Traumatic Ray-Tracheids in *Cunninghamia sinensis*.¹

BY

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With Plate XXXI.

IT is usual at the present time among perhaps the greater number of botanists to regard the Coniferales as an ascending series, beginning with the Taxineae, as relatively the most primitive, and passing through the Cupressineae and Taxodineae to the Abietineae, the most highly specialized and modern. This view is based on the greater simplicity of structure of the first-named tribe and the more complex organization of the latter. Yet there is practically nothing in the palaeobotanical evidence which really gives it support. Moreover, it is beginning to be realized that apparent simplicity of structure is by no means a reliable criterion of greater antiquity. In fact, quite the opposite conclusion more often results from the consideration of the extinct older forms. For example, the Calamites were infinitely more complicated in both their reproductive and vegetative structures than is their living survivor, the genus *Equisetum*. Similarly, the organization of the Lepidodendroids was very much more elaborate than is that of any of the existing representatives of the Lycopodinean stock.

The study of reversions, especially of those which are susceptible of experimental treatment, has become of increasing importance in morphology, for if in a presumably more ancient, because more simply organized group, it can be shown that reversions to a type of structure possessed by a more complicated related group may be experimentally produced, it becomes at once extremely probable that the more highly organized forms are the more ancient. This conclusion becomes a certainty if it is supported by a considerable body of collateral evidence, especially if such evidence is derived from the study of extinct forms.

The complicated structure of the medullary rays in the existing Abietineae, composed of both parenchyma-cells and so-called ray-tracheids, as well as the very elaborate system of ligneous resin-canals found in the tribe, are considered by many as evidence of extreme specialization and

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consequent modernity. This complexity of organization is found also in the reproductive organs of the group. Penhallow has called attention, however (Anatomy of North American Coniferales, American Naturalist, vol. xxxviii, p. 341, 1904), to the presence of the characteristic marginal ray-tracheids of the Abietineae in the Cupressineous genera, *Juniperus*, *Cupressus*, and *Thuja*. They occur in the following species in a sporadic and uncertain manner, *Juniperus nana*, *Cupressus thuyoides*, and *C. nootkatensis*, and in *Thuja japonica*. They are also found in certain of the Taxodineae. In his Comparative Anatomy (Eng. Trans., p. 490) De Bary describes their presence in the monotypic genus *Sciadopitys*. More recently Gothan (Just Jarhresberichte, vol. 31, p. 848), in a review of a work by the present author on the genus *Sequoia*, mentions the sporadic occurrence of marginal tracheids in the old wood of *Sequoia gigantea*. Finally the writer has observed the presence of marginal tracheids in the wood of *Cunninghamia sinensis*, under conditions to be described below. It will appear from the above that both in those genera which at present it is customary to include under the Cupressineae, and in those which are united under the Taxodineae, there are somewhat numerous instances of the occasional occurrence of marginal ray-tracheids, such as are a characteristic feature of the living Abietineae. The genus *Cunninghamia*, as will be shown below, is of particular interest in this connexion, because it apparently offers the first case in which the conditions affecting the appearance of marginal tracheids have been elucidated in the case of the Cupressineae and Taxodineae.

Figure 1, Plate XXXI, represents a transverse section of the wood of *Cunninghamia sinensis* under a moderate degree of magnification. The affinities of the wood are easily inferred from the considerable number of resin-cells, appearing as dark dots among the tracheids, and the absence of resin-canals, such as are found in those Abietineae which more nearly resemble *Pinus* in their internal organization. It is the view of Professor Penhallow that the resin-canals of such forms as *Pinus* have been derived from a concentration of resin-cells, such as are found in *Cunninghamia* and other Cupressineous and Taxodineous genera. That this view can scarcely be maintained will be shown at a later stage. Attention was first drawn to the presence of ray-tracheids in *Cunninghamia* in longitudinal radial sections of a branch fourteen years old and rather over a centimetre in thickness. The segment of the branch was between two and three centimetres in length, and presented no unusual features in the first eleven years of growth. In the last three years, however, there occurred here and there rays, characterized by the presence of marginal tracheids. Not more than two such rays were seen in any section, but in the considerable number of sections examined they showed themselves as distributed throughout the entire length of the piece of wood. In one case marginal tracheids were found on both upper and lower sides of the ray, but in the other instances

they were present on one side only, and that generally the lower one, as inferred from the outgoing leaf traces. Fig. 2, Plate XXXI, shows one of the rays with marginal tracheids under a moderate degree of magnification. The ray in question passes through three annual rings, of which the innermost (on the left of the figure) is considerably narrower than the remaining two. In this example the marginal tracheids appear on one side of the ray only, and are confined to the two internal annual rings. In other cases marginal tracheids have been found in the outer ring as well. Fig. 3, Plate XXXI, shows a portion of the same ray illustrated in the last figure, covering the median annual ring, more highly magnified. It is now possible to distinguish clearly that the marginal ray-cells present characteristic features on one side of the ray, in the absence of the protoplasm found in the remaining cells of the ray, and their relation to the tracheids of the wood by typical bordered pits, smaller in size than those which connect tracheid with tracheid. Fig. 4, Plate XXXI, shows a part of Fig. 3, still more highly magnified. In this figure it is possible not only to make out the connexion of the marginal ray-tracheids with the tracheids of the wood by means of typical bordered pits, but also the fact that the ray-tracheids are related to the protoplasmic ray-cells along their lower horizontal wall by unilateral bordered pits similar to those found in the horizontal walls of ray-tracheids in *Pinus*, where they come in contact with parenchymatous ray-cells. In only one or two instances have bordered pits been found in the terminal walls connecting the ray-tracheids with one another. Generally these walls are entirely free from pitting. The ray-tracheids of *Cunninghamia* resemble those described by Penhallow in *Cupressus*, *Juniperus*, and *Thuja* in being without the dentate projections characteristic of the Hard Pines, and found also by De Bary in the case of *Sciadopitys* (loc. cit.).

The discovery of ray-tracheids in the wood of the branch of *Cunninghamia* under discussion led to the examination of the rest of the woody cylinder for the same phenomenon. It was found that the rays, with tracheids, occurred in only about half of the circumference of the stem, and were quite absent in the remainder. The half of the woody cylinder without the rays possessing ray-tracheids showed clearly the presence of wound-cap, consisting of three years' growth and beginning inwardly with a typical wound-callus. Fig. 5, Plate XXXI, shows a longitudinal section through this region. Near the middle of the section is a dark stripe, representing the wound-callus. On the left of this is the normal wood formed previously to injury. On the right is the wound-cap, consisting of three years' growth, terminating outwardly in the phloem, which appears as a dark stripe. It is to be noted that the wound-cap is characterized by a considerable increase in the number of medullary rays present over that found in the normal wood. Fig. 6, Plate XXXI, shows a more magnified image of the radial

section of the wound-cap. The very numerous rays are readily distinguished as dark transverse stripes. It is possible to make out that none of those shown in the figure is provided with ray-tracheids. The amount of wood parenchyma is also abnormally large in the region of the wound-cap. Sections from the opposite side of the stem are characterized by a more normal amount of wood parenchyma and a normal number of medullary rays. The latter in some instances, as has been described above, show the presence of ray-tracheids. A careful examination of this and other fragments of wood has failed to reveal the presence of ray-tracheids, except in the region representing the annual rings formed after injury and in the part of the circumference of the wood more remote from the actual wound.

It appears from the account given in the paragraphs above that in the genus *Cunninghamia* there are found, in definite relation to injury, marginal tracheids in the rays such as are typical of the Abietineae. It would perhaps be possible to regard these as a mere abnormality did they not also occur in other representatives of the Cupressineae and Taxodineae. Their presence is apparently significant. In the Abietineous genera, *Pinus*, *Picea*, *Pseudotsuga*, and *Larix*, not only are marginal tracheids a characteristic feature of the rays of the normal wood, but ligneous resin-canals likewise occur normally. In the Abietineous genera, *Cedrus*, *Tsuga*, *Abies*, and *Pseudolarix*, ray-tracheids are normally present in only the two first named genera. Resin-canals are entirely absent in all four in the mature wood, *except as the constant accompaniment of injury. In the first year's growth of the root, and in a few cases in the cone axis and in the first year's growth of vegetative branches*, resin-canals occur normally in the four last-mentioned Abietineous genera. It is a reasonable conclusion on ordinary biological principles to consider, on the basis of the evidence of the living Abietineae alone, that the presence of ligneous resin-canals is ancestral for that tribe, and that the normal occurrence of resin-canals in the first annual ring only, as a result of injury to the mature wood, in the genera, *Cedrus*, *Tsuga*, *Abies*, and *Pseudolarix*, represents phenomena of recapitulation and reversion respectively. This view is much strengthened by the consideration of the fossil forms. It has been recently shown by the present writer that there are the best of reasons from the anatomical palaeobotanical side for regarding *Pinus* as the oldest of the living Abietineae, and as related to the archaic genus *Prepinus* (Jeffrey, E. C., Structure of the Leaf in Cretaceous Pines, Ann. Bot., vol. xxii, pp. 207-20, 1908). *Prepinus*, in the anatomical structure of its leaf, a feature recognized on all hands to be most important and significant, shows a remarkable detailed resemblance to certain Cordaitales. In this genus the structure of the wood, so far as the presence of resin-canals is concerned, was identical in structure with living and Cretaceous Pines. Further, Fliche has obtained structural evidence for the existence of *Cedrus*

in the Infracretaceous, this being the oldest well authenticated record of the occurrence of any of the four genera, *Cedrus*, *Tsuga*, *Abies*, and *Pseudolarix* (Fliche, P., Études sur la Flore fossile de l'Argonne, Bull. Soc. Sci. Nancy, 1896). Fliche's observations are all the more significant, because it is precisely the genus *Cedrus* which on anatomical and experimental grounds we should regard as the most ancient of its series, for by its wound reactions it shows a closer relationship to *Pinus* than any of the three allied genera, in that the traumatic resin-canals occur in both the horizontal and vertical planes, instead of in the vertical plane only, as in the remaining three (Jeffrey, E. C., Comparative Anatomy and Phylogeny of the Coniferales, II, Abietineae, Boston Society of Nat. Hist. Memoirs, 1905). It follows both because there are strong reasons for regarding *Pinus* as a very old representative of the Coniferous stock, and because *Cedrus*, *Tsuga*, *Abies*, and *Pseudolarix* show clear indications of descent from ancestors possessing at least the ligneous characteristics of *Pinus*, that there are good reasons for regarding the Abietineae as an ascending series, beginning with more complicatedly organized forms like *Pinus*, and terminating with simplified genera like *Abies* and *Pseudolarix*. The views stated here are in strong opposition to those expressed by Penhallow in his recent works. They seem, however, to rest on sound anatomical and palaeobotanical evidence. Professor Penhallow has not brought forward any good evidence for his view that the ligneous resin-canals of *Pinus* and its allies are derived from aggregations of the resin-parenchyma, which is found in the Taxodineae and Cupressineae. His view is that the resin-canals appear first as imperfect cysts in the wood and afterwards become organized into a perfect system of resin-canals, such as is characteristic of *Pinus*. Professor Penhallow has failed to recognize that his resin-cysts are always of traumatic origin, and are not a normal feature of wood structure as he assumes. Further, if we for the sake of argument were to admit Professor Penhallow's hypothesis, we should encounter the difficulty that the resin-canals not only have to develop from the imperfect cysts, but that these have in the course of evolution to become connected with each other and with the perfect cortical system of resin-canals, since in *Pinus* not only the ligneous canals form a complete system, but these are also in continuity with those found in the inner bark. There is every reason to believe that, in the forms with resin-canals less perfectly developed among the Coniferales, we have rather to do with the isolation of parts of a once complete system as the result of degeneration than the opposite process, as is indicated by Professor Penhallow's hypothesis. Further, not only in the matter of the degeneracy of the ligneous resin-canals are *Pseudolarix* and *Abies* the uppermost terms of the Abietineous series, but also in the loss of the other characteristic feature of the living Abietineae, viz. the marginal tracheids of the medullary rays. In *Pseudolarix* marginal tracheids have quite disappeared, while in

Abies the only well authenticated record of their occurrence is in *A. balsamea* (De Bary, Comparative Anatomy, Eng. Trans., p. 490), a record confirmed by Penhallow (Manual of North American Gymnosperms, pp. 88, 258, Boston, 1907).

After having discussed the evolutionary history of the Abietineae in relation to the development of ligneous resin-canals and the presence of marginal ray-tracheids, a necessary preliminary on account of the clear and definite character of the evidence in this tribe, we are in the position to return to the sporadic marginal tracheids of certain Cupressineae and Taxodineae. Attention has already been called to the observations of De Bary, Penhallow, and Gothan in regard to the occurrence of marginal ray-tracheids in these tribes. Professor Penhallow has suggested that their presence in the cases described by him is the first step, so far as this feature is concerned, in an upward evolution, which ends in the genus *Pinus*. If we add to his observations the recorded presence of marginal tracheids in three Taxodineous genera, we shall have to assume, if we adopt his hypothesis, that this upward evolution has begun independently in six distinct genera. It appears extremely unlikely on general grounds that *Sequoia*, *Sciadopitys*, *Cunninghamia*, *Cupressus*, *Juniperus*, and *Thuja* should each of them independently have varied in a direction leading towards the elaborate wood structure of *Pinus*. It seems more probable and more in accordance with accepted biological principles that the various Taxodineous and Cupressineous genera under discussion have all inherited their ray-tracheids as vestigial characters from a common ancestry. This view of the case is strengthened by a consideration of the mode of occurrence of ligneous resin-canals in the genus *Sequoia*. It has been shown by the present writer (Memoirs Boston Soc. Nat., vol. v, No. 10, 1903) that in *S. gigantea* resin-canals appear normally in the wood of the female cone and in the first years' growth of vigorous vegetative branches and traumatically as a result of injury in the mature wood. In *S. sempervirens* they occur only as the result of wounding. It appears highly probable that *S. gigantea* is the older of the two existing species of the genus. This is rendered probable by the more abundant occurrence of resin-canals in this species, and by the fact that it shows the presence of marginal ray-tracheids which have not yet been found in *S. sempervirens*. The presence of resin-canals in the first annual ring and in the cone-axis of *S. gigantea* would on this interpretation constitute an example of recapitulation, while the traumatic resin-canals which are found in both species, as well as the marginal tracheids of *S. gigantea*, should be regarded as reversions to the ancestral type of wood.

The strongest evidence, however, that neither *Sequoia* nor any other Taxodineous or Cupressineous genus has been the ancestor of the general Abietineous line is furnished by recent discoveries in Mesozoic Botany.

Dr. Arthur Hollick and the present writer have been engaged for some time on a Monograph of the Coniferales from the Lower Cretaceous beds of Kreischerville, Staten Island, N.Y., which is now in the press. The generally accepted view in regard to *Sequoia* is that it appeared geologically at a very early period and antedated *Pinus*. Remains, which have been referred by Zeiller and others to *Sequoia*, from their external features alone, are found as far back as the Jurassic, and in the Cretaceous such fossils become exceedingly numerous. As a result of the study of material with structure preserved, both of leafy twigs and cone-scales, we have come to the conclusion that the forms from the Cretaceous, which have been referred to *Sequoia* as well as to the somewhat similar genus *Geinitzia*, are really not of Taxodineous affinities at all but are Araucarian Conifers. This conclusion has been reached not only because the species in question show no Taxodineous features, but from the much more important consideration that the internal organization both of the twigs and cone-scales is entirely Araucarian. It is significant in this connexion to note that the foliage shoots, referred subsequently to *Sequoia* and *Geinitzia*, were originally put, on account of their habit, under the genus *Araucarites*. Indeed, it would not occur to any one familiar with the foliage shoot of the living *S. gigantea* to refer to it the leafy twigs, with four-sided falcate leaves, of the *Sequoia Reichenbachii* and *Geinitzia* types; the reference in fact seems to have resulted from the discovery of the cones of these Mesozoic forms, which present a superficial, although by no means a detailed resemblance to those of *Sequoia*. We have also shown in the memoir already referred to that a number of other well-known Cretaceous or Mesozoic genera, commonly referred to Taxodineous or Cupressineous affinities, such as *Thuyites*, *Widdringtonites*, *Brachyphyllum*, *Frenelopsis*, *Newberry*, and in all probability *Voltzia* as well, are in reality Araucarian Conifers, and have no close relationship with any of the modern species which they simulate in habit. There is in fact no structural evidence, in view of these newly discovered facts, for the occurrence of the living *Sequoia* earlier than the Tertiary, since it is only from this level that woods of the true *Sequoia* type have been described by Knowlton, Penhallow, and others. It of course follows, unless there were other better authenticated representatives of the Taxodineae and Cupressineae in the Mesozoic, that neither of these groups could possibly have furnished the ancestry of *Pinus*, which is geologically so very much older. It is true that there are numerous Cupressinoxyla in the upper Mesozoic, but there is no good reason to regard these as having belonged to the Cupressineae or Taxodineae, rather than to the Podocarpaceae. We have never found twigs with this type of wood structure, in the Kreischerville deposits, with their leaves attached. This fact rather points to the woods in question having belonged to the Podocarpaceae.

Still another fact must be kept in mind in this discussion, viz. that the wood of early Cretaceous Pines had not yet acquired the marginal tracheids which are found in those of late Cretaceous and later epochs (E. C. Jeffrey and M. A. Chrysler, On Cretaceous Pityoxyla, Bot. Gazette, vol. xlii, pp. 1-14). This conclusion follows not only from the study of the wood-structure of Lower Cretaceous Pityoxyla, but also from a consideration of the anatomy of the first year's growth of vegetative branches and of that of the cone-axis of living Pines, where their marginal ray-tracheids are late in appearing (vegetative branches) or are almost entirely unrepresented (cone-axes). It is further significant in this connexion to note that Conwentz has described the very much retarded appearance of the marginal tracheids in the amber-containing Pityoxyla (Late Eocene or Early Oligocene) of the Baltic amber deposits. This author states that the marginal tracheids are quite absent in the earlier annual rings of the branches and only appear at a late stage of growth (Monographie d. Baltischen Bernsteinbäume, p. 53). The primitive absence of marginal ray-tracheids in the genus *Pinus* makes it still more difficult to accept the hypothesis of Penhallow (Anatomy of North American Gymnosperms, Am. Naturalist, vol. xxxviii, pp. 696-708. Manual of N. A. Gymnosperms, pp. 122-71, Boston, 1907), that this genus and its allied genera have come from Cupressineous or Taxodineous ancestors, which have developed ray-tracheids and resin-canals as well. Moreover *Pinus*, or a closely-allied genus, according to the observations of Goeppert (Revision meiner Arbeiten, Bot. Centralblatt, vol. V, p. 405, 1881) and of Professor Penhallow himself (North American Species of Dadoxylon, Trans. Roy. Soc. Canada, ser. 2, vol. vi, 1900), already possessed ligneous resin-canals in the Palaeozoic.

We can in fact only conclude from all the evidence at our disposal, that *Pinus* and its nearer allies are among the oldest of living Conifers, and that its ancestors possessed ligneous resin-canals already in the Upper Palaeozoic and Lower Mesozoic. Further it acquired marginal tracheids in the later Cretaceous long before the true Sequoias or their allies had come into existence. Since the Taxodineae and Cupressineae, according to our most accurate and recent information, appeared long after the Abietineae, it is neither necessary nor logical to consider any sporadic Abietineous features which they may present, such as the normal and traumatic resin-canals of the living species of *Sequoia* or the marginal ray-tracheids of *Sciadopitys*, *Sequoia*, *Cunninghamia*, *Cupressus*, *Juniperus*, and *Thuja* as indicating that the Abietineae have been derived from either of these groups. On the contrary, the rational explanation of these peculiar features of structure in the Taxodineae and Cupressineae appears to be that they are vestigial or reversionary structures, indicating that these tribes have had an Abietineous ancestry. It is clear from the palaeontological evidence that if the two tribes in question came from the Abietineae,

it must have been at the earliest in the very late Cretaceous or the early Tertiary after the Abietineae had developed both ligneous resin-canals and marginal ray-tracheids. The structure of the female cone in the three tribes under discussion quite favours this view. In the Abietineae the megasporangiate cone is made up of pairs of superimposed scales with oppositely oriented fibrovascular systems. The female cones of the Taxodineae and Cupressineae are made up of single scales, but these contain a double system of fibrovascular bundles oriented as are those of the two distinct scales of the Abietineae. The conditions observed suggest naturally that in the Taxodineae and Cupressineae we find the fusion of two organs, which are still free in the more primitive Abietineae. A consideration of the gametophytic structure in the tribes under discussion apparently leads to a concordant conclusion, for we find both the microgametic and megagametic conditions much more simplified in the Taxodineae and Cupressineae than they are in the Abietineae.

SUMMARY.

1. Marginal ray-tracheids, similar to those characteristic of the Abietineae are sometimes present in *Cunninghamia*.

2. In *Cunninghamia* the ray-tracheids are traumatic in their origin and are most numerous in the region of the injured annual rings diametrically opposite to the wound-callus.

3. The ray-tracheids of *Cunninghamia* present a general resemblance to those described by De Bary, Penhallow, and Gothan, in the Taxodineous or Cupressineous genera, *Sciadopitys*, *Sequoia*, *Cupressus*, *Juniperus*, and *Thuja*.

4. The ray-tracheids in the genera mentioned constitute additional evidence for the derivation of the Taxodineae and Cupressineae from the Abietineae, and on this hypothesis are to be regarded as vestigial or reversionary.

5. All the evidence goes to show that the Taxodineae and Cupressineae did not exist before the very end of the Cretaceous or more probably before the beginning of the Tertiary.

It gives me much pleasure to offer my thanks to the Director of the Royal Gardens, Kew, and to my friend Mr. L. A. Boodle of the Jodrell Laboratory, Kew, for material secured there on a visit to England two years ago.

EXPLANATION OF PLATE XXXI.

Illustrating Professor Jeffrey's paper on Traumatic Ray-tracheids in *Cunninghamia sinensis*.

- Fig. 1. Transverse section of the wood of *Cunninghamia sinensis*. $\times 50$.
- Fig. 2. Longitudinal section through three annual rings of the same, showing a ray with marginal tracheids. $\times 60$.
- Fig. 3. Longitudinal view of part of the same section. $\times 180$.
- Fig. 4. Longitudinal section of a part of the same more highly magnified. $\times 500$.
- Fig. 5. Longitudinal section through wounded region of a branch of *Cunninghamia sinensis*, showing normal wood on the left and wound-cap on the right. $\times 25$.
- Fig. 6. Longitudinal section through the wound-cap of the same. $\times 60$.

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Huth, coll.

Jeffrey, Edward C. 1908. "Traumatic ray-tracheids in *Cunninghamia sinensis*." *Annals of botany* 22, 593–602.

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