On the Origin of the Herbaceous Type in the Angiosperms.¹

BY

ARTHUR J. EAMES, A.M.

Austin Teaching Fellow in Botany in Harvard University.

With Plate XIV.

IN those dicotyledonous stems where increase in thickness results in the formation of a solid woody cylinder, the latter has been considered to be the result of the fusion of a ring of separate fibro-vascular bundles by the extension of the fascicular cambium across the intervening tissue, and by the formation of xylem by this interfascicular cambium. Thus, apparently, the woody type of stem arises directly by the increased lignification and the enlargement of a stem which is, in its early structure, typically herbaceous. We may cite Sachs' 'Lehrbuch der Botanik', p. 131 (1874), and Gray's 'Structural Botany', p. 73 (1879), as illustrating this method of development. This widely accepted view is evidently not the correct one, however. On the contrary, the herbaceous stem seems to be the higher type, and its separate bundles appear to have been derived from the woody cylinder by reduction, and by the dissection of the latter into a group of individual strands. In proof of this there is much evidence, both direct and indirect.

Palaeontological evidence, in that no undoubted herbaceous fossil remains are known from the older periods, points to the modern development of this type. Further, the only surviving representatives of the arborescent Cryptogams which flourished in the Palaeozoic are herbaceous or semi-herbaceous in habit and structure. Their survival is probably due to an adjustment to modern conditions, this adjustment involving the loss of secondary growth, and the acquisition of a low or prostrate habit. *Isoetes* and *Lycopodium* may be compared with the ancient tree-like Lepidodendrids. As an herbaceous survivor of the arborescent Calamitean stock, *Equisetum* is another good illustration of the same principle. Secondary growth has practically disappeared and a stem structure simu-

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 39.

lating that of an herbaceous dicotyledon has been produced. Evidence has been brought forward¹ in proof that the bundles of this stem correspond to the primary structure of the Calamite stem. Such reduction appears highly significant.

Among the Cryptogams these changes seem to have produced more resistant plants—forms better fitted for the struggle, with new plant-groups and with new conditions. Likewise among the Angiosperms, the latest dominant vegetation, the herbs are the more adaptable and more efficient forms. Maturity is reached very early, with the least possible expenditure of material for vegetative structures; and, further, a larger amount of seed, in proportion to the size of the individual and the space it requires, is produced. Evolutionary progress can be rapid among such forms. Among herbaceous plants the annual would then be the type of highest development. It is significant that those members of the Dicotyledons now generally considered the lowest are largely trees and shrubs, and that most of the Compositae outside the tropics are herbaceous. The vast majority of the Monocotyledons are herbs. Proof that the anatomical structure of the stem of the herbaceous Dicotyledons is the highest type within that group will add further evidence to that which leads to the opinion that the Monocotyledons are the more recent group of the Angiosperms.

If, from the solid cylinder, the stem with a ring of separate bundles has been evolved by reduction and dissection, it may be asked what factor has caused the change, or given the impulse that brought about so great a transformation. The process is to be attributed to the leaf-trace and its influence. It has been accomplished by the local transformation of secondary xylem into parenchyma below and above the entering leaf-trace; by the elimination of segments of the protoxylem; by the loss of the interfascicular cambium; and, finally, in some Dicotyledons and in the Monocotyledons, by the disappearance of the fascicular cambium also. Along with the elaboration of interfascicular parenchyma by the transformation of secondary wood—essentially a development of huge rays—goes, *pari passu*, the gradual elimination of radial parenchyma within the xylem segments thus set off. The bundles of the Monocotyledons universally, and those of many herbaceous Dicotyledons, are thus entirely destitute of rays. This loss of rays is very gradual, and in some instances, at any rate, takes place by the transformation of the ray cells into a vertical parenchyma system, the elements gradually changing shape, so that the long axis, at first horizontal, ultimately becomes vertical. As a final step, these ray-like series break up into aggregate, or solitary, rows of wood-parenchyma cells, the ray form thus disappearing.

The investigations made by the writer on these points have so far been

¹ Eames, A. J.: On the Occurrence of Centripetal Xylem in *Equisetum*. Ann. Bot., vol. xxiii, 1909.

confined chiefly to the Rosaceae, with the examination of several vines, some members of the Ranunculaceae, and a few plants from other families.

A general ability to transform xylem into parenchyma exists in a number of families among the Dicotyledons. It has been shown¹ that the formation of the large rays in *Quercus* is due largely to such a change. Further, Mr. I. W. Bailey, in a paper contemporaneous with this, shows that the *leaf-trace* gives the impetus, by the influence of which woody plants form these additional masses of amyliiferous parenchyma, and acquire thus the advantage of greatly increased storage capacity. This influence extends always for a considerable distance below, and also to a less extent above, the exit of the trace. The initial stage of parenchymatization is often the cutting out from the xylem cylinder opposite the trace of a segment which may ultimately be transformed more or less completely into parenchyma. In the woody Rosaceae similar conditions exist; whereas, in herbaceous representatives of the family, parenchymatization occurs in the same regions and in much the same way, but is carried much further.

Some of the woody members show conditions similar to those described by Bailey in the Cupuliferae. Species of *Rubus*, especially of the subgenera *Idaeobatus* and *Cylactis*, possess more abundant rays with some compounding in the regions below the leaf-traces, and *Rubus spectabilis* shows compounding well developed. *Potentilla palustris*, in its prostrate or procumbent stem, presents very suggestive conditions. In the segment of the xylem directly below the exit of each leaf-trace there is a decided lack of vessels and an agglomeration of rays (Fig. 1). Moreover, at these regions the annual ring dips inward strongly, as is always the case in the formation of radial parenchyma in mass in connexion with compounding and compounded rays. Further, this leaf-trace influence, so strikingly manifested in the corresponding inward dip of the annual ring, extends always down *through one*, and often through *several* of the *internodes*. Above the leaf-gap there is disturbance for only a very short distance. Conditions in the upright stem of this species will be discussed below.

In the species described above we are dealing with forms in which the woody cylinder is as yet fairly strong. Some of the herbaceous perennials of the Rosaceae hold perhaps the greatest interest in connexion with this problem—for example, certain species of *Potentilla*, the genera *Geum*, *Agrimonia*, *Sanguisorba*, and others. Among these plants we find two kinds of stems: a stout, subterranean, or creeping perennial stem, with large storage capacity; and more slender, erect, aerial, annual stems, arising from the perennial portion usually as lateral branches. The perennial stem is, in most cases, of the woody type, with certain modifications due to adaptations as a storage organ, whereas the erect annual stem is more or less completely of herbaceous texture. These two kinds of stems are of very

¹ Eames, A. J.: On the Origin of the Broad Ray in *Quercus*. Bot. Gazette, vol. xlix, 1910.

different anatomical structure, and serve to show transitional stages between the two extreme types.

Sanguisorba canadensis, L., illustrates several points very well. The woody cylinder of the rootstock consists of a series of bundles, very unequal in size, and somewhat irregular in shape, all connected by a strongly marked interfascicular cambium. Many of these bundles, however, are much modified; their cambium has ceased to form xylem at various stages and with much irregularity, and has laid down parenchyma thereafter instead. Fig. 2 illustrates this condition. In some of them, after the formation of primary wood is completed, parenchyma replaces the secondary xylem entirely, or with the exception of a very few scattered vessels or fibres. In the aerial stem the bundles are reduced in size, and the stem resembles the herbaceous type more closely. At the base the connecting interfascicular cambium is clear; in higher parts of the stem it gradually dies out. Fig. 3 shows a stage where only slight evidences of its activities are found; and in the upper portions of the aerial axis there is no trace of cambial activity between the bundles. (The plants studied were of mature growth.)

The genus *Geum* shows, in the few species examined, an interesting series in the aerial stems from forms with solid, though thin, woody cylinders to those possessing an herbaceous type of organization. The rhizomes of all species of *Geum* are similar to the underground stem of *Sanguisorba*. *G. virginianum*, L., the most woody of the species studied, has, throughout the most of its upright stem, a cylinder that is unbroken, save, of course, by brief leaf-gaps; but at the top there is a partial separation of the woody cylinder into fascicular segments. The upper portions of the stem of *G. canadense*, Jacq., have small, widely separated bundles, quite typically herbaceous, although the rest of the stem is structurally like that of *G. virginianum*. *G. triflorum*, Pursh, and *G. rivale*, L., have the aerial stem, with the exception of a very short piece at the base, dissected into separate bundles. This condition will be further discussed below.

The chief interest in the genus *Agrimonia* lies in the ray development. The structure of the central cylinder of the rhizome and aerial stem of the three species which were examined, *A. striata*, Michx., *A. gryposepala*, Wallr., and *A. mollis*, Britton, is not very different from that of *Geum virginianum*. The rays of the rootstock consist of ray cells, typical in size, shape, and position. Conditions in the aerial stem are very different however. A cross-section of such a stem of *A. striata* shows numerous, well-marked uniseriate rays. But in the tangential section no rays seem to exist. That which resembles ray tissue in transverse section appears in this section as wood parenchyma. Rows of parenchyma cells, narrow and much elongated vertically, extend for long distances in the stem—through one internode at least. The radial section shows, however, that these long rows

of cells are arranged in radial sheets like normal ray cells. In the genera and species mentioned above various stages intermediate between the typical ray cell and the condition found in *A. striata* occur; the change of position of the long axis from horizontal to vertical is very gradual, the cells apparently becoming square as a first step.

In the genus *Potentilla* we have a considerable range from the shrubby *P. fruticosa*, L., to the annual or biennial *P. monspeliensis*, L. But the reduction of the central cylinder has not been extreme; in the aerial stems of these plants separate bundles occur, so far as the investigations of the writer have gone (in fifteen species), only in the stolons of *P. Anserina*, and in the erect stems of *P. palustris*. However, the rootstocks of several species—for example, *P. monspeliensis*, L., *P. pumila*, Poir., *P. intermedia*, L., and *P. pennsylvanica*, L.—especially show a dissection of the central cylinder into alternating segments of xylem and parenchyma. These parenchymatous segments, however, are not entirely transformed, for each has a small group of xylem elements on its medullary border. This type of structure is somewhat similar to that of the rhizomes of *Sanguisorba* and *Geum*, mentioned above. The explanation of such a condition is best obtained from the seedling. Serial sections of the seedling stem show the small centrad groups of xylem which subtend the large segments of parenchyma to be leaf-traces. As in *Quercus*, a segment of the central cylinder is set off for some distance below the passing out of a leaf-trace by the formation of large rays resulting from xylem parenchymatization. A progressive change of the xylem of this segment into parenchyma occurs upwardly towards the point of exit of the trace; more and more of the secondary xylem becoming transformed until only the primary tissue is left. This now subtends pure parenchyma, through which it passes out as the leaf-trace. In the older plant with its crowded leaves these segments, which are somewhat longitudinally extended, overlap, giving the appearance shown in Fig. 5. That these parenchymatous segments in reality represent xylem-transformations is clear, not only because all stages of development can be followed, but because scattered groups of lignified elements and solitary vessels or tracheides often appear in them. All that is necessary to produce a typical herbaceous stem from this structure is to reduce the size of the normally lignified xylem segments; many semi-herbaceous forms have such a reduced xylem system. In a stem with a thin xylem ring, the setting off of the leaf-traces alone is sufficient to form the discrete bundle system of the herbaceous type.

That such is definitely the case sometimes is exemplified by two cases among the plants examined. For a short distance above the base the erect, fertile branches of *Potentilla palustris* and *Geum rivale* have a continuous woody cylinder. This becomes broken up into bundles very quickly—within a centimetre or less from the rhizome. Serial sections

through this region show that the dissection is due to the cutting out of the leaf-traces which are set off one, two, or three internodes below their exit; and that the traces of the lowermost leaf are first set off, then those of the others in succession. Fig. 4 shows this process at the base of the upright stem of *G. rivale*. That is, the bundles of the herbaceous stem thus formed represent leaf-traces and segments of the original cylinder, the common bundles of the stem. The short distance within which these traces first appear separately and the large number connected with each leaf complicate the interpretation of conditions here considerably. It is to be noted that some of the traces extend as such through two or three internodes. The condition here, especially in *Potentilla*, seems significant. The prostrate biennial or perennial stem has an unbroken central cylinder, a small, but thoroughly typical woody stem, and the same condition is found in the seedling. The central cylinder of the erect, annual stem, very soon after its derivation from the solid cylinder of the rhizome, breaks up to form the type of stem characteristic of annual plants.

Some members of another group of plants, the vines, deserve attention at this time, because they have been used as examples to show the supposed development of the solid woody cylinder by the fusion of originally separate and distinct bundles. In such forms as *Clematis* we find several large bundles separated by broad rays, but lacking within the bundles themselves all rays, even the uniseriate or primary rays. It is probable that this structure is one of adaptation to the habit of the plant. By the enlargement of the interfascicular rays sufficient ray parenchyma may have been acquired, causing the rest to disappear. In support of this view may be cited the case of *Vitis*. The mature wood of *Vitis* possesses ordinarily only large or secondary rays—for example, the species *V. vinifera*, L., *V. labrusca*, L., and *V. aestivalis*, Michx. The seedlings of the first two species, however, show distinct uniseriate rays rather abundantly in the substance of the bundle. Further, similar uniseriate or primary rays occur in the mature wood of *V. californica*. This appears to be clear evidence bearing on the suppression of these small rays. This condition in the fibro-vascular segments of *Vitis*, and probably also of *Clematis*, moreover, is homologous with that demonstrated above in the higher herbs, where the bundles have lost all internal rays, and the interfascicular parenchyma is very greatly developed.

We have thus considerable evidence pointing to the derivation of the herb from the woody plant. A solid tubular cylinder has been shown by Jeffrey,¹ from investigations made upon the Ranunculaceae, Nymphaeaceae, and Saxifragaceae, to be the primitive condition of the stele in the Angiosperms. Similar conditions have been disclosed by the study of the seed-

¹ Jeffrey, E. C. : The Morphology of the Central Cylinder in the Angiosperms. Trans. Canad. Inst., vol. vi, 1899.

ling in *Potentilla*, *Fragaria*, *Agrimonia*, and other Rosaceous genera. Inasmuch as these forms, especially those studied by Dr. Jeffrey, are herbaceous, the dissected cylinder seems to be clearly indicated as a recent modification. What, then, has given rise to the story of the fusion of the bundles into a ring, universal in our textbooks, and so commonly taught? A few forms only have been examined because these seemed to show well the desired relations; and it is true, indeed, that the illustrations chosen, viz. *Clematis*, *Aristolochia*, and *Quercus*, seem to vouch for the conventional view of the derivation of woody plants from herbs. Often diagrams are inserted in textbooks without specification of the plant used. *Clematis* and *Aristolochia*, which are apparently the usual basis of such diagrams, are vines—plants with a structure peculiar to themselves. They can hardly be considered types illustrating the growth of the xylem mass in woody Angiosperms in general.

In *Quercus*, another commonly used type, on the other hand, the writer could find no distinct bundle structure, as some diagrams would indicate. The protoxylem is not confined, as is usually stated, to a few projections of the xylem into the pith, but is distributed in many small groups, which appear nearly or quite simultaneously close together along the edge of the pith. The latter is strongly angled, and at some points along its edge slightly greater primary growth may occur, representing leaf-traces in the stem. Mr. Bailey's paper, which will appear with this, explains clearly the structural conditions in this genus which have led to its use to illustrate bundle-fusion. It is to be remembered that here we have a row of protoxylem groups, small, but close together, encircling the pith. External to these groups arises a continuous cambium ring, which forms xylem and medullary rays, the latter continuous with the pith between the protoxylem groups. Other rays not reaching the pith appear, of course, later in the wood.

In *Aristolochia*, the plant probably most used to illustrate bundle fusion, an examination of the very young stem showed that protoxylem groups arise at very nearly or quite the same time at a number of definite points (about twelve) where later the bundles form. A cambium ring arises outside these as in *Quercus*, forming first opposite the protoxylem, and then extending across the interfascicular tissue. This rapidly forms xylem in the bundles, and lengthens radially the wide medullary rays. It lays down, however, no new intermediate bundles. Those already formed become wider as the stem increases in size, and compress the rays somewhat. New large rays appear in the original bundles, dividing them externally. In comparison with *Quercus* we find the chief differences to be a restriction of the protoxylem to definite points, and the consequent formation of fewer, but very much larger medullary rays, that is, rays reaching to the pith. Moreover, this stem is marked

by the complete absence of primary wood rays in the fibro-vascular segments.

In *Clematis* the stem shows a definite number of bundles in the internode—twelve in *C. virginiana*, L., the species studied—alternately large and small. These lesser intermediate bundles are examples of those which are said by various writers to be laid down by the interfascicular cambium, and serve to fill the gaps between the original bundles, completing the solid cylinder. Lignification, indeed, appears first in the six large bundles (which are 'common' bundles), forming protoxylem. In the six smaller bundles the protoxylem is perhaps not formed within the internode proper, though in the node itself, and for a short distance above, it is well developed. Such a condition may be responsible for the view that the so-called 'interfascicular bundles' in general lack protoxylem. The cambial ring develops as before, appearing first in the bundles, and apparently only very slightly, if at all, sooner in the large than in the small ones, which can be seen outlined in the rapidly differentiating tissue. The interfascicular cambium is then formed, and increase in thickness proceeds as usual. No new bundles are formed, and only large rays occur. In comparison with *Aristolochia* we find the important differences to be an almost complete localization of the protoxylem in those large bundles from which the leaf-traces arise to pass out at the node directly above.

These three plants, so commonly chosen to illustrate the fusion of bundles in the formation of a woody cylinder, present a good series for the demonstration of the opposite view. The arrangement of the protoxylem in the stem of *Quercus* is very similar to that in the Gymnosperms, the larger leaf-traces, and ray changes influenced by them, causing the characteristic differences. The formation of large, originally compound, rays, setting off segments of the central cylinder, has been noted above as the cause of the misunderstanding of the course of development in this genus. In *Aristolochia* and *Clematis* we find the protoxylem more and more localized; but, as stated above, these two plants belong to a class generally admitted to be highly specialized. There seems to be evidence, in the unquestionable suppression of the small rays, of a considerable evolutionary advance in the vines. Of the two genera at present under discussion the writer has been unable as yet to examine seedlings for ray development and location of protoxylem. The evolution of vines seems to have been along a line somewhat similar to that followed by the herbs. Use has been made by both of localization of protoxylem and of ray-parenchyma. The herb has also extended the transformation of xylem into parenchyma, and so has widened its interfascicular rays and reduced the size of its bundles. These changes remove the necessity for intra-fascicular wood rays, and they disappear gradually, becoming completely

obsolete only in small bundles. The reduction in size of the herbaceous stem, together with its slight development of xylem and lack of necessity for storage parenchyma, removes the demand for cambial activity. The cambium then disappears, first, naturally, in those regions where it gives rise to tissue no longer typically fibro-vascular. Its complete disappearance finally occurs when the bundles themselves have become much reduced.

SUMMARY.

The prevailing view concerning the origin of the solid woody cylinder of the Angiosperms is, that its formation results from the fusion of a group of originally separate bundles; that this is accomplished by the extension of the cambium arising within those bundles across the interfascicular tissue, thus completing a cambium ring which subsequently develops the continuous cylinder. Instead of this, however, a reverse process seems to have occurred. A primitively solid cylinder has been reduced and dissected to form the type characteristic of dicotyledonous herbs—a ring of small, separate bundles. In favour of this view there is much evidence, both direct and indirect. The anatomical structure of fossil forms and parallelism in development in cryptogamic groups still living points in this direction. Direct development proof is supplied by some of the more herbaceous members of the Rosaceae, particularly the herbaceous perennials.

Further, there has apparently been a complete misunderstanding of the structure of some of the plants chosen to illustrate in textbooks the evolutionary development of the stem, as, for example, the case of *Quercus*. Diagrams of other plants of somewhat similar structure do not always indicate the particular plant they represent, and err perhaps too much on the diagrammatic side. Two genera very commonly illustrated in this connexion, *Aristolochia* and *Clematis*, seem at first glance to offer evidence in support of the older theory. But consideration of them as members of a class that is presumably highly developed, the vines, comparison with each other and with other chosen illustrative plants, together with a careful developmental and anatomical study, shows that whatever light is to be obtained from them in these matters aids in the formation of the opinion that the fascicular type of central cylinder has been derived from the unbroken woody cylinder of the lower Dicotyledons.

Herbaceous plants, especially annuals, are clearly very efficient forms. They have probably arisen as an adaptation to modern conditions, and their adaptability, together with rapid and greatly increased reproduction, has much facilitated their evolutionary progress.

The impetus for so great a change seems, in large part at least, to have been given by the leaf-trace. This has been effected by the transformation of small or large masses of secondary xylem into storage parenchyma in those segments of the woody cylinder directly related to the leaf-trace.

The first step in this process has been the formation of compound rays in connexion with the trace. In the next stage whole segments of the central cylinder in relation to the leaf-trace become transformed entirely into parenchyma with the exception of the primary wood (which is the trace in the stem). Thus there is obtained a stem with alternating segments of typical xylem and parenchyma, the latter with tiny groups of typical xylem elements on their centrad sides, or, in other terms, alternating large and very small bundles, the latter being leaf-traces. The leaf-trace segments, before their transformation, were first delimited laterally by transformation of xylem in narrow radial bands. This, in stems with thin xylem rings, is in itself sufficient to produce the herbaceous structure. When a cylinder is thus split up, the cambium ring remains unbroken for some time, the interfascicular portions actively forming parenchyma. As the plant becomes more and more herbaceous these segments of the cambial layer become less active and finally disappear. Later, the fascicular cambium, too, is suppressed, and the highest type of bundle, very small and without secondary growth, is formed. Along with this great increase of interfascicular parenchyma goes a gradual disappearance of rays from the diminishing bundles, so that the highest type lacks rays completely. Most of these points are exemplified by certain herbaceous perennials belonging to the Rosaceae; their two kinds of stems, subterranean and perennial, aerial and annual, have proved favourable for such demonstrations.

The writer desires to express his thanks to Mr. I. W. Bailey for opportunity to observe and compare ray development in many woody plants, and to Dr. E. C. Jeffrey for material and for suggestions and advice during the investigation.

DESCRIPTION OF PLATE XIV.

Illustrating Mr. Eames's paper on the Herbaceous Type in Angiosperms.

(It is suggested that a hand lens be used in the examination of these figures.)

Fig. 1. *Potentilla palustris*. Portion of cross-section of prostrate perennial stem, showing segment below exit of leaf-trace. $\times 40$.

Fig. 2. *Sanguisorba canadensis*. Portion of cross-section of rootstock, showing two bundles connected by interfascicular cambium, that on the right consisting in large part of parenchyma. $\times 50$.

Fig. 3. *Sanguisorba canadensis*. Portion of cross-section of mature aerial stem, showing portions of two bundles, with slight evidence of interfascicular cambial activity. $\times 100$.

Fig. 4. *Geum rivale*. Cross-section of base of fertile aerial stem, showing dissection of a thin central cylinder by leaf-traces. $\times 15$.

Fig. 5. *Potentilla pennsylvanica*. Cross-section of rootstock, showing alternating segments of xylem and parenchyma. $\times 12$.

Fig. 6. *Potentilla pennsylvanica*. Portion of cross-section of rootstock, showing alternating segments of xylem and parenchyma, the latter with leaf-traces either passing out, or upon their medullary border. $\times 25$.

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Huth coll.

Eames, Arthur J. 1911. "On the origin of the herbaceous type in the angiosperms." *Annals of botany* 25, 215–224.

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