The Evolutionary History of the Foliar Ray in the Wood of the Dicotyledons : and its Phylogenetic Significance.¹

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With Plates LXII and LXIII.

EVOLUTION OF THE FOLIAR RAY.

IN 1909 Mr. Eames (4) and the writer (1, 2, and 3) conducted a series of investigations upon the broad rays and so-called 'false rays' of the Fagales. The conclusions drawn from these studies have since been published, and may be summarized briefly as follows :

1. Oaks from the Miocene of California are characterized by possessing 'false rays', such as are a distinctive feature of the wood of a large number of living representatives of the Betulaceae.

2. The mature wood of certain Live Oaks of America and Japan possess large rays which are composed of congeries of smaller rays.

3. *Alnus rhombifolia*, Nutt., and *A. maritima*, Muehl, develop in the older wood large homogeneous sheets of ray parenchyma homologous to the large rays of oaks with deciduous foliage.

4. The earliest formed secondary wood of seedling oaks and alders possesses solely uniseriate rays, such as are a characteristic feature of coniferous plants and many other Gymnosperms.

5. In the mature wood of different species of *Alnus* a perfect series of stages occur, which demonstrate the 'building up' of a homogeneous sheet of ray parenchyma from congeries of uniseriate rays and the parenchymatization of fibres included between them.

6. In the development of individual alders and oaks a similar progressive series of compounding stages occur in passing from the younger to the older portion of the stem.

7. Wood which possesses highly developed types of compound ray tissue when injured severely reverts to the primitive uniseriate condition,

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and in subsequent growth a recapitulation of the compounding process occurs.

8. Upon the basis of the comparative and developmental anatomy of living and fossil plants and the phylogenetic significance of seedlings and traumatic regions, the uniseriate ray appears to be the primitive type of ray structure in the Fagales, and the large sheets of ray tissue, either of the homogeneous or aggregate type, have developed from them by a process of aggregation and fusion.

In subsequent investigations by the writer (1, 3) additional evidence was secured in regard to the origin and development of these structures and their effect upon the stem.

1. Small twigs of *Quercus*, *Alnus*, *Carpinus*, and *Betula* revealed upon the removal of the bark a striking and diagrammatic relation between the sheets of aggregate or compound tissue and the traces of the leaves.

2. A study of the development of ray structures in the Fagales made by means of transverse and tangential serial sections cut through the seedling, young and mature twigs, and large stems, showed the leaf to have been the stimulating influence in the formation of these large sheets of storage tissue.

3. The latter originated as aggregations of uniseriate rays in the immediate vicinity of the leaf-traces, and have been 'built up' and extended vertically and horizontally considerable distances from the node.

4. The large sheets of aggregate or compound tissue which may be called *foliar rays*, in view of their origin about the entering trace, have an important effect upon the development of the stem, since their rate of growth is in most cases less rapid than that of the rest of the xylem (Pl. LXII, Fig. 2). This is generally expressed by a strong retarding influence upon the growth of adjacent radii of lignified tissue and produces a marked 'dipping in' of the outline of the annual rings in their vicinity (Fig. 2).

5. The retarding influence of foliar rays is most diagrammatically expressed in small mature twigs of oaks with deciduous foliage, in the stems of certain highly specialized Angiosperms of vine-like and semi-herbaceous habit, and in the fluted trunk of the Blue Beech, *Carpinus caroliniana*, Walt. In the case of the Blue Beech large groups of approximated foliar rays of the 'false type' produce by their retarding effect upon growth the large furrows which are a characteristic feature of the bole of this tree, the ridges corresponding to the segments in which foliar rays are feebly developed or absent. In the mature twigs of oaks with deciduous foliage there are strongly developed foliar rays related to the lateral traces of the leaves. These lateral leaf-trace rays extend downwards through several nodes, and owing to the phyllotaxy of the plant (see Pl. LXIII, Fig. 15), sheets of storage tissue are formed which are relayed from node to node in ten more or less continuous vertical lines along the stem. As is shown in

Fig. 15 the ten sheets of ray tissue are distributed in five pairs of approximated rays. This approximation of the lateral leaf-trace rays enables their concentrated retarding influence upon growth to depress the included segment of tracheal tissue below the general contour of the stem (Pl. LXII, Fig. 3, and Pl. LXIII, Figs. 13, 15). In addition to the lateral leaf-trace rays foliar rays are developed in oak and other plants in relation to the median traces of the leaf. However, in oak these rays are in most cases less strongly developed in the young twig than are the rays related to the lateral traces.

6. The origin and development of foliar rays show clearly that the statements of Sanio, Sachs, and de Bary, pointing to the origin of large rays as inclusions of fundamental tissue or ground parenchyma between putative fibro-vascular bundles and the development of so-called fascicular and interfascicular segments from supposed fascicular and interfascicular cambiums, lead to extremely misleading conclusions.

7. All segments of the stem are essentially 'fascicular', since in the seedling plant of primitive Dicotyledons the stele is an undivided tubular cylinder without indication of the putative fascicular and interfascicular segments and large rays.

8. The development, in relation to the traces of the leaves, of large sheets of storage tissue from congeries of uniseriate rays has a strong dissecting effect upon the stele, producing the supposed fascicular and interfascicular segments of oak, vines, and semi-herbaceous plants.

Eames (5), in an investigation of herbaceous and semi-herbaceous Angiosperms, secured interesting evidence which indicates strongly that herbaceous Angiosperms have been derived from forms which possessed strongly developed secondary growth. In the life-history of many plants there occurs a transition from a tubular stele, in younger portions of the plant, to a ring of separate fibro-vascular bundles in subsequently formed parts of the stem. For example, the prostrate biennial or perennial stems of *Potentilla palustris*, Scop., as well as the seedling plant, possess an unbroken central cylinder, whereas the cylinder of the erect annual stem a short distance above the rhizome breaks down into a typically herbaceous ring of separate bundles. The herbaceous type of central cylinder has resulted, therefore, from the reduction in size of Dicotyledonous plants in later geological periods, coupled with the evolution of foliar rays whose dissecting effect has been progressively increased.

More recently Professor Groom (6) has published the results of an investigation upon the annual ring and medullary rays of *Quercus*. There are certain fundamental objections to the conclusion reached by Professor Groom, that 'it is impossible at the present to decide whether in *Quercus* the broad-rayed or the narrow-rayed type was primitive'.

In studying lines of evolutionary modification in plant structures it is essential not only that a careful study be made of the comparative anatomy

of normal mature plants, but in addition an intensive study is necessary of the development of structures during the life-history of individual plants. Such developmental studies should be made to cover numerous species selected from as many genera and families as possible. Furthermore, since ancestral characters are known to persist in the seedling, reproductive axis, leaf, and first-formed portion of vigorous mature shoots of plants which have suffered vegetative reduction, and to be recalled in traumatic regions of plants which have been similarly reduced, it is essential that these regions be examined with particular care. Finally, palaeobotanical material, when available, must be regarded as an invaluable check upon conclusions of phylogenetic significance reached from living material.

It is unfortunate that Professor Groom's conclusions are based upon rather narrow foundations. The material used by him consisted evidently almost exclusively of mature oak wood, a large part of which was composed of American species cut from a collection in the possession of this Laboratory. An extensive study of the development of ray structures in the life-history of different species of oak (such as was made by Eames in the case of certain vines and species of the Rosaceae, Ranunculaceae, and other families, and by the writer in the case of many species of the following genera of the Fagales, *Quercus*, *Pasania*, *Alnus*, *Betula*, *Corylus*, *Carpinus*, *Ostrya*, *Castanea*, *Castanopsis*, and *Fagus*) was not attempted by Professor Groom. Nor did he examine those regions of the plant which retain ancestral characters.

In view of these facts certain criticisms by Professor Groom of the results secured by Eames and the writer are of interest. Professor Groom states: 'From the point of view of the assumption that the seedling is a seat of phylogenetically early structure features, these facts lose their significance if it be shown that a similar "linking up" of small rays to form large ones takes place in older parts. I find that such a "linking up" does take place, at least in connexion with some of the rays of the inner rings of the twigs of *Quercus Robur*, L.'

It is necessary at this point to emphasize the important fact that the foliar ray has reached varying stages of aggregation and fusion in different species of the Fagales. In *Alnus japonica*, Sieb. et Zucc., *A. rhombifolia*, *A. maritima*, and many evergreen oaks the foliar ray is of the *aggregate type* composed of congeries of smaller rays more or less imperfectly fused. The first-formed wood of the seedling possesses solely uniseriate rays, and the development of foliar rays is a progression in the direction of compounding. In most oaks with a distinctly deciduous foliage and in certain somewhat ring-porous evergreen oaks from the western and south-western part of the United States, the foliar ray is of the *compound type*, composed largely of a nearly homogeneous mass of parenchyma. In the highest types of this group the fused or compound condition of the foliar ray occurs except

in primitive parts, e. g. the seedling. In passing from these regions to subsequently formed portions of the stem the development of the foliar ray tissue is a progression in the direction of compounding. The significant facts to be kept in mind are that in *Quercus* the first-formed wood of the seedling possesses solely uniseriate rays, the development of foliar rays is a progression in the direction of compounding, and more primitive stages of the 'linking-up' process occur in the young plant. The 'linking up' of small rays to form large ones in the first rings of the twigs of *Quercus Robur* does not invalidate seedling evidence, since in this species the solidifying of the foliar ray may not have worked back to the region of the pith in the early wood of the stem and branches.

An unfortunate difficulty has been introduced by Professor Groom: that the broad solid ray may be primitive in oak, since it apparently undergoes subdivision in many cases. In view of the progression in the direction of compounding which occurs in the development of ray structures in the life-history of oak, alder, and other genera of the Fagales it is difficult for the writer to concur in this turning of the *foliar compound ray* inside out. That the foliar ray is dissected into shallower sheets of ray tissue in passing horizontally from the young to the older portions of a thick stem is true for all species of the Fagales. This is as true for species in which foliar rays are of the aggregating type as for those higher types in which nearly homogeneous masses of fused ray tissue are related to the traces of the leaves. In 'exogenous' stems which are increasing rapidly in circumference a multiplication of elements, fibres, vessels, parenchyma, and rays must occur with added layers of growth. Therefore the dissection of foliar rays is essential to maintain the proper proportion of ray tissue in the older zones of the stem. However, the impulse which produces this dissection of foliar rays is fundamentally different from that which results in the evolution of storage tissue in relation to the traces of the leaves, and cannot be considered evidence for believing that the broad, solid type of ray is primitive in *Quercus*. Both phenomena are often active in the same foliar ray. For example, in *Alnus rhombifolia*, *Quercus virginiana*, Mill, or *Q. densiflora*, Hook. and Arn., foliar rays of the aggregate type are gradually 'built up' in passing from the vicinity of the leaf-trace to the mature portion of a wide stem, yet a dissection of this aggregating mass of tissue takes place in the older wood, resulting in the formation of 'lower' and *more numerous* sheets of compounding tissue.

In this connexion Professor Groom's conclusions in regard to '*Quercus* (*Pasania*) *fenestrata* (*Q. spicata*)' are of interest: 'In *Q. fenestrata* these characteristic high rays are often approximated in pairs, and between the two rays forming a pair the boundary of the annual ring is much nearer the centre of the stem than it is elsewhere (Pl. LXXXV, Fig. 12). Moreover, the space between the two rays forming a pair is devoid of vessels. These

three sets of facts denote that in some way the pair of high rays, together with the tissue between them, is equivalent to a single broad ray; and the very considerable inward dip of the annual ring between the two rays finds simplest explanation in the assumption that in the ancestor the complex mass represented solely ray tissue.' This conclusion is somewhat remarkable in view of the facts pointed out by the writer in a former paper, that the depressed segments of the oak stem are produced (see Pl. LXII, Fig. 3, and Pl. LXIII, Figs. 13 and 15) by the concentrated retarding effect upon growth of two closely approximated foliar rays. Since these rays are usually related to the traces of different nodes it is difficult to conceive of their origin from the dissection of a single large ray. The writer recently examined material of *Quercus spicata*, sent from India by courtesy of Mr. R. S. Pearson, Imperial Forest Economist, and is unable to agree with Professor Groom in stating that vessels are absent from the depressed segments included between approximated pairs of foliar rays. Professor Groom for some unexplained reason completely ignores the important relation of the leaf-trace to the formation of large rays, although he refers to the paper by the writer in which this evolutionary process was described.

Since conducting the investigations which have been summarized earlier in this paper a more comprehensive study has been made of Dicotyledonous plants. This investigation has included not only numerous species of the more primitive or supposedly primitive families, but also of the higher or supposedly more recent families. The material used comprised not only species from the temperate regions of North America, Europe, China, and Japan, but in addition representatives of a more tropical flora from India and Australasia. In connexion with instruction upon the anatomy of American woods material of practically all American trees and larger shrubs has been examined. This investigation has confirmed strongly the conclusions reached in regard to the origin, development, and dissecting effect of foliar rays, and has served to emphasize the important part that these structures have played in the evolution of modern Angiosperms. As might naturally be expected in viewing this evolutionary movement from a broader and clearer standpoint, certain obscure and imperfectly understood features have been clarified.

That the evolution of the foliar ray occurred in the early history of Angiosperms is seen from the fact that the most convincing evidence of the compounding process is confined largely to primitive Dicotyledons or to regions of phylogenetic significance, and from the fact that in the majority of woody Angiosperms this primitive type of foliar ray has been changed structurally or completely reduced. This conclusion is further emphasized by the occurrence of well-developed foliar rays in Angiosperms of the upper Cretaceous (11).

In the light of recent investigation the foliar rays appear to have

developed as aggregations of uniseriate rays about the persistent leaf-traces of evergreen plants of the warmer Mesozoic times. These sheets of storage tissue were subsequently extended increasingly greater distances from the leaf-traces, and gradually compacted by the coalescing and enlargement of the uniseriate rays and the parenchymatization of fibres included between them. Rays of this primitive type which occur side by side with uniseriate rays have persisted to the present time in certain of the more primitive Dicotyledonous families, e.g. Fagales, Casuarinaceae.

DIFFUSION OF THE FOLIAR RAY.

With changes of environment during later geological periods the primitive foliar ray was modified in the evolution of the majority of modern trees and shrubs. This change consisted in the diffusion of the constituent smaller rays of the aggregate sheet of foliar ray tissue. Evidence of this transition, as has been shown by Thompson (12), has persisted in certain Dicotyledons and is particularly well shown in the Casuarinaceae and Ericaceae. In certain species of *Casuarina*, e. g. *C. equisetifolia*, L., *C. glauca*, Sieber, &c., the typical primitive foliar ray of the aggregate type exists in the younger portion of the stem, but in passing to the older portion the individual rays of the aggregation are diffused throughout the wood. A similar condition exists in *Rhododendron punctatum*, Andr., *Ledum groenlandicum*, Retz., and *Kalmia angustifolia*, L. In somewhat higher types, *Fagus atropunicea*, Sud., and *Platanus occidentalis*, L., the foliar rays have been diffused throughout the wood and evidence of the former congeries has been lost. However, serial transverse and tangential sections show that the diffused parts of the former aggregate ray are related to the leaf-traces. It is to be emphasized in view of the conclusions drawn by Groom from Jost's (8) study of *Fagus sylvatica*, L., that the so-called broad, high rays of *Fagus* represent diffused and enlarged portions of former foliar aggregate rays. In the majority of higher Dicotyledonous trees and shrubs the process of diffusion is so complete that evidence of the former connexion between the multiseriate rays and traces of the leaves has disappeared entirely.

REDUCTION OF THE FOLIAR RAY.

In the wood of a large number of Dicotyledonous plants the foliar ray, either in its aggregate, compound, or diffused form, occurs with the primitive uniseriate ray. There are, however, numerous exceptions to this general rule. Thus the uniseriate ray is seen to disappear entirely from the wood of certain highly specialized Angiosperms (5). Furthermore, individual species of many families of Dicotyledons are characterized by possessing only uniseriate rays. In Pl. LXII, Fig. 1 is illustrated the tangential section of the mature wood of the common American Chestnut, *Castanea dentata*,

(Marsh) Borkh. It will be observed that the wood is characterized by the primitive type of ray structure. A similar condition is found to exist in other members of the Cupuliferae. Thus the mature wood of *Castanea pumila*, (L.) Mill, *Castanopsis hystrix*, A.DC., *C. Indica*, A.DC., *Alnus acuminata*, H.K.B., *A. mollis*, Fernald, *A. yasha*, Matsum, &c., possess characteristically only uniseriate rays. In view of the fact that the first-formed wood of primitive Dicotyledonous plants possesses only uniseriate rays and the foliar ray has been 'built up' from congeries of small rays, it might naturally be supposed that the plants under consideration possessed the primitive type of Dicotyledonous wood from which have been evolved the higher and more complex forms. However, before accepting this supposition as a correct one, a more detailed examination of their structure is necessary. The fallacy of inferring that less complex plants are of necessity more primitive has in recent years been clearly illustrated by the study of the comparative anatomy of living and fossil plants. The pines, which, owing to their complex structure, have been commonly considered the most recent of Coniferous plants, have been shown to be very old geologically, and the supposedly primitive Cupressineae are now known to be of comparatively recent origin, and to have been evolved from more complex ancestors. In other words, in the evolution of living plants may be traced the gradual reduction and disappearance, as well as the origin and development, of specialized tissues. Among Coniferous plants the reduction of resin canals and ray tracheides can be observed in the Abietae, Cupressineae, and Taxodineae, as well as the evolution of ray tracheides and wood parenchyma in the Pineae. Similarly, among Araucarian plants there exists the reduction of resin canals and Abietineous pitting. It is, therefore, to be expected that among living Dicotyledons reduced forms occur with less complex structures than those of more primitive forms from which they have been derived, and an examination of those regions which are known to retain ancestral characters is essential in determining their real phylogenetic position.

FIRST-FORMED WOOD OF VIGOROUS MATURE TWIGS.

In Fig. 4 is illustrated the cross-section of a vigorous mature shoot of *Alnus mollis*. It will be observed that in the first annual ring are numerous large rays of the foliar type. These rays gradually die out in the second and third annual layers of growth, and the wood of the older portion of the twig possesses only the uniseriate rays characteristic of the mature wood of the species. In the first annual ring of twigs of normal growth the large rays are absent and the wood resembles that of the mature stem. Since the phylogenetic importance of the first annual ring of vigorous branches of plants which have suffered vegetative reduction has been pointed out by Jeffrey (7) in the recapitulation of resin

canals in *Sequoia washingtoniana*, (Winsl.) Sud., it is to be inferred that the foliar ray has undergone a process of reduction in the alder under consideration. Furthermore, since similar conditions exist in other lower Dicotyledons which possess only uniseriate rays in the mature wood, the conclusion is reached that a considerable number of plants, although not in reality primitive, have reverted by the reduction of the foliar ray to a type of ray structure which characterized primitive Angiosperms.

VIGOROUS MATURE ROOTS.

Fig. 6 illustrates a cross-section of a vigorous mature root of *Castanea dentata*. Six more or less feebly developed large rays (x) radiate from the clusters of protoxylem. A similar condition is illustrated in Fig. 7, a cross-section of a vigorous root of *Alnus yasha*. In this root five much reduced aggregate rays (x) are seen to radiate from five clusters of protoxylem. In view of the phylogenetic importance of vigorous mature stems the persistence of large rays in vigorous mature roots is significant.

THE NODE.

In primitive plants which possess well-developed foliar rays these structures originate in the vicinity of the leaf-trace and gradually 'build up' and enlarge in passing from the earliest formed wood of the node to that of the more mature portions of the plant. Fig. 5 illustrates a cross-section of the node of *Alnus yasha*. The foliar ray, which is strongly developed near the leaf-trace and in the first annual layer of growth, gradually disappears in the older wood. This reduction rather than compounding of ray tissue, which occurs also in *Castanea*, *Castanopsis*, *Alnus mollis*, and *A. acuminata*, indicates, as do the vigorous ramifications, that the foliar ray was once well developed in these plants and has gradually disappeared except from regions which are known to retain primitive characters. The retention of the foliar ray at the node is to be expected, since ancestral characters have been shown by Scott, Jeffrey, and others to persist in the vicinity of the leaf. The nodes of vigorous mature stems are, therefore, particularly favourable regions for the recapitulation of primitive features, and retain indications of the existence of foliar rays after they have disappeared from the rest of the stem.

TRAUMATIC REGIONS.

Valuable evidence confirming the phylogenetic importance of the recapitulation of primitive characters in the regions just mentioned is afforded by a study of the traumatic reactions of the wood of these plants. It has been pointed out above that severe injuries, in wood which possesses well-developed foliar rays, produce a reversion to primitive stages of aggregation and fusion or to the uniseriate condition. From

this it might naturally be inferred that injuries to the wood of these reduced plants would recall the foliar type of ray. That such is indeed the case is shown by Fig. 8, a cross-section of the wood of *Alnus mollis*, cut in the immediate vicinity of a severe injury. The injury has obviously produced a large aggregate ray which may be clearly recognized by its retarding influence upon the growth of neighbouring elements and the distinct sag in the outline of the annual rings. A similar condition is illustrated in Fig. 9, a cross-section of the mature root of *Alnus mollis*. The wood at the lower side of the photomicrograph, which was formed before the injury occurred, possesses only uniseriate rays, but in the upper portion of the figure may be seen numerous aggregate rays which originate at the injury. Additional illustrations of the traumatic recurrence of large rays have been observed by the writer in *Castanea*, *Castanopsis*, and *Alnus*, as well as in woods which have replaced the compound or aggregate by the diffuse type of foliar ray. Fig. 10, a cross-section of the outer portion of an insect gall in a mature twig of *Ostrya virginiana*, (Mill) Koch., illustrates the recurrence of an aggregate ray in a type of wood that possesses normally only small bi- and triseriate and uniseriate rays.

CONTOUR OF MATURE TWIGS.

There remains for consideration a striking piece of evidence in regard to the reduction of the foliar ray in lower Dicotyledonous plants. A characteristic and important feature of the foliar ray is its retarding influence upon the growth of neighbouring radii of the stem (see Figs. 2 and 3). This influence is so strongly developed in many plants that the depression in the outline of the annual rings which marked the former position of the foliar ray persists for some time after the disappearance of the ray. The writer has shown (3) that the fluted stem of the Blue Beech, *Carpinus caroliniana*, Walt., is produced by congeries of aggregate rays whose concentrated retarding influence upon the growth of certain radii produces the large grooves in the stem. A careful study of this plant shows that the foliar rays of the aggregate type are gradually being replaced by the diffuse condition. (In the closely allied genus *Ostrya* the diffuse condition is dominant.) In specimens growing under unfavourable conditions the writer has found large stems from which the aggregate ray has disappeared almost completely. However, the characteristic flutes remained, although less strongly developed. These plants were later cut down, and during subsequent growth of the stump (by means of stool shoots) congeries of aggregate rays were recalled in the depressed segments of the new layers of growth. The stimulation of the injury and surplus supply of food substances in the root produced evidently a reversion to conditions which existed before the plant suffered vegetative reduction. In Pl. LXIII, Fig. 17, a cross-section of a vigorous mature shoot of *Castanea pumila*,

may be seen five depressed segments. In this twig the foliar ray has disappeared except from the immediate vicinity of the leaf-traces. The normal twig possesses a circular outline, and the foliar ray is not conspicuously developed at the node. This recurrence of depressed segments in vigorous shoots of *Castanea* indicates that five pairs of approximated lateral leaf-trace rays existed formerly in the mature twigs of these plants, and have disappeared except from the nodes of very vigorous stems. In *Castanopsis* indications of depressed segments which were once a well-developed feature of the plant persist in the normal mature twigs. A cross-section of the node of *Castanopsis hystrix* is illustrated in Pl. LXIII, Fig. 16. Two segments (y) are more strongly depressed upon the upper side of the photomicrograph, due to the fact that the rays related to the lateral leaf-traces are persistent at the node. Owing to the phyllotaxy of the plant the three remaining segments (x) are less strongly depressed. Fig. 14 shows a cross-section of the mature stem of *Castanopsis indica*. In this species the five depressed segments are more persistent between the nodes, and indicate that the reduction of the foliar ray is less complete in this plant than in the preceding species. In Fig. 13 may be seen the cross-section of a mature twig of *Castanopsis tribuloides*, a plant whose structure resembles that of *Quercus*, since the lateral leaf-trace rays are strongly developed in the wood of small twigs. A careful study of the life-history of the plant reveals the fact that the aggregated rays are disappearing in many portions of the root and stem. In Pl. LXII, Figs. 11 and 12 are illustrated the remains of aggregate rays which were once strongly developed by the cambium to maintain the proper proportion of ray tissue in the widening stem and root. These facts, considered in connexion with evidence afforded by the recapitulation of primitive characters which occur in vigorous mature ramifications, nodes, and traumatic regions, point conclusively to the reduction of foliar rays in certain Fagales, and indicate that *Castanopsis* and *Castanea* are reduced members of the oak family, just as *Alnus mollis*, *A. acuminata*, and *A. yasha* must be considered reduced species of the genus *Alnus*.

The uniseriate rayed species of the Salicales (9) and Sapindales (10) have been studied by Miss Holden, and have been found to represent a reduced condition where complex ray structures have been lost in a reversion to the primitive uniseriate type, but among the higher families of Dicotyledonous plants the uniseriate condition has resulted largely from the reduction of foliar rays of the diffused type rather than of the aggregate or compound types.

SUMMARY AND CONCLUSIONS.

1. The central cylinder of primitive Angiosperms was a tubular cylinder or siphonostele which possessed strongly developed secondary growth.

2. The wood of the most primitive Angiosperms possessed only uniseriate or linear rays, such as are a well-developed feature of the wood of Conifers and other Gymnosperms.

3. During the warmer times of the Mesozoic sheets of storage tissue were 'built up' from congeries of uniseriate rays, about the persistent leaf-traces of evergreen Angiosperms, and were subsequently extended vertically and horizontally considerable distances from the node.

4. This primitive type of foliar ray tissue has persisted, in more or less unaltered form, in certain species of primitive families of the Dicotyledons, e. g. Casuarinaceae, Fagales, &c.

5. With changes of environment in later geological periods storage conditions were fundamentally modified in the wood of Dicotyledons.

6. In the evolution of the majority of living Dicotyledonous trees and shrubs the individual units (varying greatly in size owing to the enlargement and fusion of the original uniseriate rays which formed the incipient aggregation) of the aggregating mass of foliar ray tissue have been diffused more or less uniformly throughout the stem, and evidence of their former relation to the traces of the leaves has disappeared, except from certain primitive forms, e. g. Casuarinaceae, Ericaceae, Fagales, and Platanaceae.

7. In a comparatively limited number of forms the primitive foliar ray of the *aggregate type* has been progressively compounded or solidified, and has resulted in the formation of foliar rays of the *compound type* composed of homogeneous masses of parenchyma, e. g. oaks with deciduous foliage, *Casuarina Fraseriana*, Miq., *Alnus rhombifolia*, &c.

8. In many families of Dicotyledons species exist in which a reversion to the primitive uniseriate condition has occurred as a condition of reduction from foliar rays.

9. Evidence of the reduction of the foliar ray in the Fagales consists of a more or less complete series of progressively reduced species, and of the persistence or recurrence of foliar rays in regions of phylogenetic significance in forms which are very completely reduced.

10. The importance of experimental plant morphology in the study of phylogeny is clearly illustrated by the Fagales. In its later history the family has suffered vegetative reduction. At the same time storage conditions have been fundamentally changed in the family, resulting in modification of the sheets of aggregated ray tissue which originated about the

persistent leaf-traces of more luxuriant ancestors. In modern species the foliar ray of the primitive aggregate type has been or is in the process of being *reduced*, *diffused*, or *compounded*. Rapid accumulation of nutritive substances, such as occurs in mature twigs of unusual vigour or in regions where traumatic stimulation exists, tends to produce a reversion to ancestral structure. Thus in reduced forms the foliar ray is relegated to the first annual rings of vigorous mature roots and shoots. Similarly, in species which have suffered reduction or diffusion, the foliar aggregate ray may be recalled traumatically. Furthermore, species which possess foliar rays of the aggregate or compound type under the stimulus of a slight injury accelerate the 'building-up' process. However, diametrically different results are secured by slow or impaired nutrition. Under conditions of this sort the reduced or diffused condition is hastened by the arrested development of the primitive foliar ray. This is clearly shown in specimens of the Blue Beech which have been grown under unfavourable conditions, and by the fact that the common *Alnus incana* in the northern and colder part of its range has suffered more complete reduction of the foliar aggregate ray than in the warmer southern part. Arrested development due to impaired nutrition occurs also in plants which possess foliar rays that are of the compound or nearly compound type. Thus *severe* injuries in the oak produce a reversion to primitive stages of aggregation and fusion or to the uniseriate condition.

11. *Castanea* and *Castanopsis* are reduced members of the oak family, just as *Alnus mollis*, *A. acuminata*, and *A. yasha* must be considered reduced species of the genus *Alnus*.

12. Owing to the important part that the foliar ray has played in the structural development of Dicotyledons, the study of its evolution and reduction yields evidence significant in a natural classification of Angiosperms.

13. A more detailed consideration of the comparative anatomy and phylogeny of Dicotyledonous plants indicates conclusively that the existing conceptions of the origin and development of the woody cylinder of Angiosperms must be fundamentally modified to agree with actual conditions which exist among the higher seed plants.

In conclusion, the writer wishes to express to Major Gage, I.M.S., Superintendent of the Royal Botanic Gardens at Calcutta, to Mr. G. H. Cave of the Lloyd Botanic Garden at Darjeeling, and to Mr. R. S. Pearson, Imperial Forest Economist at Dehra Dun, his keen appreciation of their courtesy in sending valuable material of Indian plants. To Dr. Jeffrey the writer is much indebted for material and kind assistance in the course of the investigation, and to Mr. James Austin for assistance in photomicrography.

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EXPLANATION OF PLATES LXII AND LXIII.

Illustrating Mr. Bailey's paper on the Foliar Ray.

PLATE LXII.

Fig. 1. *Castanea dentata*. Tangential section of the mature wood, showing the uniseriate rays. $\times 60$.

Fig. 2. *Casuarina*, sp. Transverse section of the mature stem, showing the depression in the outline of the xylem produced by an aggregate ray. $\times 20$.

Fig. 3. *Castanopsis tribuloides*. Transverse section of the mature stem, showing a small segment of wood which is depressed by two closely approximated foliar rays. $\times 20$.

Fig. 4. *Alnus mollis*. Transverse section of a mature vigorous twig, showing numerous rays of the aggregate type in the first and second annual layers of growth. $\times 20$.

Fig. 5. *Alnus yasha*. Transverse section of the node of a mature twig, showing a well-developed aggregate ray in the vicinity of the leaf-trace. The ray is seen to die out in the third annual ring. $\times 20$.

Fig. 6. *Castanea dentata*. Transverse section of a vigorous mature root, showing the retention of aggregate rays. $\times 20$.

Fig. 7. *Alnus yasha*. Transverse section of a vigorous mature root, showing the retention of aggregate rays. $\times 20$.

Fig. 8. *Alnus mollis*. Transverse section of the mature stem in the vicinity of a severe injury, showing a large aggregate ray which has been recalled traumatically. $\times 40$.

Fig. 9. *Alnus mollis*. Transverse section of the mature root, showing aggregate rays recalled by a severe injury. $\times 20$.

Fig. 10. *Ostrya virginiana*. Transverse section of an insect gall in a mature twig, showing the traumatic recurrence of an aggregate ray. The ray produces a sag in the outline of the xylem and is capped in the phloem by a dark-coloured cluster of sclerenchyma. $\times 100$.

Fig. 11. *Castanopsis tribuloides*. Transverse section of the mature wood of the stem, showing the remains of a once strongly developed aggregate ray. $\times 60$.

Fig. 12. *Castanopsis tribuloides*. Transverse section of the mature root, showing evidence of the reduction of aggregate rays in the root. $\times 60$.

PLATE LXIII.

Fig. 13. *Castanopsis tribuloides*. Transverse section of a mature twig, showing the strongly depressed segments produced by well-developed approximated foliar rays. $\times 10$.

Fig. 14. *Castanopsis indica*. Transverse section of a mature stem, showing the persistence of five well-developed depressed segments. $\times 10$.

Fig. 15. *Quercus velutina*. Transverse section of a mature twig, showing five small depressed segments which are produced by five pairs of closely approximated lateral leaf-trace rays. $\times 20$.

Fig. 16. *Castanopsis hystrix*. Transverse section near the node of the mature twig, showing the persistence of two strongly depressed segments (y) which are related to the lateral leaf-traces of this node. Indications of the three other depressed segments (x) are more or less feebly developed. $\times 10$.

Fig. 17. *Castanea pumila*. Transverse section of a vigorous mature twig, showing the retention of five depressed segments after the disappearance of the foliar rays. $\times 10$.

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x.

x.

x.

x.

x.

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17.

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