On the Origin of the Multiseriate Ray of the Dicotyledons.¹

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With Plates LXXVII and LXXVIII.

THE medullary rays of dicotyledonous plants present several distinct types. The simplest of these is but a single cell wide, and for this reason is called a *uniseriate* ray. It is similar to, and, in part at least, homologous with, the usual type of ray found in gymnospermous plants. A second type is two or more cells wide, and accordingly is known as *multiseriate*. Such a ray is of widespread occurrence in the Dicotyledons. Still another type, recently designated the *compound* ray, is much broader than either of the foregoing, and consists of an extensive homogeneous mass of parenchyma. This is the type which gives to the oak wood, for example, its characteristic grain. Finally, closely associated with the compound ray, one finds in certain woods an aggregation of uni- and multiseriate rays, to which the term '*false*' ray has been applied.

The inter-relationships and evolution of these different types of rays have recently formed the subject of a series of investigations in this laboratory. Eames² has demonstrated from a study of the structure of fossil and seedling oaks, as well as from comparative evidence, that the broad type of ray has arisen by a progressive fusion of uniseriate rays and an accompanying transformation of the included fibres and wood parenchyma into ray parenchyma. That is to say, in the ancestral oaks, and in primitive regions of modern oaks, only uniseriate rays may be found, and these by a process of fusion have given rise to the modern broad oak ray. Bailey³ has emphasized the perfect series of transitions in this process furnished by the false rays of the Cupuliferae, and has shown that the factor at work in the development of the compound ray has been the influence of the leaf-trace. The most natural and convenient place for

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 43.

² Eames, A. J.: On the Origin of the Broad Ray in *Quercus*. Bot. Gaz., xlix, March, 1910, No. 3, pp. 161-7.

³ Bailey, I. W.: The Relation of the Leaf-trace to the Formation of Compound Rays in the Lower Dicotyledons. Ann. Bot., Jan. 1911, pp. 225-241.

the storage of the food manufactured in the leaf is, of course, in the stem adjacent to the leaf-trace. Accordingly the storage organs, i. e., the rays, at this point in the stem have been enormously developed, especially in view of the probable persistent habit of the leaves of Angiosperms during the warmer Mesozoic times. Then, following its development at the leaf-trace, the broad ray has spread throughout the plant. Bailey has also suggested that the further development of compound rays at the expense of the woody cylinder has given rise to the herbaceous habit among Angiosperms. The same conclusion was reached by Eames¹ after an investigation of herbaceous and semi-herbaceous forms. This aspect of the work has resulted in a conclusion exactly the reverse of the commonly taught Sachsian hypothesis of the development of the woody cylinder from the herbaceous type by the filling in of the interfascicular regions through the activity of the so-called interfascicular cambium.

It will be observed that the only kind of ray not included in these investigations is the multiseriate type, that intermediate in size between the uniseriate and compound types. It is the object of this paper to determine the origin of this ray and to establish its position in the general scheme of ray development in the Dicotyledons. In carrying on the investigation it was found that the Ericaceae presented very favourable conditions, and this family was studied in detail. Confirmatory evidence was found in many other groups.

The origin of the multiseriate ray is epitomized in Pl. LXXVII, Fig. 1. This is a photograph of a transverse section of *Rhododendron punctatum* (Andr.) just above the level of exit of the leaf-trace. All the rays in the section are seen to be uniseriate except the conspicuous group at the top, which is directly above the leaf-trace. At this point we see next to the pith a broad compound ray which during its course through the wood breaks up progressively into several smaller multiseriate rays. Otherwise stated, the group of multiseriate rays has originated by the breaking up of a compound ray.

A tangential view of this group of rays is presented in Fig. 2. At the bottom of the field is the leaf-trace, and extending upward from it completely through the field and for a long distance beyond is the aggregation of multiseriate rays. A small group also extends for a very short distance below the trace. Complete series of such tangential sections through the node from the bark to the pith show that all the multiseriate rays in the branch are associated in this manner with the traces. Complete series of transverse sections through the node show that the solid type of broad ray is not present at the pith through the whole vertical extent of the group, but at the upper extremity multiseriate rays arise directly from the pith.

¹ Eames, A. J.: The Origin of the Herbaceous Type in Angiosperms. Ann. Bot., Jan. 1911, pp. 215-224.

In this species, then, almost the whole of the woody cylinder possesses only uniseriate rays ; the multiseriate ones occur only in association with the leaf-trace and arise by the dissection of compound rays.

A similar condition is found in *Ledum groenlandicum* (Oeder) and is represented in Fig. 3. Only one side of the woody cylinder is shown, with the edge of the pith at the extreme bottom of the figure. The horizontal spreading of the multiseriate rays with the increase in diameter of the stem is almost diagrammatic. Following the breaking up, the resulting rays may widen by their own growth and split again. The tangential view is given in Fig. 4. This section was taken further from the pith than Fig. 2, and consequently more horizontal spreading of the rays has taken place. As in *Rhododendron punctatum*, all the multiseriate rays in the stem arise in association with the leaf-traces.

An important additional step is seen in Fig. 5, which is a photograph of a section of *Kalmia angustifolia* (L.), at the nodal region. In this species three traces arise at approximately the same level. One of their corresponding large rays is seen unbroken at the lower left of the figure. Above and at the lower right the breaking-up process has taken place. The result is that considerably more multiseriate rays occur in the adult wood than in the aforementioned species. Furthermore, at the right of the figure are to be seen two multiseriate rays which are not associated with the others. A series of sections would show, however, that in reality these are associated with a leaf-trace of a lower node. As may be seen in the tangential section (Fig. 6), the group of rays extends for a long distance above the trace, in fact up to and beyond the next trace. This overlapping of the groups of rays gives the appearance in question and assists in distributing the multiseriate rays throughout the wood. Another important fact in this connexion is that the groups of rays in their course outward through the wood extend continually higher vertically, so that in a tangential section as far out as the bark they are much higher than in one at the pith.

Still more conspicuous overlapping and vertical extension of the rays may be observed in *Chaemadaphne calyculata* (Moench). In this species and in *Kalmia angustifolia* it is often difficult to observe the solid oak type of ray even at the pith. This stage is apparently omitted, the multiseriate rays often arising in a group from the pith above the leaf-trace.

In other species of the Ericaceae, for example in *Vaccinium corymbosum* (L.), multiseriate rays may be found which are not in association with the leaf-trace but which arise quite independently at the pith or in the wood. The natural inference is that the habit of forming multiseriate rays, arising as indicated, has become firmly fixed upon the cambium, which may then form this type quite apart from the influence of the leaf-trace. The uniform distribution of the multiseriate type throughout the wood will then

be a matter of course. Nevertheless, one still finds the breaking-up process taking place at the leaf-trace. Pl. LXXVII, Fig. 7, which is a photograph of a section above the node in *Vaccinium corymbosum*, shows a broad ray at the bottom being dissected into the numerous multiseriate ones seen at the top. In addition to these, other multiseriate rays are visible at the left and right which are quite independent of the broad ray. In *Vaccinium corymbosum*, therefore, the breaking up of the broad ray at the leaf-trace takes place as previously described, and in addition new rays arise quite independently of the leaf-trace. The adult wood will therefore be characterized by a rather uniform distribution of multiseriate rays, although here and there one may observe a slight grouping, the result of the breaking up of a compound ray.

A tangential view of the condition existing in *Vaccinium corymbosum* is given in Fig. 8. The leaf-trace is visible at the extreme lower edge of the figure, and the ray in the process of dissection above it. Independently arising multiseriate rays are to be seen at the left and right.

A similar condition is present in *Gaylussacia resinosa*, except that the solid type of ray is more evanescent.

It is obvious that the net result of the process of dissection of compound rays and the fixation on the cambium of the habit of forming the dissected type will be the uniform distribution of the latter type throughout the wood. Such a condition one finds to exist in many species of the Ericaceae; for example, *Clethra alnifolia* (L.) (Fig. 9). At the bottom is the pith, and throughout the wood are multiseriate rays intermixed with uniseriate ones. Fig. 10 shows the condition in tangential section, the multiseriate rays being strikingly uniform in distribution. Furthermore it is important to notice that the leaf-trace at the bottom of the figure is no longer accompanied by a compound ray or by an aggregation of multiseriate rays. This plant presents, therefore, the completely developed condition of the multiseriate ray of the Dicotyledons.

Among other Ericaceous plants presenting equally well developed conditions may be mentioned *Andromeda floribunda* (Pursh), *Lyonia ligustrina* L. (DC.), *Leucothoe racemosa* L. (Gray).

To summarize the conditions found in the Ericaceae: The breaking up of compound rays into smaller multiseriate ones is of common occurrence. In some species only one such group may be seen in a given section. Then by the occurrence of several traces at the same level, by the overlapping of rays from traces at different levels, by the vertical extension of groups of rays with the increase in size of the stem, and above all by the acquired habit of forming multiseriate rays independently of the leaf-trace, the multiseriate rays become uniformly distributed throughout the stem, and the dissection process is lost.

Turning now to other groups of Dicotyledons in which the compound

ray is well developed, one finds the evidence equally conclusive. Among the Proteaceae, *Grevillea* and *Hakea* have been examined. The wood of *Grevillea robusta* for some distance from the pith possesses typical large rays of the oak type, which extend vertically for long distances. They are not confined to the vicinity of the leaf-traces as in the Ericaceae, but are uniformly distributed throughout the wood. A short distance from the pith they become divided into two or three smaller rays by the intrusion of fibres. Fig. 11 shows a broad ray at the bottom being split in this manner into two smaller rays. In any given section two or three such rays can usually be seen undergoing division.

In *Hakea* sp. the conditions are almost identical with those described for *Grevillea robusta*. Fig. 12 shows the division taking place in this species, three smaller rays being formed at the top.

These two examples are sufficient to show that the dissection process occurs in the Proteaceae and that it is probably of widespread occurrence in the family. Importance is added to this by the fact that the broad rays are much better developed here than in the Ericaceae.

In regard to the Casuarinaceae the story is much the same. The early formed wood of *Casuarina glauca* possesses very large solid compound rays, as may be seen in Pl. LXXVIII, Fig. 13, which is a photograph of a tangential section of this species taken very close to the pith. The homogeneous rays immediately become traversed by strands of fibres in the form of a network (Fig. 14). The strands increase in size and number, with the result that the remnants of the original broad ray gradually become smaller and scattered uniformly through the wood. The ultimate condition is shown in Fig. 15, in which there is no indication of a broad ray, but in its place a typical multiseriate-rayed wood. This condition is reached at a distance of two or three centimetres from the pith.

In *Casuarina equisetifolia* the broad rays are never so well developed as in *C. glauca*, and become broken up much sooner. Fig. 17 shows the typical broad ray for this species, and Fig. 18 the aggregation of smaller multiseriate rays resulting from its dissection. A section still further from the pith would show a uniform distribution of small multiseriate rays.

An undetermined species of *Casuarina* presented the same phenomenon. It appears, therefore, that the conditions described are normal for the family. The obvious conclusion is that the Casuarinaceae formerly possessed broad rays and are replacing them by smaller multiseriate ones.

In the broad-rayed genera of the Fagaceae the breaking-up process is sometimes apparent and resembles slightly that found in *Casuarina*. At the pith of *Fagus ferruginea* broad rays extend for extremely long distances vertically, as may be seen in Fig. 19. The two rays visible here extend far beyond the limits of the figure. A short distance from the pith strands of fibres begin to cross the rays obliquely and divide each into

a vertical series of lower rays. The beginning of this process is shown in Pl. LXXVIII, Fig. 20, which is a photograph at the same magnification of a section taken further from the pith of the same branch. Still further out the separating strands increase in size, with the result that the low rays or segments of an original high ray are gradually pushed apart. This continues until the condition found in the adult (Fig. 21) is attained. Here the rays are scattered through the wood and give little suggestion that they have originated from the oblique dissection of vertically elongated compound rays. Owing to the obliquity of the dissecting fibres the process cannot usually be well observed in transverse sections. Occasionally, however, the fibres are sufficiently vertical to make the process visible in favourable sections. This is especially true in the European Beech, *Fagus sylvatica*. In Fig. 22, taken from a section of the latter species, the broad ray in the centre of the field is undergoing the oblique division.

Even in certain species of the oak itself, in which the broad rays reach their maximum development, the beginning of their dissection may be seen. In *Quercus bicolor*, for example, in the later formed wood of very old trees the rays begin to undergo oblique division.

In *Platanus occidentalis* the conditions are almost identical with those described for *Fagus ferruginea*.

If the smaller multiseriate rays have originated as suggested, it is to be expected that typical multiseriate-rayed forms would exhibit some evidence of their derivation from a broad-rayed ancestry. Such evidence has been found in many forms. As a first example we may take the case of *Carpinus japonica*. This species is characterized by the possession of multiseriate rays. Yet occasionally one may find in the seedling the broad oak type of ray. Fig. 23 shows such a ray at the bottom of the field dividing to form the two smaller rays at the top. Obviously we have in this primitive region a recapitulation of the process by which multiseriate rays have originated.

Ostrya virginiana, the hornbeam, which is likewise characterized by the possession of multiseriate rays, furnishes a second example. Fig. 24, from the root of a seedling, shows the retention in this species also of the broad type and its division into the smaller type. Moreover, wounded seedlings of *Ostrya* occasionally exhibit broad rays in the wood formed immediately after injury. This phenomenon is to be regarded as a traumatic reversion and, together with the observation just recorded, is interpreted to mean that the multiseriate-rayed *Ostrya* is descended from forms which possessed broad rays.

The conditions in the genus *Betula*, which has been investigated by Professor Jeffrey, lead to exactly the same conclusion. Species such as *B. populifolia* (Marsh) possess compound rays of the so-called false type throughout the ordinary wood. Others, such as *B. alba* (L.), possess them

only as a passing phase in the seedling, and have thereafter only smaller multiseriate rays. Others again, such as *B. papyrifera* (Spach), do not normally possess compound rays even in the seedling, but a wound in the latter region will recall them. Finally, *B. lutea* (Michx.) and *B. lenta* (L.) never have them even in severely wounded seedlings. The various species of *Betula* thus exhibit in an admirable manner the loss of compound rays and their replacement by those of the multiseriate type. The actual breaking up cannot be observed so well as in the forms previously described, for the compound rays usually die out rather abruptly.

Mr. I. W. Bailey, who is now investigating the loss of compound rays, finds among other things that the chestnut (*Castanea*), though possessing in the adult wood only uniseriate rays, shows undoubted evidence of having once possessed compound rays. He also finds that in *Castanopsis* the evidence is even more striking.

All these examples from the Cupuliferae show that, upon investigation in the proper regions, relics in one form or another of a broad-rayed ancestry may be found. Nor is the evidence lacking in other groups. In the Juglandaceae broad rays have been observed in seedlings of *Carya*. A tangential view of such a ray undergoing division is presented in Fig. 16. It is probable that investigation in the proper regions will also reveal their presence in many other families of the Dicotyledons.

In this connexion the work of Miss Holden¹ on the uniseriate-rayed Sapindales is noteworthy. She finds that *Aesculus*, which is normally characterized by the possession of uniseriate rays, may possess rays of much larger size in the petiole of the leaf, in the root, and in the reproductive axis. From these observations she concludes that this simple-rayed form is simple not primitively but by degeneration from a broader-rayed type.

CONCLUSIONS.

We have seen that the members of the Ericaceae exhibit in an extremely diagrammatic manner the breaking up of compound rays into smaller multiseriate ones, and the stages by which typical multiseriate-rayed plants completely lacking compound rays in the normal adult wood have been derived. Among forms with broad rays the dissection process is apparently widespread, being figured in the Casuarinaceae, Proteaceae, and Fagaceae, as well as in the Ericaceae. Among plants possessing normally only the smaller multiseriate rays the actual process may be observed in the regions of retention of ancestral characters, and where the actual process is lost, relics are still retained of the broad-rayed ancestry. From all sides, then, the conclusion seems inevitable that the multiseriate

¹ Ruth Holden: Some Features in the Anatomy of the Sapindales. Botanical Gazette, ined.

rays of the Dicotyledons have originated by the breaking up of the compound type.

That the elaborate system of compound rays should have been modified seems but reasonable. The influence at work in the development of the compound, aggregate, or foliar ray was originally the demand for the storage of assimilates descending from the large leaves of the earlier Angiosperms. It was natural that in the warmer climate of Mesozoic time, when the leaves probably persisted for a number of seasons, the storage devices of the wood should be mainly centred about the leaf-traces. In later epochs, however, with the advent of a severer winter season and the consequent acquirement of the deciduous habit in connexion with the leaves, the organization of the storage system about the leaf-traces as permanent centres would no longer be advantageous or desirable. Besides being less unwieldy, the system of smaller rays affords equally large capacity for storage and a more convenient general relation between conducting, supporting, and storage tissues.

It should also be emphasized that there has been abundant opportunity in point of time for the complete evolution of the system of multiseriate rays, not only because the compound type is characteristic of the most primitive Dicotyledons, but also because multiseriate rays were already in existence in the Cretaceous. Stopes and Fujii¹ have described many woods of this type from the Cretaceous of Japan.

The general course of ray development would then be as follows: Starting with a primitive uniseriate-rayed condition, the broad rays have been built up by a process of compounding primarily about the leaf-trace and extending from here throughout the wood. From this condition two courses take their origin. On the one hand the continued development of the compound ray at the expense of the woody cylinder has resulted in the ultimate production of the herbaceous condition. On the other hand the forms which remained arborescent replaced the compound rays by a system of smaller multiseriate rays with its more uniform distribution of ray parenchyma. The typical ray structure of the more recent arborescent Dicotyledons accordingly appears to be the multiseriate condition. It is obvious that ray structure will supply a valuable criterion in considerations of phylogeny and classification.

SUMMARY.

1. The production of multiseriate rays by the breaking up of the ancestral broad compound type may be observed in many families of the Dicotyledons (Ericaceae, Casuarinaceae, Fagaceae, and Betulaceae).

¹ Stopes, M. C., and Fujii, K.: Studies on the Structure and Affinities of Cretaceous Plants. Phil. Trans., Series B, vol. cci. pp. 1-90.

2. Originating from the breaking up of compound rays, the multiseriate ray has spread throughout the wood in the higher dicotyledonous Angiosperms.

3. Reversion to the ancestral compound type of ray may be observed in the seedling, root, &c., of dicotyledonous plants which are characterized by the multiseriate type.

4. The multiseriate ray represents the most recent development in ray structure among the Dicotyledons.

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EXPLANATION OF PLATES LXXVII AND LXXVIII.

Illustrating Mr. Thompson's paper on the Origin of the Multiseriate Ray.

PLATE LXXVII.

Fig. 1. *Rhododendron punctatum*. Transverse section above the node, showing broad ray breaking up into several multiseriate rays. $\times 12$.

Fig. 2. The same. Tangential section, showing leaf-trace and group of rays above it. $\times 25$.

Fig. 3. *Ledum greenlandicum*. Transverse section above node, showing the splitting up of broad ray and horizontal spreading of the multiseriate rays. $\times 12$.

Fig. 4. The same. Tangential section, showing the multiseriate rays above the leaf-trace. $\times 25$.

Fig. 5. *Kalmia angustifolia*. Transverse section through the nodal region, showing unbroken broad ray, two groups of multiseriate rays resulting from the breaking up of broad rays, and two multiseriate rays extending up from a lower node. $\times 12$.

Fig. 6. The same. Tangential section, showing the group of multiseriate rays above the leaf-trace. $\times 25$.

Fig. 7. *Vaccinium corymbosum*. Transverse section, showing breaking up of a compound ray and independently arising multiseriate ones. $\times 45$.

Fig. 8. The same. Tangential section. $\times 45$.

Fig. 9. *Clethra alnifolia*. Transverse section, showing uniform distribution of multiseriate rays. $\times 50$.

Fig. 10. The same. Tangential section, showing the same uniform distribution, and also absence of aggregation above the leaf-trace. $\times 50$.

Fig. 11. *Grevillea robusta*. Transverse section, showing splitting of broad ray. $\times 60$.

Fig. 12. *Hakea* sp. Transverse section, showing splitting of broad ray as in *Grevillea robusta* (Fig. 11). $\times 60$.

PLATE LXXVIII.

Fig. 13. *Casuarina glauca*. Tangential section close to the pith, to show the large compound ray. $\times 45$.

Fig. 14. The same. Tangential section some distance from the pith, to show the network of fibres which breaks up the compound ray. $\times 45$.

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Fig. 15. The same. Tangential section of the adult wood, to show the absence of broad rays and presence of multiseriate type. $\times 45$.

Fig. 16. *Carya* sp. Tangential section of seedling, showing presence of broad rays. $\times 45$.

Fig. 17. *Casuarina equisetifolia*. Tangential section close to the pith, showing broad ray. $\times 45$.

Fig. 18. The same. Tangential section further from the pith than Fig. 17, to show the group of multiseriate rays resulting from the breaking up of a broad ray. $\times 45$.

Fig. 19. *Fagus ferruginea*. Tangential section near the pith, to show the broad unbroken rays. $\times 45$.

Fig. 20. The same. Tangential section, showing the vertical dissection of a broad ray by oblique fibres. $\times 45$.

Fig. 21. The same. Tangential section of adult wood. $\times 45$.

Fig. 22. *Fagus sylvatica*. Transverse section, showing oblique dissection of a broad ray. $\times 60$.

Fig. 23. *Carpinus japonica*. Transverse section of a seedling, showing a broad ray splitting into two of the multiseriate type. $\times 60$.

Fig. 24. *Ostrya virginiana*. Transverse section of the root of a seedling, showing a broad ray splitting into three of the multiseriate type. $\times 60$.

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Thompson, W. P. 1911. "On the origin of the multiseriate ray of the dicotyledons." *Annals of botany* 25, 1005–1014.

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