the resin canals just described are more often found in the upper scales of the cone. The outer system of ducts, unlike the inner one, never extends down into the axis of the cone, although it may pass far up in the bundles into which the fibrovascular tube of the base of the scale breaks above.

In figure 13, plate 69, is seen a transverse section of the upper broad portion of the fructiferous scale. The scale is covered on both the upper and the lower surfaces with a layer of periderm. In the fundamental tissue of the scale are numerous large resin passages as well as numerous sclerenchymatous cells. There are present two systems of fibrovascular bundles oriented in opposite directions, of which the upper series is less well developed and consists of somewhat smaller bundles. Along the upper margin of the lower set of bundles, which are the better developed, can be seen small, light dots which mark the position of intrafascicular resin ducts. These are continuous with those described above as occurring in the lower portion of the woody skeleton of the scale. Resin canals are much more commonly present in the lower series of bundles of the flattened upper part of the fructiferous scale than they are in the upper series, possibly on account of the greater robustness of the former. Figure 14, plate 69, shows a portion of the same section more highly magnified. The structure of the fundamental tissue can be more clearly seen. It consists of parenchymatous elements, of long sclerenchymatous elements present in cross section, and of large resin passages. Within the inner boundary of the woody tissue of most of the lower bundles can be seen one or more resin ducts. These are absent from the upper bundles. Figure 15, plate 69, represents another part of the same section. The fundamental tissue presents no difference from that shown in the preceding figure; but the bundles which belong to the lower series, towards the margin of the scale, are obviously united by strands of tissue running from their inner borders. The tissue in question is made up of transfusion cells. The smaller terminal bundles of the extreme upper portion of the fructiferous scale of *S. gigantea* are all more or less completely united at their inner borders by transfusion cells. The bundles likewise frequently terminate in transfusion tissue as well. Occasionally towards the lower part of the course of the bundles, as they become united into the fibrovascular tube of the base of the scale, the enormously developed transfusional borders of the bundles bend inwards and fuse more or less completely together, giving rise to a peculiar pseudomesarch type of bundle such as is shown in figure 16, plate 69. In this figure, two resin canals are to be seen in the secondary wood. Subtending the part of the secondary wood containing the two resin ducts, is a mass of parenchyma which is enclosed incompletely on the opposite side by wing-like extensions of the secondary xylem. These are in turn completely covered by a thick zone of very dense transfusion tissue. The phenomenon just described is not of very common occurrence and in all probability no very great morphological importance is to be attached to it.

The Seedling of *S. gigantea.*

Figure 17, plate 70, reproduces a transverse section of the woody portion of a five year old seedling of *S. gigantea*, collected by Prof. Asa Gray in the famous Calaveras grove of Big Trees, during his visit to California in 1872. I owe this duplicate specimen to the kindness of my colleague, Prof. B. L. Robinson, curator of the Gray herbarium. Four annual rings are shown in the figure. The resin cells which are so conspicuous in the wood of the adult stem are much less strikingly present in the seedling, and resin ducts are entirely absent even from the first annual ring. Through the kindness of Dr. Joseph L. Goodale, I have had the opportunity of examining several other seedlings of *S. gigantea*, grown on his estate at Ipswich. In none of these did I find any indication of the presence of resin canals in even the first annual ring of woody growth.

Effects of Wounds on the Woody Tissues of *S. gigantea.*

Figure 18, plate 70, represents part of a transverse section of a wounded root of *S. gigantea*, in which the wounded area has become completely callused over. Towards the right in the figure, may be seen a mass of callus tissue. In the ring of growth just below the callus, is to be made out a long row of traumatic resin ducts stretching completely across the figure. The annual ring containing the resin canals, although axial to the callus, was formed subsequently to the wounding of the tissues, as was made out by examining the whole line of injury. The resin ducts are quite similar to those occurring normally in many of the *Abietineae*, and are generally surrounded by but a single layer of cells. Of these cells some are normal glandular cells, such as usually surround the lumen of resin canals where they occur in the wood of the *Abietineae*, while others are "resin cells," and are distinguished by their thick and strikingly pitted walls. In figure 19, plate 70, is represented part of the outer margin of the wood in a transverse section of the peduncular portion of the cone of *S. gigantea*. Very large resin canals appear along the inner border of the vernal wood in the last annual ring. These are surrounded by secretory cells; but as the figure was made from dry material the latter have almost completely collapsed. The formation of true resin canals in this case was due to the same cause as in the root just described above. I have seen a large number of instances of the formation of traumatic resin canals in the wood of both the root and the stem of *S. gigantea* and consequently am of the opinion that it is quite a usual result of injury. It should be added, however, that the formation of parenchymatous wood containing a large number of resin cells and ordinary parenchyma cells is even more commonly present in the case of wounds. This is especially the case with large exposed wounds on the aerial portions of the stem, where there is much necrosis and drying out of the woody tissue. In smaller wounds, however, where there is not too great an exposure of the ligneous cylinder to desiccation, the formation of the traumatic resin passages described above is very common. It should be noted finally that the traumatic resin canals of *S. gigantea* are formed in the vernal wood and in this respect are in contrast to those occurring in *S. sempervirens* under similar conditions, which, as will be shown later, make their appearance in the autumnal wood. I have found examples of the formation of resin canals in the phloem of *S. gigantea*, as well as in the wood, and as the result of a similar cause. I have discovered no instance of the occurrence of resin ducts in the fibrovascular cylinder of this species, except in the first year's growth of vigorous young branches of adult trees and in the axis of female cones (as described in earlier paragraphs), which could not be clearly traced to a previous injury. It seems extremely probable that the formation of traumatic resin canals in *S. gigantea* is to be regarded as a case of reversion to an ancestral condition, especially in view of the mode of occurrence of normal resin canals in certain instances as described above. The arguments in favor of this view, however, are best deferred to a later stage.

Traumatic Resin Canals of the *Abietineae*.

It seems necessary in the meantime to refer preliminarily to certain other facts of a similar nature which have been made out in the case of the *Abietineae*, in a series of researches of which the present investigation forms a part. It has long been known that resin ducts are generally absent in the wood of the Abietineous genera, Abies, Tsuga, and Cedrus, and that they are replaced in many instances by resin cells. For the present the first-named genus will alone be considered; for as I hope to show subsequently, the other two genera resemble it very closely in the features which are of interest in this connection. *Abies firma* is described by Prantl (Engler u. Prantl, Nat. pflanzenfamilien, Coniferae, 1889, p. 37) as differing from the other species of Abies in normally possessing resin ducts in its wood. Penhallow (*op. cit.*) has more recently described the presence of resin canals, occurring in isolated annual rings of *Abies nobilis* and *Abies bracteata*. I have been able to confirm these observations in the beautiful series of sections of North American woods published a few years ago by Professor Penhallow. The resin ducts occur in long tangential rows in both the last-named species. I have myself examined a number of species of the genus Abies, and have found resin canals of very frequent occurrence under conditions to be more fully described on another occasion. For the present, however, it may be stated that resin ducts are extremely apt to be present in the female reproductive axis of various species of Abies, even when they are quite absent from the woody tissues of the ordinary vegetative stem. For example, in *Abies grandis*, according to Penhallow, there are no resin ducts present in the wood. Figure 20, plate 70, shows the general structure of the woody axis of the upper portion of the female cone of *A. grandis*. The specimen from which the figure was made, was secured at the Gray herbarium, and as a consequence the tissues have suffered a good deal from long desiccation. Nevertheless, indubitable resin ducts can be clearly made out in large numbers in practically the whole circumference of the woody cylinder of the cone. They are of quite the normal type and are surrounded by glandular cells which still retain the remains of their protoplasm. The section through the small upper end of the cone axis was chosen because it permitted of showing the structure of the *whole* of the ligneous portion of the tissues of the cone on a sufficient scale of magnification to make clear the presence and mode of distribution of the resin canals. In figure 21, plate 70, is seen a similar view of the woody tissues in the cone of *Abies balsamea*. This species is devoid of resin ducts not only in the wood of the vegetative axis but also in that of the cone. The figure in this case was made from material which had been properly preserved. Figure 22, plate 70, is made from a section through an injured root of a small tree of *Abies balsamea* growing in the Botanic garden of Harvard university. The figure includes all the xylem as well as a portion of the phloem of the injured root. There is an interruption of continuity in the latter tissue on the lower side, due to an incised wound which was made in all probability by a spade used in digging the soil about the tree. The woody tissue is likewise interrupted in the same region as the phloem, and on one side the last annual ring is separated for some distance from the tissues below. There is a considerable formation of resinous tissue along the inner margin of the last annual ring on both sides of the wound, which takes the form of resin cells. Farther away from the wounded portion, on the left, the resinous tissue gives place to a tangential row of resin ducts continuous through almost half the circumference of the root, and passing on the right into a narrow zone of resin cells, which are in turn continuous with the thick mass of resinous tissue on the immediate border of the wound. The center of the root is occupied by a resin duct surrounded by resinous cells, such as is commonly found in the axial wood of the root in the genus Abies (de Bary, Comp. anat., 1884). My investigations on this genus, although not yet complete, show that resin canals occur very frequently in the female reproductive axis, even when they are quite absent from the wood of the vegetative stem and from the root as well, except in the axial primary wood as just mentioned above. In all cases where I have been able to make the experiment, however, I have succeeded in bringing about the formation of resin canals as a result of injury, in the wood of species of Abies which are normally without them, even in their reproductive axis. It is interesting in this connection to note that certain fungous diseases causing injury to the wood of species of Abies produce the same result. It seems necessary to record the traumatic reactions of the woody tissues of the genus Abies because, as I shall attempt to show at the end of this essay, they supply an interpretation of the similar phenomena in the case of Sequoia.

The Leaf of *S. gigantea*.

In figure 23, plate 70, is seen part of a section through the base of the leaf of *S. gigantea*. In the center of the figure lies the leaf trace flanked by the two lateral wings of transfusion tissue, which are so characteristic of the lower part of the foliar bundle in Sequoia and its allies. Above and below the leaf trace are masses of collenchymatoid tissue. The feature of greatest interest in the figure is, that contrary to other described coniferous leaf traces, the foliar bundles of *S. gigantea* contain a resin duct. The duct is quite of the normal type and is surrounded by a single, almost complete row of resiniparous cells. In some cases, however, as is often found in the resin canals of the Sequoias, the parenchymatous lining of the canal is far from being continuous, and the tracheids as a result often abut directly on its lumen. It must not be supposed that resin ducts occur in all the leaf traces of *S. gigantea*, for this is not the case. They appear only to be present in the bundles of the very large leaves of exceptionally vigorous branches of mature trees (*i. e.*, trees which have already ripened seed). All the material which I have, showing this feature, came from the Gray herbarium of Harvard university; but in spite of the necessarily bad condition of preservation consequent on its origin, there seems to be no reasonable doubt as to the nature of the canals, which I have described above as resin ducts. The longitudinal range of the resin ducts of the foliar bundles of the largest leaves in mature trees of *Sequoia gigantea* is quite limited; for they appear only after the leaf trace has passed quite out into the cortex of the branch, and indeed after it has traversed a considerable part of its upward and outward course. There is as a consequence no communication between the resin ducts of the first annual ring of wood in the branches and those appearing in the leaf traces. Like the other modes of occurrence of resin canals described above, there is an entire absence of correlation with other similar tissues. The resin ducts of the leaves disappear again very shortly after the leaves have emerged from the surface of the branches, so, as has just been stated above, the longitudinal course of the resin canals of the leaf traces, where they occur, is very short indeed.

The Stem of *Sequoia sempervirens*.

Penhallow (*op. cit.*) has noticed the occurrence of continuous tangential rows of what he terms "imperfect resin ducts" in the wood of the old stem of *S. sempervirens*. The phenomenon seems to be extremely rare, for I have found very few examples although a large number of different specimens of the wood of this species has been examined in this connection. Professor Penhallow has been so kind as to send me a very good example illustrating this peculiarity, and as it is much more striking than any other I have seen, all the accompanying figures of the mature wood of *S. sempervirens* are made from this material. In figure 24, plate 70, a part of a transverse section of the wood of *S. sempervirens* is represented under a low magnification. There are four annual rings present in the figure. Mingled with the tracheids in all the four woody rings are numerous resin cells, such as have been described above in *S. gigantea*, and such as occur commonly in the other *Taxodineae*. The autumnal wood in *S. sempervirens* forms a much thicker zone than in *S. gigantea*, which is the cause of the greater weight and strength of the wood in the former species. In the second annual ring from the top of the figure are to be seen the resin ducts first described for *S. sempervirens* by Penhallow (*op. cit.*, p. 39, pl. 6, fig. 2). They are obviously situated in the autumnal wood and in this respect present a marked contrast to those of *S. gigantea* described in the foregoing paragraphs, for in the latter species they occur in the vernal portion of the annual ring. In their distribution the resin canals in the present instance resemble those formed as the result of injury in *S. gigantea*, species of Abies, *etc.*, and form a continuous tangential zone, such as is characteristic of traumatic resin canals. Figure 25, plate 71, shows a portion of the annual ring containing resin ducts more highly magnified. There is obviously a sharp transition from the autumn wood to that of the following spring in the size of the tracheids and the thickness of their walls. There are numerous resin cells on the outer margin of the autumnal wood. Farther inwards, the autumnal tracheids give place to parenchyma cells, which, on account of the fact that the material is from the heart wood of an old tree, are quite devoid of protoplasmic contents. They are unmistakable, however, since their walls are composed of cellulose and stain a deep blue with haematoxylin. About the lumina of the resin ducts, the parenchymatous cells are as a rule strongly pitted and closely resemble the resin cells of the medullary rays in certain Conifers.

In figure 26, plate 71, is shown a transverse section of a young branch of *S. sempervirens* from material sent to me by Dr. A. A. Lawson of the Botanical department of Leland Stanford university. The bases of four leaves clearly appear on the margin of the figure. These originate from the branch by a flat base in contrast to the rounded mode of origin found in *S. gigantea*. In two of the leaves there are obviously three resin canals in the mesophyll, another point of contrast to *S. gigantea* and most of the other *Taxodineae* and *Cupressineae*, where there is as a rule but a single resin duct in the parenchyma of the leaf, and immediately under the fibrovascular bundle. The material from which the illustration has been made was cut and preserved in California on the 2d of May. The growth of the present year's ring of wood has begun and has already reached a considerable thickness. Branches of *S. gigantea* cut from trees at the same spot and at the same time show scarcely any signs of the commencement of cambial activity. The slowness of initiation of cambial activity in the Big Tree is no doubt one, at least, of the causes of its greater hardiness. There are no resin ducts to be seen in the wood of the young branch, appearing in transverse section in the figure, and in this respect the illustration might stand for any branch of *S. sempervirens*; for I have not found even in the most robust ramifications of the mature trees of this species any indication of the resin canals, which are so often present in the first annual woody ring of *S. gigantea*.

Traumatic Resin Ducts in *S. sempervirens*.

In some of the specimens sent me by Dr. Lawson from the arboretum of Leland Stanford university the phenomenon of fasciation was present. As this feature of *S. sempervirens* has recently been fully described by Pierce (Studies on the Coast Redwood, Cal. acad. sci., 1901), it will not be necessary to refer to it here. The wood in most of the fasciated specimens was quite normal as regards the absence of resin canals; but in the subterranean portion of a dead branch which had taken on the flattened mode of growth so characteristic of fasciation, numerous resin ducts were found in tangential rows. The shoot in question had obviously been injured and the appearance of resin canals is doubtless to be correlated with the diseased condition of the tissues. Figure 27, plate 71, is made from a section through this branch. There are two annual rings present and it is in the first of these that the resin ducts are to be seen. The ducts are in tangential rows and are situated in the autumnal wood just as in figure 25, plate 71. In figure 28, plate 71, are represented some resin canals from another section of the same material, highly magnified. The resin ducts are obviously surrounded for the most part by cells still containing protoplasm and a nucleus, although in some cases the tracheids abut directly on the lumen of the resin canal. The structure of the ducts shown in the figure is quite typical of the resin passages I have found in the Sequoias in general. It is a fact of considerable interest in the present connection, that the resin ducts first described by Penhallow for the wood of the old stem of *S. sempervirens* occur in the same tangential rows which are found in the obviously injured stem of the species under discussion, and under similar circumstances in the *Abietineae* as well. It is often the case that traumatic resin canals extend far above and below the actual spot of injury and it accordingly seems extremely probable that the rows of imperfect resin canals found in the otherwise quite normal fragments of wood of *S. sempervirens* are really due to an injury above or below the region from which the pieces of wood have been taken.

The Reproductive Axis of *S. sempervirens*.

In figure 29, plate 71, is represented the fibrovascular cylinder of the lower third of the reproductive axis of *S. sempervirens*. Although the cone from which the section was made had long shed its seeds, and had assumed an almost black hue from long exposure to the weather, there are obviously no indications of annual rings in the photograph. While the absence of annual rings does not absolutely prove that there are no additions to the secondary wood of the reproductive axis after the first year, still it appears very probable from the state of affairs in the cones of the other living species of Sequoia that such is the case. This view of the matter is further strengthened by the occurrence of perfectly normal annual rings in the vegetative organs of *S. sempervirens*. The question can, however, only be finally settled by the study of the growth of cones in the field. There are no annual rings in the peduncular portion of the cone of the species under consideration and in this respect it also presents a contrast to *S. gigantea*, where, as has been described above, there are numerous annual rings in that region of the reproductive axis. Further, resin ducts are entirely absent from all parts of the wood of the cone of *S. sempervirens*. Figure 30, plate 71, shows the structure of a cross section through the base of a cone scale of this species. The dense wood of the tubular central cylinder of this portion of the fructiferous scale shows no evidence of the presence either of the annual rings or of resin ducts, which are such notable features of the cone scales of *S. gigantea*. The specimen shown in figure 30 is quite typical in these respects; for I have examined a number of cones from different sources, without finding any examples of the occurrence of either of these structures. In figure 31, plate 71, appears a portion of a transverse section of the upper third of the cone scale of *S. sempervirens*. The large bundles along the lower side of the figure belong to the lower series. They are very much larger than those near the upper surface of the scale and are inversely oriented.

In the species under consideration there is a very much greater relative reduction of the upper series of bundles than is the case in *S. gigantea*. The commissures of transfusion tissue, which are so marked, especially in the lower bundles of the cone scales of the latter species, are much less well developed in the Redwood. The fibrovascular bundles of the fructiferous scales of *S. sempervirens* show no annual increments of growth and never contain resin ducts.

The Root of the Sequoias.

Figure 32, plate 71, illustrates the structure of a small root in *S. gigantea*. It is obviously pentarchous in its organization and very much resembles a root of *Pinus strobus* or some other Abietineous species with large polyarch roots. The protoxylem groups, however, which occupy the apices of the five rays of the primary wood, differ from those of species of Pinus, *etc.*, in not embracing resin ducts. Although the roots of the species under consideration are generally pentarchous, examples are not infrequently found in which there are only four rays of primary wood. This state of affairs also occurs in *Pinus strobus*. The primary root of all seedlings of *S. gigantea* which I have examined is of the tetrarchous type. I have never found resin canals present in the secondary wood of this species except as the result of injury.

The root of *S. sempervirens* is so similar to that of *S. gigantea* as scarcely to merit a separate description. The symmetry of the root is, however, almost always tetrarchous and the various histological elements are somewhat larger than in the latter species.

Conclusions.

In the foregoing paragraphs, attention has been called to the occurrence of resin ducts, under certain definite conditions, in the wood of Sequoia. In *S. gigantea*, which in all probability is the more primitive of the two surviving species, resin canals are constantly present in the wood of the peduncle, of the axis, and of the scales of the female cone. They also frequently occur in the first annual ring of the more vigorous branches of adult trees. Resin ducts likewise are sometimes found in the leaf traces of the larger leaves of well nourished, mature individuals. Finally, it is possible to bring about the formation of resin canals in tangential rows as the result of injury to the woody cylinder of the root stem and cone of *S. gigantea*. The resin ducts occurring in the various situations cited above, form entirely separate systems which do not communicate in any way with each other. In *S. sempervirens*, in contrast to the species just referred to, there are no resin canals in the woody tissues either of the reproductive organs, or of young branches, or even of vigorous leaf traces. In *S. sempervirens*, resin ducts appear only as tangential rows in isolated annual rings, probably in all cases in response to injury to the tissues of the wood.

The occurrence of resin canals in the reproductive axis of *S. gigantea* is in all probability to be regarded as an ancestral feature. It is significant in this connection that certain species of Abies, which have no resin ducts in the wood of their vegetative organs, retain them in the ligneous cylinder of their cones, *e. g., A. grandis, A. nobilis, etc., etc.* In the case of these species the presence of resin ducts as a general feature of structure of the wood in the order to which they belong, justifies the conclusion that the occurrence of resin canals in the wood of the female reproductive axis is an ancestral character, which has disappeared in the wood of the vegetative stem. A parallel case is presented by the peculiar mesarch bundles found by Dr. Scott in the peduncle of the cones in certain Cycads (The anatomical characters presented by the peduncle of *Cycadaceae*, Ann. bot., 1897, vol. 11). Bundles of this nature were present in the medullary crown of the vegetative axis of certain of the primitive fossil Gymnosperms and of the Cycadofilices. In the living Cycads, mesarch bundles have disappeared in the vegetative stem, but are sometimes retained in the reproductive axis and quite generally in the vegetative and reproductive leaves. In *S. gigantea*, resin ducts retained in the wood of parts of the female cones, likewise occasionally occur in the leaf traces as well, thus presenting a striking parallel to the mesarch bundles of the Cycads, in the manner of their distribution. The presence of resin canals under certain quite definite conditions in the first annual ring of the branches of *S. gigantea*, supplies a further argument for regarding the occurrence of resin ducts in the wood of this species as the retention of an ancestral feature, for it is only natural to find such a character reappearing in the *first* zone of woody growth of the young branch. This conclusion is also confirmed by the presence of a similar feature in the young branches of certain Abietineous species to be subsequently described.

The phenomena of injury furnish additional evidence in favor of the view that the ancestral stock from which the Sequoias have been derived, was characterized by the presence of ligneous resin ducts, for it appears justifiable to regard the formation of tangential rows of traumatic resin canals in the injured wood of both living species of Sequoia as a reversion to an ancestral condition, especially in view of the phenomena described in the last paragraph. This explanation of the phenomena resulting from injuries to the woody tissues in the species under discussion is confirmed by the fact that similar traumatic resin ducts are commonly formed as the result of injury to the wood in the *Abietineae*, in contrast to the *Cupressineae, etc.*

The hypothesis that the Sequoias have come from ancestors characterized by the presence of resin ducts in their woody tissues, receives a further support from the consideration of the anatomical structure of certain fossil species of Sequoia. Penhallow has described the presence of resin canals in the wood of *S. langsdorfii* (Notes on the Cretaceous and Tertiary plants of Canada, Proc. and trans. roy. soc. Canada, 1902, series 2, vol. 2, p. 44–45). The wood of this species, known heretofore only by its foliage and its fruit, is described as having occasionally imperfect resin ducts in its autumnal wood. Unfortunately the author does not figure nor further describe the distribution of the resin ducts in question, so it is not possible to have an opinion as to whether they were of traumatic or of normal origin. The resin canals in the case of *S. langsdorfii* had a longitudinal course in the wood. Quite recently, Professor Penhallow has announced the occurrence of radial resin canals in the wood of another species of Sequoia; but as yet no published account has appeared.

It seems highly probable, if the various arguments advanced above are valid, that the Sequoias have come from a stock characterized by wood penetrated by resin canals. If this probability be granted, the question immediately arises, whether they have come off from the same stock as the *Abietineae*, which have as a striking anatomical peculiarity the presence of resin canals in their ligneous tissues. At first sight this would appear to be an unlikely hypothesis; for the *Abietineae* are generally regarded (*cf.* Potonie, Pflanzenpalaeontologie, 1899, p. 322; Coulter and Chamberlain, Morphology of Spermatophytes, 1901, p. 108; Strasburger, Coniferen und Gnetaceen, 1872, p. 265; *etc.*) as a very modern order of the Coniferales. The reasons for this view are, however, not entirely apparent, for the genera Pinus and Cedrus appear in the infra-Cretaceous, and are thus as far as the palaeontological record at present goes, synchronous in their first appearance with Sequoia (R. Zeiller, Palaeobotanique, 1900, pp. 271 and 277). Further, so competent a judge as Dr. Scott states that "on the whole, it is impossible in the present state of our knowledge, to say which tribe or family of the Coniferae is the most ancient" (Studies in fossil botany, 1900, p. 483).

Much importance is justly attached to the structure of the female cone in the classification of the Coniferales, and any hypothesis of the phylogeny of the group must accordingly harmonize with the facts gathered from this source, *when properly interpreted.* In the *Abietineae*, the female cone is made up of double superposed scales. The most generally accepted explanation of the morphological nature of each pair of superposed scales is that the upper ovule-bearing scale represents the fusion of a pair of leaves, belonging to a reduced axis, axillary to the lower subtending bract (for an admirable account of this difficult question, see Worsdell, Structure of the female "flower" in the Coniferae, Ann. bot., 1900, vol. 14). This hypothesis finds a strong support from the standpoint of comparative anatomy, and as has recently been aptly stated by Professor Coulter, the clear and parallel case of reduction of an axillary (vegetative) shoot in

Sciadopitys is almost a demonstration of its accuracy. The hypothesis which explains the ovuliferous scale of the *Abietineae* as a reduced and modified short shoot (brachyblast), is likewise in harmony with teratological evidence, for in the so called proliferous cones of certain *Abietineae*, the ovuliferous scale becomes more or less completely transformed into a leafy bud and the subtending bract into an ordinary vegetative leaf. It is a curious and interesting fact, which does not seem to have been properly considered in regard to its bearing on the phylogeny of the Coniferales, that cases of proliferous female cones are confined, in the present state of our knowledge, to the *Abietineae* and the *Taxodineae* (Penzig, Pflanzenteratologie, 1894, vol. 2, p. 485–514). To those who accept the brachyblastic theory of the nature of the ovuliferous apparatus in the Coniferales, this state of affairs must appear weighty evidence in favor of the view that the *Abietineae*, and the *Taxodineae* as well, are somewhat primitive orders of the group, for there would naturally be the greatest tendency to reversion and the clearest anatomical evidence of the shoot value of the ovuliferous scale in the orders which are nearest to the ancestral stock.

In the case of the *Taxodineae*, the scales of the female cone are not superposed in pairs but consist of single, generally more or less thickened ovule-bearing organs, in which there is present a *double* system of bundles consisting of an upper and a lower series oriented in opposite directions, as are those of the separate superposed scales of the *Abietineae*. The generally accepted description of the state of affairs in the cone scales of the *Taxodineae*, is that there is a fusion of the ovuliferous and sterile bracts. It is scarcely logical to speak of organs as being "fused" unless they were originally separate. The view that they were primitively separate, superposed scales in the ancestral stock of the *Taxodineae* is strengthened by a consideration of the anatomical facts in the case of the genus Sequoia; for it is not easy to conceive that the series of massive bundles near the upper surface of the cone scale in this genus is arising *de novo* for the benefit of the reproductive organs, since the ovular bundles are extremely small and quite out of all proportion to the fibrovascular strands of the upper system from which they take their origin. The more reasonable explanation seems to be that the thick, single scale which bears the ovules in the case of most of the *Taxodineae*, is made up of a fusion of two separate scales which existed in a more primitive group, probably the *Abietineae* or their parent stock. This view of the matter receives further support from the peculiar manner of the occurrence of resin ducts in the woody tissues of living and fossil Sequoias.

It would be anticipating unduly the results to be recorded in subsequent memoirs on the Coniferales, to express more than a provisional opinion as to the position of the genus Sequoia but this much may be safely stated. The anatomy of living and fossil species of Sequoia goes to show that the genus has come from a stock possessing ligneous resin ducts, such as prevail in the *Abietineae* of the present day. It may be urged that this in itself is a very small point. Reply may be made that the mesarch structure of the primary woody bundles of the more primitive Gymnosperms and the adhesion of the stamens to the calyx in the *Rosaceae* are likewise small points, yet no well informed botanist doubts that they are important taxonomic criteria. It appears to be rather the significance than the magnitude of anatomical or morphological features which makes them of classificatory value. The peculiar and apparently most significant mode of occurrence of resin canals in the wood of the Sequoias points to their derivation from an Abietineous stock, which may of course have been ancestral not only to the Sequoias but also to the living genera of the *Abietineae* as well. This conclusion appears to be supported by a consideration of the structure of the female cone in the *Abietineae, Taxodineae,* and the Coniferales in general. Finally the derivation of the Sequoias from an Abietineous source is in no way contradictory to the palaeontological record.

SUMMARY.

1. Typical resin ducts occur in the wood of the peduncle, axis, and scales of the female cone of *Sequoia gigantea.*

2. Resin ducts are likewise present in the first annual ring of vigorous branches of adult trees of the same species. Resin ducts are normally absent in all the branches of immature trees.

3. Resin ducts are also found in the leaf traces of very vigorous leaves of adult trees of *Sequoia gigantea.*

4. Resin ducts are entirely absent from the wood of all parts of the cones of *Sequoia sempervirens.*

5. The same statement holds true of the branches and leaves of this species.

6. Resin ducts appear in tangential rows in the wood of root and shoot in both *Sequoia gigantea* and *Sequoia sempervirens* as a result of injury to the tissues.

7. A consideration of the mode of occurrence of resin ducts in the Sequoias leads to the conclusion that they are an ancestral feature of structure in the wood.

8. The anatomy of the vegetative organs and floral organs of the living Sequoias points strongly to their derivation from an Abietineous stock. This conclusion receives confirmation from what is known of the anatomy of the fossils, and finally is not in contradiction to the palaeontological record.

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Cambridge, Mass.

Explanation of Plates.

All the figures are from photomicrographs.

PLATE 68.

Fig. 1. Transverse section of the wood of *Sequoia gigantea*. × 50.

Fig. 2. Transverse section of a branch of a young tree of *S. gigantea*. × 60.

Fig. 3. Transverse section of a vigorous branch of an adult tree of *S. gigantea*. × 40.

Fig. 4. Transverse section of the medullary region of a similar branch. × 100.

Fig. 5. Medullary region of a similar branch from another adult tree of *S. gigantea*. × 50.

Fig. 6. Transverse section of the woody portion of the peduncle of an old cone of *S. gigantea*. × 30.

Fig. 7. Transverse section of the central portion of the same. × 50.

Fig. 8. Higher region of the peduncle of the same cone. × 30.

PLATE 69.

Fig. 9. Transverse section of the medullary region between those shown in figures 6 and 8. × 50.

Fig. 10. Transverse section through the axis of the cone of *S. gigantea*. × 40.

Fig. 11. Transverse section of the woody axis of the base of a cone scale in *S. gigantea*. × 50.

Fig. 12. Transverse section of the woody axis of another cone scale of *S. gigantea*. × 50.

Fig. 13. Transverse section through the upper portion of a cone scale of *S. gigantea*. × 3.

Fig. 14. Transverse section of part of the same. × 50.

Fig. 15. Transverse section of another part of the same. × 50.

Fig. 16. Transverse section through an abnormal bundle of the cone scale of *S. gigantea*. × 60.

PLATE 70.

Fig. 17. Transverse section of the woody part of the axis in a five year old seedling of *S. gigantea*. × 40.

Fig. 18. Transverse section through part of an injured root of *S. gigantea*, showing the formation of traumatic resin ducts in a tangential row. × 40.

Fig. 19. Transverse section through part of the peduncle of a wounded cone of *S. gigantea*. × 50.

Fig. 20. Transverse section of the upper portion of the woody axis of a female cone of *Abies grandis*, showing the presence of resin canals. × 40.

Fig. 21. Transverse section through the woody axis of the cone of *Abies balsamea*, showing the absence of resin ducts. × 35.

Fig. 22. Transverse section through the central portion of a wounded root of *Abies balsamea*, showing the presence of a tangential row of traumatic resin ducts. × 32.

Fig. 23. Transverse section through a leaf trace of a vigorous leaf of a mature tree of *S. gigantea*. × 200.

Fig. 24. Transverse section of the wood of *S. sempervirens*, showing the presence of a tangential row of resin ducts. × 35.

PLATE 71.

Fig. 25. Part of the last section more highly magnified, showing the structure of the wood and the resin ducts. × 100.

Fig. 26. Transverse section of a young branch from an immature tree of *S. sempervirens*. × 30.

Fig. 27. Transverse section of part of an injured stem of *S. sempervirens*, showing the presence of tangential rows of traumatic resin ducts in the autumnal wood. × 50.

Fig. 28. Transverse section of another similar specimen, showing details of the structure of the traumatic resin ducts. × 200.

Fig. 29. Transverse section through the woody axis of the cone of *S. sempervirens*. × 35.

Fig. 30. Transverse section through the woody portion of the base of the cone scale of the same species. × 50.

Fig. 31. Transverse section through the upper portion of the cone scale of *S. sempervirens*. × 40.

Fig. 32. Transverse section through the root of *S. gigantea*. × 40.

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