Transitional Herbaceous Dicotyledons.[1]

BY

EDWARD CHARLES JEFFREY,

Harvard University,

AND

RAY ETHAN TORREY,

Massachusetts Agricultural College.

With Plates XI–XIII and five Figures in the Text.

A NUMBER of years ago, in one of the contributions issuing from this laboratory, Eames (1) described the origin of the herbaceous type in the Dicotyledons with special reference to the Rosaceae. The conclusions reached by this author vouched for the appearance of the herbaceous condition as the result of the formation of large storage rays in relation to the entering foliar traces. The evidence presented clearly indicates the derivation of these large foliar storage rays from the union of what were originally aggregations of more or less modified ordinary rays in proximity to the leaf-strands. In the midst of these aggregations of rays the vessels become transformed first to fibres and later, together with other originally elongated elements, into parenchyma. The parenchyma originating from the transverse septation of longitudinal prosenchyma becomes more and more assimilated with the radial parenchyma in its dimensions, and in extreme cases is scarcely distinguishable from it. It is clear, if the method of origin of foliar ray described by Eames for herbaceous representatives of the Rosaceae is correct, that herbaceous forms are derived from woody or arboreal ancestors. More recently, two authors working in collaboration (2) have expressed the opinion that ‘ Although this hypothesis accounts for many of the facts in the Rosaceae, it meets with difficulty when applied to other families and is open to criticism on several counts ’.

The criticisms of the views put forward by Eames, which the authors describe as ‘ originating with Professor Jeffrey ’, are, in the words of their authors, as follows : ‘ In the first place, the transitional stages from a woody to an herbaceous condition, which it cites, and which form, indeed, the

[1] Contribution from the Laboratories of Plant Morphology of Harvard University.

[Annals of Botany, Vol. XXXV. No. CXXXVIII. April, 1921.]

strongest evidence in its support, are found *not in the aerial parts of the stem but in the underground portions.*' Further, ' The fact that intermediate stages in harmony with the theory we are criticizing *are so rare in aerial stems as to be regarded as one of its weak points* '. In a following paragraph the authors under review state, 'The fact, however, which militates most strongly against the validity of the hypothesis under discussion is that, in practically all many-bundled herbaceous stems, the interfascicular parenchyma is not subtended by tiny leaf-trace bundles, nor is the stem composed of presumably typical alternating large and small bundles, the latter being leaf-traces.'

It will be shown in the sequel that Messrs. Bailey and Sinnott are apparently ignorant of fundamental facts in regard to the organization of the aerial stem in herbs. Further, they fail to distinguish the modifications in the general topography of the axis resulting from the different degrees of advance towards the herbaceous condition, thus showing a singular lack of capacity for thinking in three dimensions. The erroneousness of their statements will, moreover, be demonstrated on the identical forms which they present as evidence for the truth of their views. In advance, this general criticism must be made of their illustrations and their deductions. They fail to realize that if there is such a thing as a leaf-ray, it would naturally occur in the nodal region of the stem, where the traces enter the axial organ. Their illustrations throughout show a surprising inability to grasp this rudimentary principle of anatomy.

Obviously a clear conception of the differences of anatomical organization between a woody and an herbaceous stem can best be obtained by comparing the nodal regions of nearly related trees and herbs. The authors under discussion have figured *Hibiscus* and *Abutilon* as examples of herbaceous types. It may quite reasonably be urged that neither of these genera, which are of tropical or sub-tropical distribution, can be regarded as typical herbs, particularly by our authors; for in the later pages of their article they have elaborated at great length the hypothesis (which however did not originate with them) of the temperate distribution of characteristic herbs. Since both *Abutilon* and *Hibiscus* are distinctly woody and tropical herbs, they obviously will supply the supreme test of the correctness of this hypothesis, emphasizing the development of foliar rays as a fundamental feature of distinction between trees and herbs.

Fig. 1, Pl. XI, shows the general organization of a year-old stem of the common Basswood (*Tilia* sp.), or Linden, as an example of the nodal conditions in an arboreal representative of the Malvales. On either side of the long axis of the pith is to be seen a depression in the inner contour of the woody cylinder, marking the situation of a foliar trace, which has just entered the axis at the node above. In Fig. 2 a part of Fig. 1 is shown under a higher degree of magnification. The foliar trace lying in its internal depression of the cylinder is obviously subtended externally by unmodified wood. The truth of this statement is confirmed by the inspection of Fig. 4, Pl. XI, which represents a tangential section through the foliar trace in its outward course through the wood. Above the trace lies a dark patch, the parenchyma of the leaf-gap, which is continuous internally with the medulla. The narrow pointed elements abutting on the lower border of the parenchymatous tissues of the leaf-gap are the tracheary elements of the foliar trace. Below the leaf-trace neither foliar ray nor any appreciable aggregation of the ordinary rays of the wood can be distinguished. It will be clear to the reader that nothing of the nature of a foliar ray is present in relation to the leaf-trace in the genus *Tilia*. Turning to the genus *Abutilon*, cited and figured by our authors in support of their view, we find in Fig. 5 a total transverse section of a year-old stem of *Abutilon* species. The plane of section is the same as in *Tilia*, namely, slightly below the node. The topography exhibited is, however, quite different, for here there are distinct parenchymatous interruptions in the continuity of the woody cylinder, three in number, corresponding to the three foliar traces entering the stem at the node. In Fig. 6, Pl. XI, one of these parenchymatous interruptions, or, as we prefer to call them, foliar rays, is shown under a higher degree of magnification. The organization of the structure in question obviously is entirely parenchymatous, and, contrary to the confident assertion of our critics, it is subtended internally by a small leaf-trace. Moreover, the node chosen for illustration belongs to the aerial stem, so that their contentions in every respect are proved erroneous on the basis of one of the genera chosen by them to illustrate the superior accuracy of their knowledge of the anatomy of Dicotyledonous herbs. Fig. 3, Pl. XI, illustrates the tangential aspect of the foliar ray in *Abutilon*. The leaf-trace is seen to be surrounded on all sides by copious parenchyma, constituting for the most part the substance of the foliar ray. A small portion of the parenchyma on the upper surface of the leaf-trace must, however, be conceded to the foliar gap. A very significant organization is presented by the lower region of the foliar ray. It will be observed that it passes gradually into the substance of the wood, and accompanying this transition is the progressive transformation of parenchymatous elements into fibres. This condition clearly indicates the fibrous origin of a considerable portion of the foliar ray. The rest of its substance must be regarded as composed of the fused normal rays of the wood. A very instructive comparison is that of Figs. 1 and 5, of Figs. 2 and 6, and of Figs. 3 and 4. In each case can be noted the relations of the leaf-trace to the organization of the cylinder in woody and herbaceous stems of close affinities. It probably will be quite clear to the reader that there is a distinct and interesting difference of organization between *Tilia* and *Abutilon*, which is most strikingly expressed in the development of specially large storage rays in the case of the latter, in relation to the entering traces of the leaves. Our critics' figure of *Abutilon* is of indifferent quality, but is clear enough to show that it does not represent conditions in the nodal regions of the stem, and as a consequence has no bearing whatever on this discussion.

Turning our attention to the genus *Hibiscus*, illustrated by their Fig. 8, Pl. XXXIX, it is clear that foliar rays are present even in their indistinct and technically inadequate figure. In view of that fact it is surprising that they should deny the existence of foliar rays in the genus *Hibiscus*. In our Fig. 9, Pl. XI, is shown a total view of a three-year-old stem of the genus under discussion. On the right can be distinctly seen a foliar ray related to a corresponding trace and extending through three annual rings. Fig. 10, Pl. XI, shows a part of the leaf-ray more highly magnified. It is distinctly a structure differentiated from the normal organization of the wood by crowding of the ordinary rays and by the absence of vessels. The leaf-ray of *Hibiscus* is in fact a typical aggregate ray consisting of crowded wood rays separated from one another by fibrous bands, which include no vascular elements. The fibres contained in the aggregate leaf-ray of the genus under discussion represent a more primitive condition than that found in *Abutilon*, since the ray is here still in the aggregate condition throughout and has not, as in the case of the latter genus, been largely transformed into the homogeneous compound type of foliar ray, by the septation of the separating fibrous bands of the aggregation of rays into storage parenchyma. It seems clear that neither *Abutilon* nor *Hibiscus* justifies the sweeping statement of our critics as to the absence of foliar rays in the aerial stems of herbs of Malvaceous affinities. It is rather surprising that our authors did not have recourse to such common types as the Hollyhock (*Althaea*) and the various Mallows to support their assertions. An examination of these forms reveals a complete agreement with the data illustrated in our figures of *Abutilon* and *Hibiscus*. Among more exotic genera showing the same conditions as regards foliar rays may be mentioned *Sida*, *Napaea*, *Abelmoschus*, *Gossypium*, *Lavatera*, &c., &c. In concluding the statement regarding herbaceous representatives of the Malvales, we may appropriately reiterate that the aerial stems of these are distinguished from arboreal forms of similar systematic affinities by the development of distinct foliar rays in relation to the entering foliar traces. Other things being equal, these are the better developed the more advanced in the herbaceous scale are the plants under examination.

Before leaving the Malvales it will be well to devote some attention to the nature of the leaf-gap, since there is obviously some confusion in certain quarters on this subject. Fig. 7, Pl. XI, shows a part of the woody cylinder of a year-old stem of *Tilia* at the level where the foliar trace is beginning to enter the stem. Internal to the trace, which appears as a black area, is a radially directed mass of parenchyma ending in the pith. This is the parenchyma of the leaf-gap. Such gaps are found more or less well developed in the secondary wood of all of the Pteropsida. On the outer (also the lower) side of the foliar trace there is no corresponding thick radial mass (see Fig. 2, Pl. XI) of storage parenchyma, except in forms provided with foliar rays (see Fig. 6, Pl. XI). Notable in this connexion, of course, are the Dicotyledonous herbs at present under discussion.

We may now consider with advantage another group in which herbaceous types occur side by side with arboreal. The Urticales will excellently serve in this connexion, because they are regarded by many, by reason of the chalazogamy which they manifest, as among the lowest of the Dicotyledons. Beginning as before with an arboreal representative, Fig. 13, Pl. XII, shows a complete view of a year-old stem of the American Elm, in the region of the node. The position of the traces is revealed by three marked depressions on the inner border of the pith. Fig. 14, Pl. XII, shows one of the leaf-segments of the woody cylinder, more highly magnified. It is clear that outside the leaf-trace the wood is practically normal in structure, showing the presence of wood rays, fibres, and vessels.

In Fig. 15, Pl. XII, is shown a total view of the nodal region of the thicker part of the stem of *Boehmeria nivea*, the so-called 'Fibre-Ramie'. This Urticaceous herb presents a marked contrast to the Elm in the nodal region, by reason of the presence of distinct and broad parenchymatous bands corresponding to the position of the leaf-traces in the stem. These are the foliar rays and are just as characteristically developed in the herbaceous representatives of the Urticales as they have been shown above to be in the Malvales. Fig. 16, Pl. XII, shows a detailed view of one of the leaf-segments of the stem and its corresponding foliar ray. The small leaf-trace is here again externally subtended by a well-developed parenchymatous leaf-ray in marked contrast to the generally woody organization of the central cylinder. The facts here, too, are as irreconcilable with the statements of our critics as they have been shown above to be for the Malvales. Fig. 17, Pl. XII, shows a higher region in the stem under a somewhat less magnification than that employed in the case of Fig. 16. In this illustration the foliar trace is still in the cortex and has not made its way into the central cylinder. A gap subtends the trace in the substance of the wood, which is of course the foliar gap. Fig. 18, Pl. XII, shows a tangential view of the leaf-ray in *Boehmeria*. It is quite obvious that the foliar trace is surrounded by a broad band of parenchymatous tissue, particularly well marked, below the trace. It is thus clear that the leaf-ray shows equally well in the tangential and in the transverse planes of section. In Fig. 19, Pl. XII, is shown a much more magnified view of the foliar ray in the species under discussion. With the increased magnification it becomes clear that the leaf-ray still reveals vestiges of its ligneous origin by the presence of fibres more or less distinctly developed. Examples from herbaceous representatives of the

Urticales of the presence of foliar rays might be multiplied, but the single illustration will suffice, particularly as one of us has recently figured the similar condition in the common Stinging-Nettle, *Urtica urens* (3).

Before taking leave of the Urticales, it will be well to figure for the *Fibre-Ramie* the result on the organization of the leaf-ray of the thinning of the stem in its upper region. Fig. 11, Pl. XI, represents an entire nodal transverse section of *Boehmeria nivea*. The leaf traces are seen, three in number, as in the stouter region of the axis. Their topographical relations are, however, modified as a result of the thinner woody cylinder. Since the cylinder of wood does not appreciably exceed in radial dimension that of the foliar trace, the mass of parenchyma radially subtending the foliar trace in the lower and thicker region of the stem is necessarily absent and the foliar storage tissues are represented only by the parenchyma, which flanks the leaf-trace on either side. This flanking parenchyma compensates for its reduced radial development by a correspondingly increased longitudinal extension. As a consequence of this condition, the cylinder in Fig. 11, Pl. XI, is much more clearly broken up into distinct bundles (naturally separated from one another by foliar rays) than is the case with the more woody lower region of the axis shown in Fig. 15, Pl. XII. Fig. 12, Pl. XI, shows a portion of Fig. 11, much more highly magnified. The foliar trace lies in the centre, and occupies an outstanding position in regard to the strands of the stem on either side, from which it is separated by the flanking foliar parenchyma.

Fig. 20, Pl. XII, shows a complete view of the nodal region of a four-year-old axis of the genus *Xanthorhiza*. This Ranunculaceous genus has been figured by the authors (*op. cit.*, Fig. 12) of the article referred to above as furnishing evidence in favour of their view that there are no foliar rays in the aerial axis of herbaceous forms. It is clear from our illustration of the stem of this somewhat woody herbaceous representative of the Ranunculaceae that there are numerous radial bands extending through all the four annual rings and corresponding to dark radially directed structures, the leaf-traces. Fig. 21, Pl. XII, shows a detail of a three-year-old stem of the same species including three foliar traces and their corresponding leaf-rays. To make the situation still more clear, a tangential view of two foliar rays with their included foliar traces is shown in Fig. 22, Pl. XII. It is thus abundantly clear that the genus *Xanthorhiza*, selected by our critics to illustrate the absence of foliar rays in the Ranunculaceae, serves them very badly in this respect, since well-developed rays are seen not only in sections through the nodal region, but almost equally well in those which pass through the internode. In fact, it may be stated that, except in the genus *Paeonia*, which is to be regarded as perhaps the most primitive representative of the Ranunculaceae proper in the Northern Hemisphere, the only rays present in the woody cylinder are those to which we have applied the name foliar. In *Paeonia* there are smaller rays of the normal woody type, as well as those of broader dimensions, belonging to the foliar category. It will be obvious to the reader that the authors under discussion have not been very fortunate in their choice of the Ranunculaceae as a group demonstrating the accuracy of their statements. It may be added that any of the Ranunculaceae possessing a reasonably well developed aerial stem clearly show the presence of foliar rays. This, for example, is true of both *Clematis* and *Thalictrum*. In the more advanced herbaceous species the situation is less obvious by reason of the thinning of the woody cylinder. In many cases, however, the situation is revealed by the anatomy of the perennial subterranean stem. It is true that our critics have rejected the evidence furnished by the anatomy of the terrestrial region of the stem in extremely herbaceous perennials. This attitude, however, rests on a fundamental misconception, which need not be enlarged upon at the present time. In the arboreal representatives of the Ranales the leaf-ray is in general as conspicuous by its absence as it is in the tree-like examples of other natural families, including both woody types and herbs.

At this stage it will be convenient to refer to a statement quoted at the beginning of this article. It is as follows: 'The fact, however, which militates most strongly against the validity of the hypothesis under discussion is that, in practically all many-bundled herbaceous stems, the interfascicular parenchyma is not subtended by tiny leaf-trace bundles, nor is the stem composed of presumably typical alternating large and small bundles, the latter being leaf-traces.' Fig. 23, Pl. XII, represents a transverse section of *Euphorbia Cyparissias*, the common garden Spurge. The margin of the medulla is crenulated by projections of the pith into the woody cylinder. Each of these bays harbours a leaf-trace which shows as a small dark dot terminating the apex of the bay. It is clear that outside each of the leaf-traces lies a well-developed foliar ray, and that these foliar rays clearly alternate with the stem segments, which are quite obviously characterized by the presence of vessels, conspicuous by their absence in the rays. It will be clear to the reader that the illustration under consideration very obviously realizes a condition stated by our self-confident critics not to exist. Almost any species of Sunflower, Aster, or Golden-rod, if sectioned in the appropriate region of the stem, would reveal similar topographical relations. In fact, hundreds of examples could be easily supplied of conditions which are cited above as impossible. The situation emphasized reveals the superficiality which unfortunately characterizes much of the recent anatomical work of the senior of our two critics.

Fig. 24, Pl. XII, exemplifies the anatomical conditions obtaining in the region of the foliar trace in *Robinia Pseudacacia*. The leaf-trace is opposed by normal wood, and there is consequently no foliar ray present in this arboreal representative of the important Legume alliance. In contrast to

Fig. 24, we find in Fig. 25, Pl. XII, a leaf-trace subtended by a remarkably well developed foliar ray. The species used here is the herbaceous *Melilotus alba.* The occurrence of foliar rays is practically universal in herbaceous and vine-like representatives of the Leguminosae, and they consequently supply good evidence in favour of the coincidence of foliar rays with the herbaceous type. Here, as elsewhere, when the aerial stem is extremely slender, a radially well developed foliar ray is found only in the thick perennial subterranean axis.

In a group like the Umbelliferae, the representatives of which in temperate regions are almost exclusively tender herbs, it is usually possible to discover radially developed foliar rays only in the persistent hypogaeous axis. The same statement holds true for a large number of other highly herbaceous orders. Obviously, in seeking a derivation of the herbaceous type from the woody, it is necessary to choose types of herbs in the first instance which are more or less woody in order to successfully trace the stages from the arboreal to the herbaceous type. Our critics have made the mistake of comparing extreme herbs with trees, and have failed to investigate with even moderate care the more important transitional forms which unite trees and herbs.

Fig. 26, Pl. XIII, illustrates the organization of the nodal region of the Scrophulariaceous genus *Gerardia.* The leaves are opposite, and corresponding to these are two opposite foliar traces. The trace on the lower side of the figure is making its way in towards the centre and is consequently subtended inwardly by the foliar gap. The upper trace by contrast has reached its final position on the margin of the pith and subtends radially a well-marked parenchymatous band, the foliar ray. In Fig. 27, Pl. XIII, is shown a detail of the foliar ray, and its contrasted structure may be compared with the ordinary wood on either hand. Almost any of the Scrophulariaceae show similar conditions as to the development of foliar rays, notably the common Mullein (*Verbascum*) and the Toad-flax (*Linaria*).

In conclusion, we may deal with the Compositae. Fig. 28, Pl. XIII, illustrates a transverse section of the foliar ray in *Solidago canadensis* from a preparation made by Miss Edith Whitaker, who has recently published an interesting contribution on the anatomy of the Golden-rods (4). A well-developed radial mass of storage parenchyma is revealed in the section. Fig. 29, Pl. XIII, also from a preparation by Miss Whitaker, reveals the tangential aspect of the foliar ray. The trace in this instance, as is indeed common in the Compositae, lies well to the top of the ray. In Fig. 30, Pl. XIII, is shown the radial view of the foliar ray. This illustration is particularly instructive. Above is shown the ordinary structure of the wood which is normally found above the region of exit of the trace in stems which are not too extremely herbaceous. Below the foliar trace, which shows as a structure pursuing an oblique and rising curved course towards the left, lies the radial aspect of the entirely parenchymatous foliar ray. To the right of the leaf-trace is shown the darker-hued parenchymatous material, which represents the soft matrix occupying the leaf-gap. The three figures described above give an accurate view in three dimensions of the foliar ray as it appears in the Golden-rod. The topography of the foliar rays is surprisingly uniform in the Compositae, and literally hundreds of instances could be furnished for illustration, exactly paralleling those shown in Figs. 28, 29, and 30. Figs. 31 and 32, Pl. XIII, show tangential views of the foliar rays in two different species of Sunflower. In Fig. 31 is revealed the tangential aspect of the leaf-ray in *Helianthus tuberosus*, a perennial species with annual aerial stems. In the substance of the leaf-ray in this species even the low power of magnification used reveals the presence of other than parenchymatous elements. In other words, the ray is of mixed constitution and still contains some of the vessels and fibres of the wood from which it was originally formed. In Fig. 32, Pl. XIII, is revealed, under the same degree of magnification as in the preceding figure, the foliar ray of the strictly annual species *Helianthus annuus*. The very much larger size of both foliar ray and its corresponding foliar trace are easily observed. The difference in dimensions observed corresponds closely with the degree of herbaceousness in the two species. *Helianthus annuus* is large, vigorous, and very herbaceous, and is able to go from seed to seed in a comparatively few weeks. Another feature of interest from the comparative standpoint, other than the greater development of both leaf-trace and the corresponding foliar ray in *H. annuus*, is the homogeneity of the ray itself, indicating a more advanced degree of transformation from the original wood into storage tissue.

In the foregoing paragraphs and their accompanying photographic illustrations a considerable variety of evidence has been supplied in support of the proposition advanced from these laboratories some years ago, that herbaceous stems, in their origin at any rate, are characterized by the presence of large foliar rays, radially subtending the foliar traces. It should be emphasized that the figures are only illustrative of an infinitely larger number of facts of a similar character, as it is obviously impossible within the limits imposed by an article in a scientific magazine to describe or cite in detail more than a comparatively few cases bearing upon the theme under discussion. An attempt has, however, been made to have the illustrations chosen thoroughly representative of the course of evolution of herbs from woody ancestors. In a good number of instances the woody or arboreal type has been figured in proximity to its herbaceous derivative so that easy comparison of the two is possible. The present authors are of the opinion that, with these illustrations before his eyes, no competent and fair-minded reader can deny the existence in typical Dicotyledonous herbs of the structures which we have called foliar rays. It will further be clear to those who peruse these lines, it is hoped, that the foliar ray, practically universally characteristic of Dicotyledonous herbs, is a compound structure derived from the aggregation of storage tissues in the region of the foliar trace, as it enters the stem at the node.

Before passing on to the diagrammatic illustrations of the derivations of transitional herbs from woody ancestors, it will be well to pass in review the figures of the article (1) which it has been necessary to discuss in the present pages.

Their first illustration of the Compositaceous genus *Arctotis* is an excellent example of the peculiarly inconsistent reasoning which characterizes the anatomical statements of our critics. After objecting strongly to the use of the decumbent stem of *Potentilla palustris* by Eames (1) in his article proceeding from these laboratories, they use the 'somewhat decumbent aerial stem of *Arctotis grandis*' in support of their own conception of the origin of the herbaceous type. Fig. 2 of their article represents the stem of the American Beech and has no bearing on the present discussion. Fig. 3, of *Hypericum aureum*, is not taken in the region where the leaf-traces enter the stem at the node, and consequently has no bearing on the matter in dispute, namely, the presence of foliar rays in relation to foliar traces. We have examined several species of *Hypericum* and have invariably found foliar rays related at the node to leaf-traces. The following figure of another species of *Hypericum* is open to the same criticism as Fig. 3. The next figures (5 and 6) illustrate the stem of the Solanaceae, but not at the node. Here, as in the Hypericaceae, well-marked foliar rays are to be seen where the leaf-traces enter the stem. Fig. 7, of *Salvia sp.*, may be taken as illustrative of the Labiatae, which are as well characterized by the presence of foliar rays as are other herbaceous orders. Figs. 8 and 9, illustrating the Malvales, have been sufficiently criticized in the foregoing pages. Fig. 10, of the stem of *Rosa rugosa*, has little bearing on the discussion. The authors do not figure any herbaceous representatives of the Rosaceae, with the exception of *Sanguisorba*, in which foliar rays are clearly present even in the aerial stem, although not shown in their illustration. The futility of their statements regarding the Ranunculaceous genus *Xanthorhiza* has been revealed in earlier paragraphs. The other illustration of the Ranunculaceae, *Delphinium*, is through too slender a stem to throw any light on the question of the origin of herbs from woody ancestors. *Acanthopanax* shows some progress towards the herbaceous condition and the formation of foliar rays, although this is not manifest in the illustration supplied by our critics. Fig. 15, illustrating the Umbelliferae, is made through the internode of an extremely herbaceous axis, and as a consequence throws no light whatever on the origin of the herbaceous type from the woody, which is naturally best elucidated by herbs of intermediate and transitional organization. Figs. 16 and 17 are characterized by the same faults as many of the others, namely, they are not taken properly in the nodal region or the stems are too slender to reveal the condition of transition of fundamental importance in the present connexion. These shortcomings are all the more serious because the two illustrations in question are all that the authors have presented for the very important herbaceous group, the Compositae. Fig. 18, a further example of the Ranunculaceae, is not from a nodal region of *Clematis*, and as a consequence naturally throws no light whatever on the typical foliar ray, which in woody herbs like the species of *Clematis* illustrated is of shallow vertical length and confined as a consequence to the region immediately below the node and the trace to which it is related.

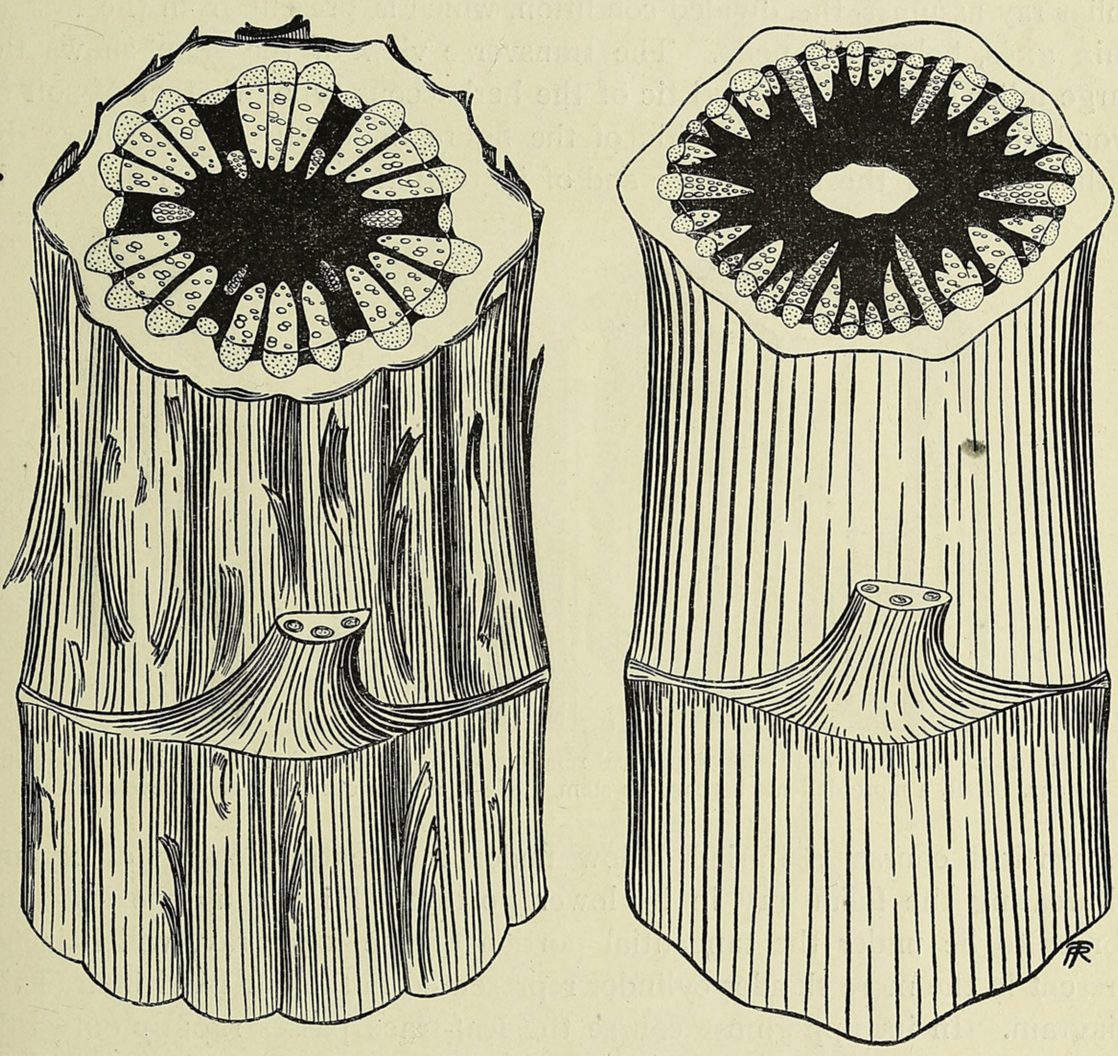
The elucidation of the results reached by the examination of transverse and longitudinal sections of transitional herbs is naturally best accomplished by means of diagrams. Text-fig. 1 shows at once the tangential and transverse aspects of three different genera of the Compositae. In the centre appears a representation of the stem of the southern woody genus *Baccharis*, in the region of the node. The leaf-trace is diagrammatically indicated by elements with spiral markings. It will be noted in the tangential aspect which faces the observer that there is only a slight concentration and enlargement of the rays of the wood in proximity to the foliar trace. On the opposite side of the transverse aspect of the central region of the diagram is shown the transverse section of a leaf-segment of a higher node. Obviously we have here to do with an aggregate ray related to the leaf-trace, since no vessels are present in the region of the cylinder radially subtending the vascular supply to the leaf. To the right in the diagram appears the nodal tangential aspect of *Bidens sp.* Here there is a considerable fusion and enlargement of the normal rays of the wood in relation to the foliar trace, and as a consequence the storage conditions are farther advanced than they are in the central segment of the diagram. No transverse section of the foliar ray is represented in the case of *Bidens*. To the left in the diagram is shown the tangential aspect of the nodal situation in the genus *Helianthus*. The storage devices here have become better developed than in *Bidens*, since a well-marked compound and as a consequence purely parenchymatous ray has made its appearance in relation to the foliar trace. A notable feature in this instance is the presence of a central tongue of unmodified wood in the lower region of the foliar ray. This structure has the effect of subdividing the leaf-ray into two in the lower part of its course. The two narrow forks of the foliar ray in many herbs run for a long distance down the stem, and as a consequence through a number of internodes. The vertical length of the foliar ray other things being equal, has a direct relation to the degree of herbaceousness of the axis. It may vary in the same stem, for in the lower aerial region, where the cylinder is thick and woody, the vertical extension of the foliar rays may be short, while the radial development is often prominent. In the upper slender portion of the same axis, on the other hand, the rays are frequently shallow radially and vertically extremely elongated.

In Text-fig. 2 are elucidated, in respectively more and less herbaceous species of *Clematis*, the topographical relations of the foliar rays. The

TEXT-FIG. 1. Centre diagram of the woody genus *Baccharis*. Left, tangential view of the node of *Helianthus*. Right, tangential view of the nodal region of *Bidens*.

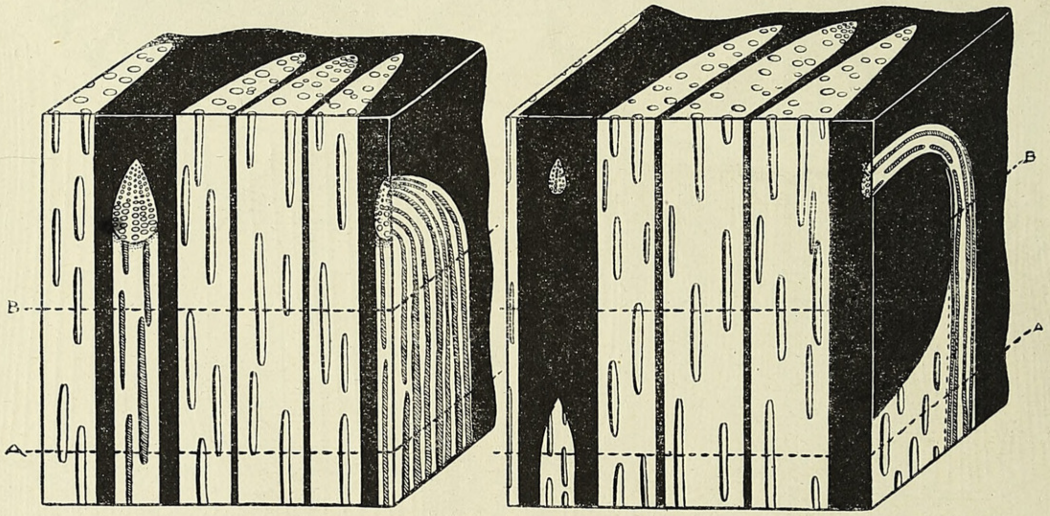
diagram to the left shows a somewhat woody species. There are six foliar traces projecting somewhat into the medullary region, to which are related radially six corresponding foliar rays. The storage tissue in these rays is mainly exterior to the foliar traces, but some of it lies on their flanks. In the right-hand figure an herbaceous species of *Clematis* is represented. Here the six foliar traces are relatively very much larger in size than they are in the companion illustration, a frequent condition of contrast between woody and herbaceous axes in the same genus. The six leaf-traces of the herbaceous stem are of such marked radial development that the foliar storage tissue is absent radially, and as a consequence is confined to a lateral position on the flanks of the traces of the leaves in their course in the stem.

Text-fig. 3 shows the situation as regards the relation of the storage rays to the foliar traces in three dimensions. The left-hand diagram repro-



TEXT-FIG. 2. Diagram of the nodal regions of a woody and an herbaceous species of *Clematis*.

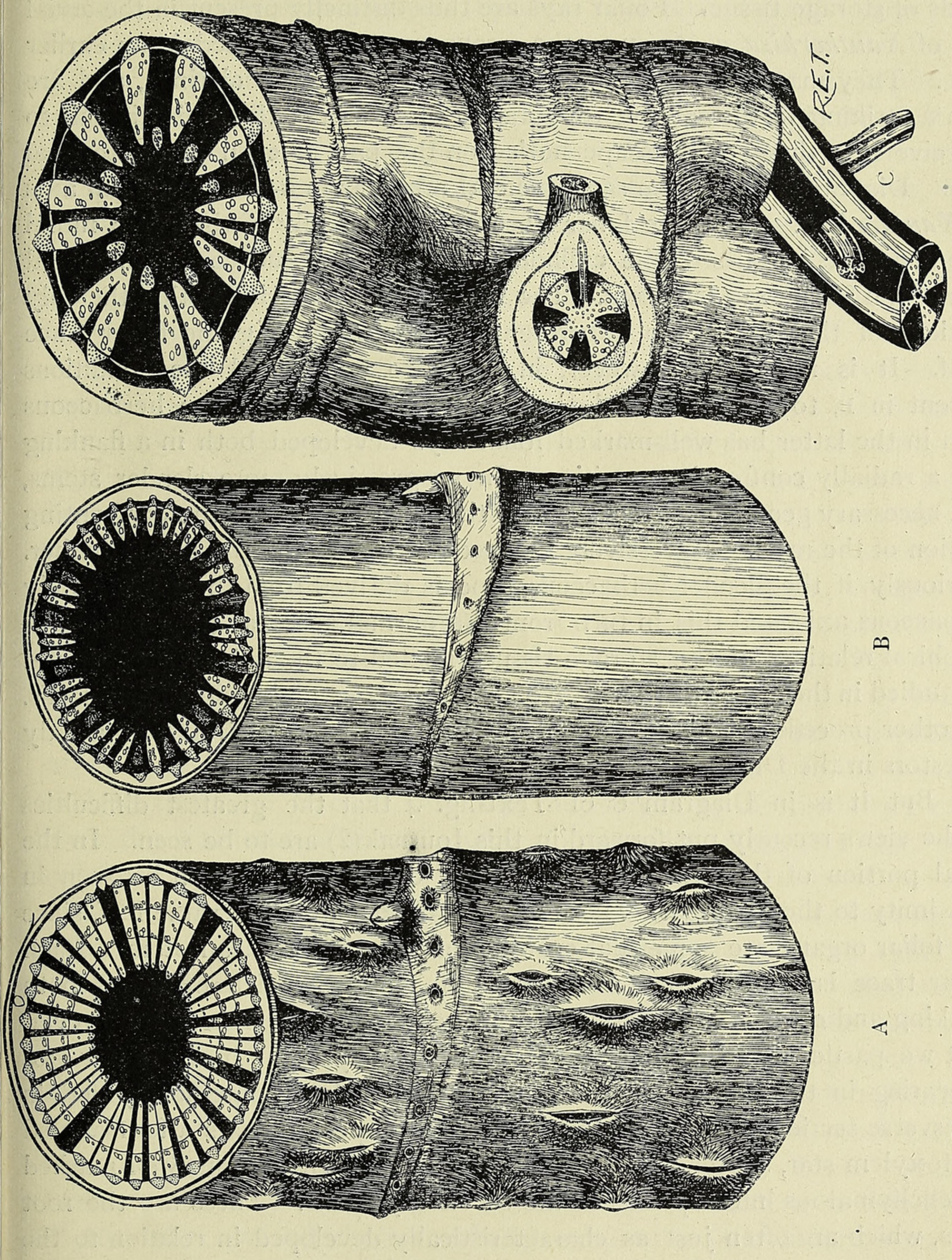
duces the topographical relations of leaf-trace and foliar ray in the slender herbaceous region of the stem. To the left of the illustration lies a foliar ray with its contained leaf-trace. The trace is represented below in tangential long section, while above, on account of the fact that it turns obliquely outwards or radially in its course towards the base of the leaf, it is seen in somewhat oblique transverse section. In the transverse view of the ray is shown a solid mass of storage tissue representing the enlarged foliar gap. To the right of the diagram under discussion is shown the radial aspect of the woody cylinder in a segment occupied by a foliar trace. The relations of the ray to the trace can be clearly seen and also the fact that the foliar trace turns somewhat abruptly radially outwards at its upper extremity. In the diagram to the right the topographical relations of the foliar trace in a more woody herbacous axis are shown, in the region of the node. To the left the foliar trace is seen only in transverse section in the tangential plane, since its vertical portion is buried deeply under the parenchyma of the foliar ray. In the lower region the massive foliar ray assumes the divided condition, which is present from the first in thin axes, below the node. The transverse view of the stem shows the large foliar gap so characteristic of the herbaceous type, whether of soft or woody texture. The right side of the figure under discussion shows the radial aspect of the foliar trace and of its related foliar ray. The trace in



TEXT-FIG. 3. Diagram of the topographical relations of leaf-trace and foliar ray in three dimensions. Left, a more delicate herbaceous stem. Right, a stem of more woody development.

its vertical course is buried below under the central tongue of xylem, bifurcating the foliar ray in its lower portion. Higher up the leaf-trace comes to lie under the tangential portion of the foliar ray, which is not present in the more slender cylinder represented in the left-hand item of the diagram. In its uppermost course the leaf-trace passes rapidly outwards, and in this region is completely surrounded by storage tissue.

Text-fig. 4 presents in its three items the general topography of thick and thin axes of the same somewhat woody aerial stem and of the more parenchymatous subterranean stem of a herbaceous perennial. A and B are constructed from thick and thin aerial stems of *Xanthorhiza*. In C appears the rhizome of a species of *Actaea*. The illustration in the last instance shows also the topography of the attached roots and their corresponding rootlets. Beginning with A, we have a stem three years old, shown in the transverse section in the region of an upper node. Below is the superficial view of another node. From this part of the diagram it is

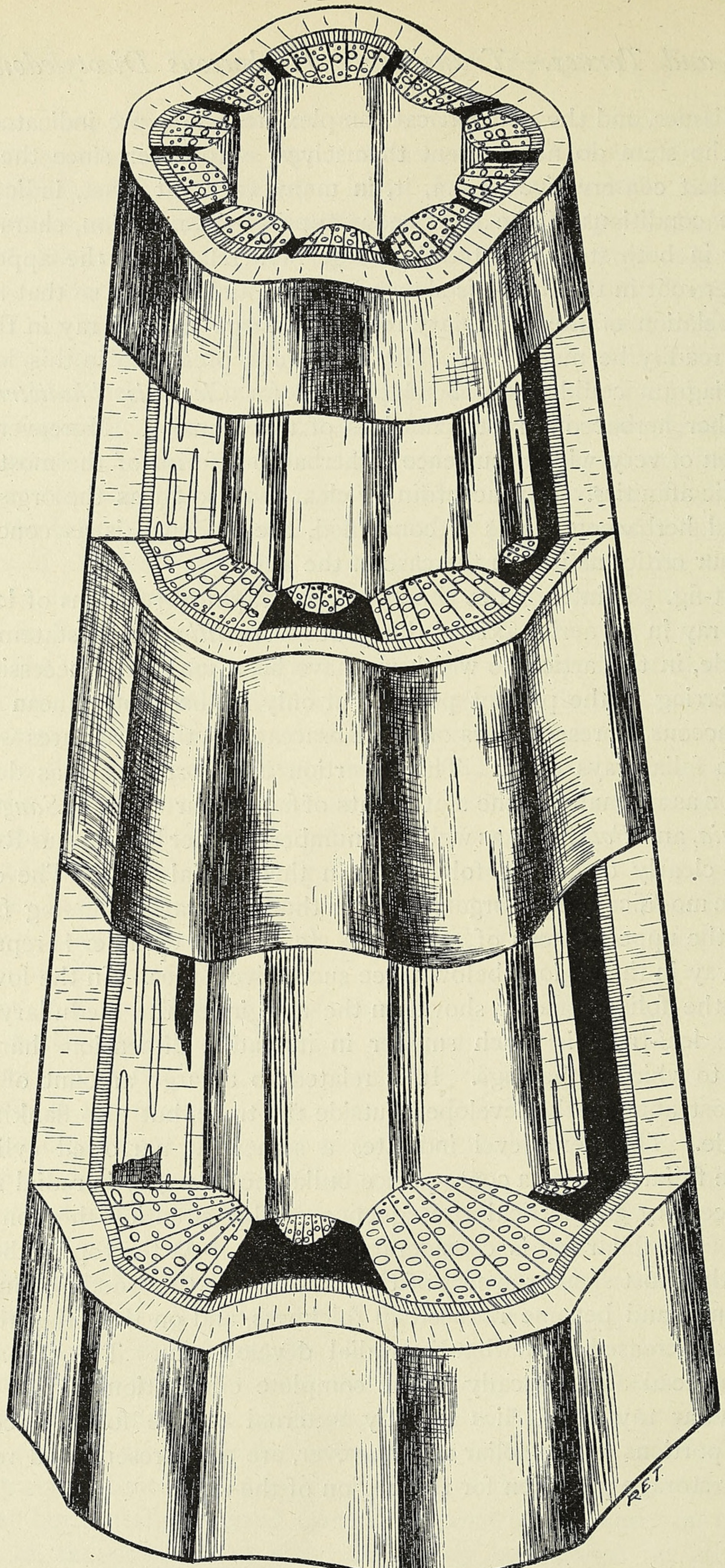


TEXT-FIG. 4. Diagram in three dimensions of thicker and thinner aerial stems of *Xanthorhiza* (A and B). Diagram of the root-stock of a species of *Actaea*, showing the topography of the rays in relation to appendages of both root and stem (C).

clear that many foliar traces enter the stem at the same node, but at somewhat different levels. The upper transverse view shows the traces in topographical relation to the foliar rays. It is clear that the latter extend through three annual rings and subtend the traces as long radial and massive bands of storage tissue. Foliar rays are thus distinctly present in the aerial axis of *Xanthorhiza*, contrary to the erroneous statement cited in an earlier page. They may extend through four or even five annual rings, and are such a striking feature of the topography of the stem that it is difficult to conceive how they could escape notice on the part of even an anatomical tyro. Diagram B shows the same general relations in a slender annual axis of *Xanthorhiza.* Here the foliar traces are practically of the same radial extent as the bundles of the cylinder, and as a consequence the tangential part of the foliar rays is absent. The result of this situation is that the only portions of the leaf-ray to be present are those flanking the foliar trace itself. It is necessary, however, in order to understand the conditions present in B, to have in mind those exemplified in A. The herbaceous stem in the latter has well-marked foliar rays developed both in a flanking and a radially confronting position. In progressively more slender stems, as a necessary geometrical result of the thinning of the axis, the confronting portion of the ray is progressively reduced and finally disappears altogether. Obviously, if the slender herbaceous type is derived from the more woody herbaceous axis, and this in turn from the normal arboreal type, the topographical relations of the storage tissues related to the foliar traces should be studied in the order of arboreal, woody herbaceous, and slender herbaceous. No other procedure is permissible if herbs are in reality derived from woody ancestors in the Dicotyledons.

But it is in Diagram C of Text-fig. 4 that the greatest difficulties to the views recently put forward in this Journal (2) are to be seen. In the axial portion of the illustration a number of foliar traces can be seen in proximity to the medulla. These do not all belong to the same leaf, since the foliar organs are somewhat crowded on the subterranean stem. Each foliar trace is related to a well-marked foliar ray, which manifests both flanking and confronting relations to the trace. It is to the roots, however, that we particularly turn our attention in this diagram. In the upper root appearing in the illustration the organ is shown both superficially and in transverse section. In the centre of the latter aspect appears a four-angled protoxylem star, subtending the projections of which are four well-marked parenchymatous interruptions of the secondary wood. These are the root rays, which are often just as characteristically developed in relation to the lateral rootlets as are similar storage rays in the stem in relation to the foliar traces. Since the woody cylinders of the lateral rootlets are from the first horizontally directed from their point of departure on one of the angles of the protoxylem, they are clearly surrounded on all sides by storage tissues, and the geometrical complexities which are indicated in the case of the stem do not present themselves. Moreover, since the root is a somewhat conservative organ, it, in many cases at least, indicates the primitive conditions of the herbaceous type of organization, characterized normally in both stem and root by large rays related to the appendages. The lower root in the figure is shown in tangential section, so that the very definite relation of the secondary root to a large storage ray in the main root can readily be made out. The conditions presented in this last item of our diagram could easily be duplicated for *Clematis*, *Thalictrum*, and many other herbaceous representatives of the Ranales. Moreover, this is a situation of very wide occurrence in herbaceous forms of the most diverse systematic affinities. It is accordingly clear that, so far as the organization of typical herbaceous roots is concerned, the evidence is as conclusively against our critics as it is in the case of the axis.

Text-fig. 5 is intended to show the topographical relations of leaf-trace and leaf-ray in an aerial axis of the genus *Potentilla*. The statement has been made, in the article to which we have been under the necessity of so often referring in the present pages, that only in the subterranean stem of the herbaceous representatives of the Rosaceae do the structures which we designate foliar rays occur. This assertion is unfortunately as devoid of foundation as are many of the statements of fact of our critics. *Sanguisorba*, *Agrimonia*, and *Potentilla*, as well as a number of other herbaceous Rosaceae, manifest clearly developed foliar rays in their aerial axes. The diagram shows the modifications in organization of the foliar ray in passing from the lower to the upper regions of the aerial stem. The cylinder is represented as cut away in the regions below three successive nodes. In the lowermost of these the foliar trace is shown on the margin of the medullary region. Here the leaf-trace is much smaller in its radial dimension than is the cylinder to which it belongs. It is related to a large amount of storage tissue, most abundantly developed outside the trace, but also flanking it on either side. The next level indicates a somewhat narrowed cylinder in which the foliar trace as a consequence bulks more largely in radial relation. As a necessary geometrical consequence of this situation the confronting portion of the foliar ray is considerably reduced. At the top of the figure appears the most slender aspect of the axis. Here the woody cylinder has on the one hand become reduced in thickness, and on the other the foliar trace has increased somewhat in radial development. These concurrent conditions lead automatically to the complete elimination of that portion of the foliar ray which lies radially external to the foliar trace. The flanking portions of the foliar ray, however, are still present, and represent the foliar storage provision for this region of the axis.



TEXT-FIG. 5. Diagram to illustrate the topographical relations of the leaf-trace to the leaf-ray at various heights in the tapering aerial stem of *Potentilla*.

Conclusions.

The various photographic illustrations and stereodiagrams supplied in connexion with the earlier pages of the present article seem clearly to justify quite definite conclusions as to the mode of origin of the herbaceous type of axis in the Dicotyledons from that of woody or arboreal texture. It seems obvious, as a consequence of the comparison of nearly related arboreal, woody herbaceous, and slender herbaceous stems, that the structures which we have called foliar rays are in the first place developed in woody herbs as a result of the clustering of ordinary rays of the wood in relation to the incoming leaf-traces. The clusters or congeries of rays, to which one of us has applied the name aggregate rays, are often characterized by the fact that vessels are eliminated in the bands of longitudinal woody elements separating the constituent members of the foliar aggregation of rays from one another. We have illustrated this condition above, in the case of the genus *Hibiscus*. It is of wide occurrence in woody or transitional herbs. A next step in the development of the herbaceous type is the transformation of the strands of fibres separating the storage units of the aggregate ray from one another into rows of parenchymatous elements which become more and more assimilated to the ordinary radial parenchyma both in their dimensions and in the relations of their axes. This condition of the foliar ray we have called the compound ray, to distinguish it from the aggregate ray from which it takes its origin. Quite often when the compound ray has been thoroughly established it still betrays its derivation from the aggregate ray by the fact that its lower portion is still largely in a condition of aggregation. As the herbaceous condition becomes more and more established, the foliar rays become not only more homogeneous, by reason of the more complete loss of identity of their originally diverse woody elements, but also more elongated in the vertical direction.

The last condition often expresses itself in transverse section, where the traces are sufficiently numerous and their accompanying foliar rays are sufficiently developed in the long axis, by a series of separate strands, more or less regularly alternating as to size, in which certain members are deep radially and woody in structure, while the alternating segments consist of relatively slender bundles subtended radially by massive storage tissues. The storage tissues also occur on the flanks of the slender bundles just referred to, which are the foliar traces in their course in the stem. This state of affairs is extremely common, for example, in the more woody lower region of the aerial stem in the herbaceous Compositae, particularly if the foliar traces are numerous and the foliar rays greatly extended longitudinally. Favourable objects on which to test the truth of this general statement are the genera *Helianthus*, *Aster*, *Lactuca*, &c., &c. Although the organization just referred to is particularly well seen in Compositaceous stems of the proper degree of advance in the herbaceous direction, it also occurs in many other groups, where the necessary conditions are realized. It is a striking example of the inaccuracy which we have often had to note in our critics that they deny the possibility of the topography which we have represented photographically in Figs. 20 to 23 for the Ranunculaceae and the Euphorbiaceae. Hundreds of similar cases could be supplied from common herbaceous types.

Another and more advanced phase of the evolution of the herbaceous type is the thinning down, in an even more marked degree, of the axis. This automatically results in the elimination of the parenchyma of the foliar ray, which radially subtends the foliar trace. As a consequence of this condition, only the flanking parenchyma of the foliar ray persists. This situation is shown in our Figs. 11 and 12, and also by Text-figs. 3, 4, and 5.

It has been maintained by our critics that the herbaceous type in the Dicotyledons is merely the result of the progressive thinning of the woody cylinder. This condition is undoubtedly true for some Vascular Cryptogams of herbaceous habit, but cannot be accepted for the Seed-plants. The Coniferales, for example, have never given rise to plants either herbaceous or vine-like, in spite of the fact that they exist often under climatic conditions extremely favourable as regards low temperature to the appearance of the herbaceous habit. The reasonable inference from this state of affairs is that the Conifers lack some fundamental feature of organization which is essential to the development of the herbaceous type among the Seed-plants. We are by no means compelled, however, to take refuge in negative evidence in this respect, for it has been shown by numerous examples drawn from woody or transitional herbs, in the foregoing pages, that a constant and in fact diagnostic feature of the herbaceous type in the Dicotyledons is the presence of those structures which we have designated foliar rays. As explained above, these arise in the first place and in many woody herbs from the accentuation of the ordinary rays of the wood in proximity to, and especially below, the entering foliar traces. These aggregations of rays, by the process of compounding, are transformed later into considerable foliar bands of longiradial storage tissue. It follows from the statement of the manner of origin of herbs in the Dicotyledons that it is the result of advance and differentiation, and is not the consequence of a mere process of degeneracy, as assumed by our critics. Angiosperms are, in fact, as has been pointed out by one of us in a recently published text-book of anatomy, characterized by the development of *dynamic* herbs in contrast to the Vascular Cryptogams, which are represented in the living *Flora* by *degenerate* herbs.

Summary.

1. The origin of the herbaceous type in the Dicotyledons is from woody or arboreal forms.

2. Woody herbs, as a consequence, throw clear light on the mode in which the herbaceous Dicotyledons have been derived.

3. In the aerial axes of woody herbs a constant and practically never-failing distinction from trees is the formation of large foliar storage rays about the incoming leaf-traces, as they pass through the woody cylinder.

4. In woody herbs the foliar storage rays are well developed in the radial direction, but their vertical extension is slight.

5. In the aerial stems of more slender and less woody Dicotyledonous herbs the foliar rays become elongated vertically to compensate for their reduced radial dimension resulting from the thinning down of the woody cylinder.

6. In rays of the type described in 5, the lower part of the radial parenchyma related to the foliar trace is often bifurcated by a tongue of unmodified wood.

7. The vertical elongation of the foliar rays and their subdivision in the manner described in 6 result in the final separation of the originally continuous woody cylinder into a series of separate strands.

8. The final stage of the herbaceous Dicotyledons is a condition in which the cylinder is thinned to such a degree that the radial extension of the foliar rays is virtually eliminated. With this condition is usually associated a great development in length of the portions of the foliar ray flanking the leaf-trace on either side.

9. Recent statements asserting the absence of foliar rays in the aerial axis of the herbaceous type in the Dicotyledons are inaccurate.

Literature cited.

1. Eames, A. J.: The Herbaceous Type in the Angiosperms. Ann. Bot., vol. xxv, No. 97, Jan. 1911.
2. Bailey, I. W., and Sinnott, E. W.: The Origin and Dispersal of Herbaceous Angiosperms. Ann. Bot., vol. xxviii, No. 112, Oct. 1914.
3. Jeffrey, E. C.: The Anatomy of Woody Plants. University of Chicago Press, 1917.
4. Whitaker, Edith S.: The Anatomy of Certain Golden-rods. Bot. Gaz., vol. lxv, No. 3, March, 1918.

EXPLANATION OF PLATES XI–XIII.

Illustrating Messrs. Jeffrey and Torrey's paper on Transitional Herbaceous Dicotyledons.

PLATE XI.

Fig. 1. Transverse section of a year-old stem of the common Linden (*Tilia*) in the region of a node, showing the absence of foliar rays such as are characteristic of woody herbs.

Fig. 2. Foliar segment of Fig. 1, more highly magnified to show the woody character of the tissues subtending the foliar trace.

Fig. 3. Tangential section of the foliar ray of the woody herb *Abutilon*.

Fig. 4. Tangential section of the foliar segment in *Tilia*, showing the absence of the foliar ray in this genus.

Fig. 5. Entire transverse section of the stem of *Abutilon* sp., showing clearly the presence of three foliar rays, corresponding to the three foliar traces on the margin of the pith.

Fig. 6. One of the foliar rays of *Abutilon* in transverse section, more highly magnified than Fig. 5. Compare this with the transverse section of *Tilia* in Fig. 2.

Fig. 7. Transverse section through part of the nodal region of the woody cylinder of *Tilia* sp., showing the foliar gap which interrupts the continuity of the wood internally to the leaf-trace.

Fig. 8. Transverse section of the foliar ray of *Oenothera biennis*, taken from the aerial region of the stem.

Fig. 9. Transverse section of the entire axis of *Hibiscus syriacus* in the region of the node. On the right is seen a foliar ray extending through three annual rings.

Fig. 10. Transverse section of part of the foliar ray shown in the preceding figure. The ray is seen to be made up of normal wood rays and of fibres, but vessels are conspicuous by their absence.

Fig. 11. Total transverse section of the slender region of the aerial axis of *Boehmeria nivea* in the region of the node.

Fig. 12. Part of the same more highly magnified to show the nature of the foliar rays in the slender region of the stem.

PLATE XII.

Fig. 13. Transverse section of the nodal region of a year-old stem of the American Elm (*Ulmus americana*) to show the absence of foliar rays in an Urticaceous woody axis.

Fig. 14. A foliar segment of *Ulmus americana*, and its internally subtending foliar trace. The absence of modification in the woody structure of the leaf-segment is very obvious.

Fig. 15. Entire transverse section of the nodal region of the stem of *Boehmeria nivea*, a woody herb of Urticaceous affinities, showing, in contrast to Fig. 13, the obvious presence of foliar rays in relation to the foliar traces.

Fig. 16. One of the foliar rays of *Boehmeria nivea* in transverse section. It is subtended internally by its corresponding foliar trace.

Fig. 17. Transverse section of the foliar gap of *Boehmeria nivea*. The leaf-trace subtends it externally in the cortex.

Fig. 18. Tangential section of the foliar ray of *Boehmeria nivea*.

Fig. 19. Part of the same, more highly magnified.

Fig. 20. Total transverse section of the aerial perennial stem of *Xanthorhiza*, showing numerous foliar rays and their corresponding foliar traces.

Fig. 21. Part of a transverse section of the same species, more highly magnified to show three foliar rays extending through three annual rings and subtended by their corresponding foliar traces.

Fig. 22. Tangential section of two foliar rays of *Xanthorhiza*

Fig. 23. Transverse section of *Euphorbia Cyparissias*, showing a clear alternation of numerous stem bundles and of foliar rays subtended by their foliar traces.

Fig. 24. Transverse section of leaf-segment of *Robinia Pseudacacia*, showing the absence of a foliar ray.

Fig. 25. Transverse section of the foliar ray in the woody herb *Melilotus alba*.

PLATE XIII.

Fig. 26. Total transverse section of the nodal region of the woody herb *Gerardia*, showing the presence of two foliar rays corresponding to the two opposite leaves. The ray on the lower side has just begun to appear.

Fig. 27. Transverse section of the foliar ray shown in the upper region of Fig. 26, more highly magnified.

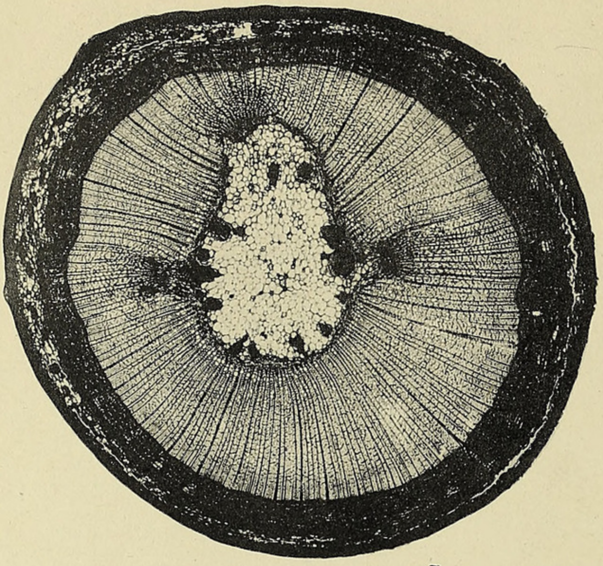
Fig. 28. Transverse section of the foliar ray in *Solidago canadensis*, from the base of the aerial axis.

Fig. 29. Tangential section of the foliar ray of *S. canadensis*, from the thicker region of the aerial stem.

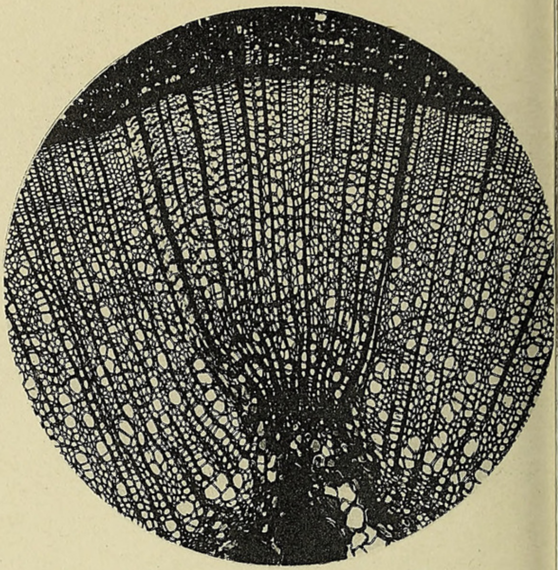
Fig. 30. Radial section of the foliar ray from the woody region of the aerial stem of *S. canadensis*.

Fig. 31. Tangential section of the foliar ray of the lower region of the aerial axis of *Helianthus tuberosus*.

Fig. 32. Tangential section from a lower aerial node of *Helianthus annuus*, showing the organization of the foliar ray. The magnification is the same as in Fig. 31.

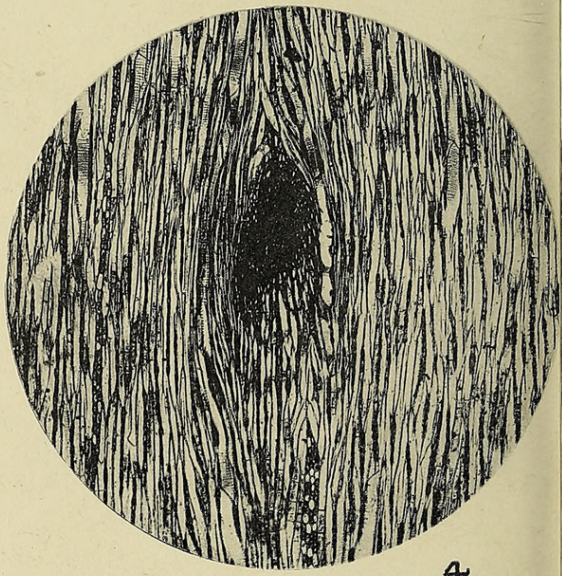


1.

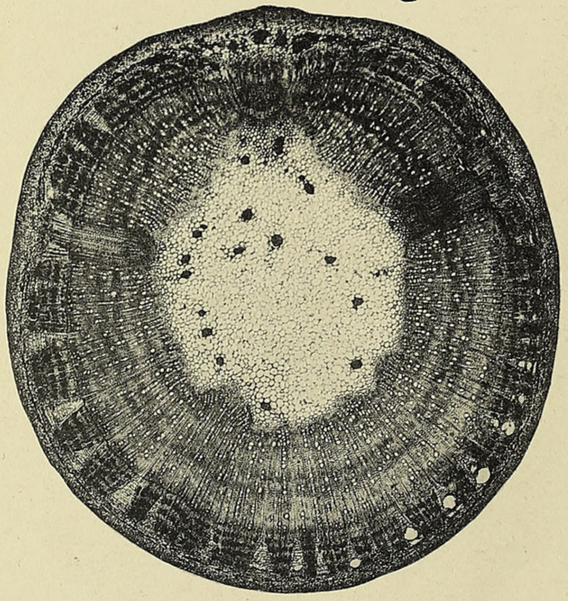


2.

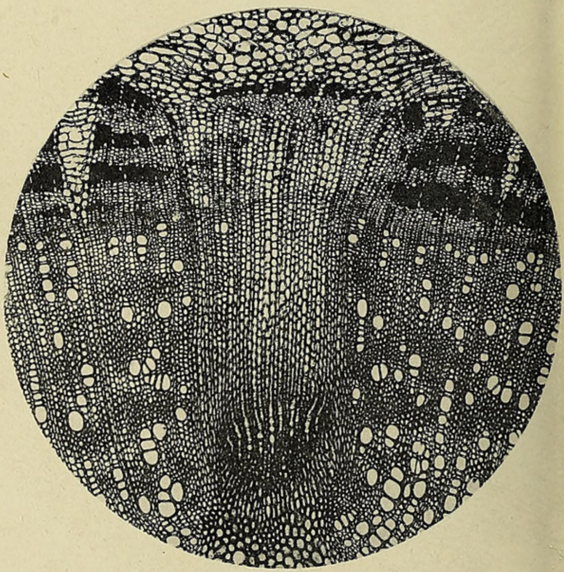
3.



4.

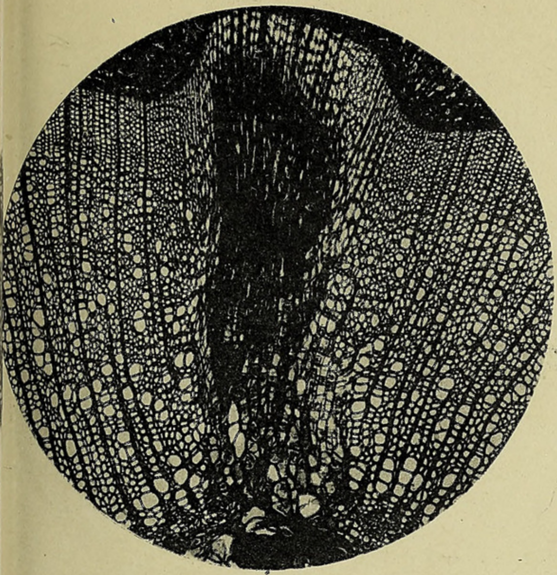


5.

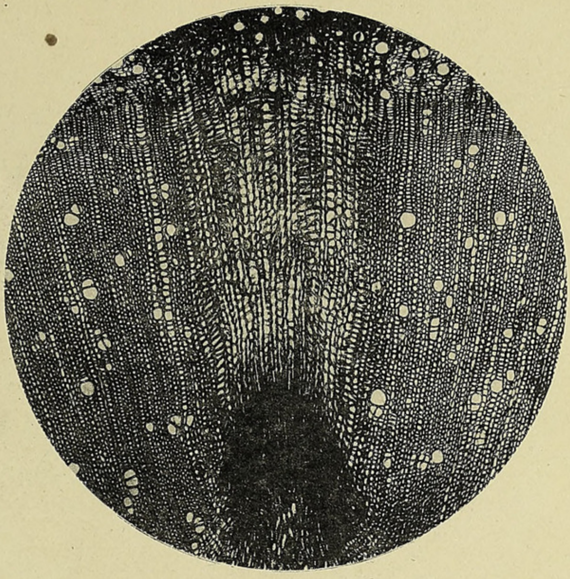


6.

JEFFREY — HERBACEOUS DICOTYLEDONS.

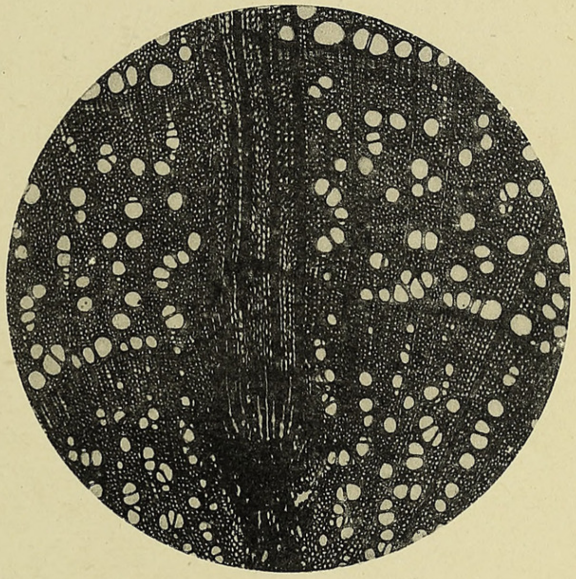


7.

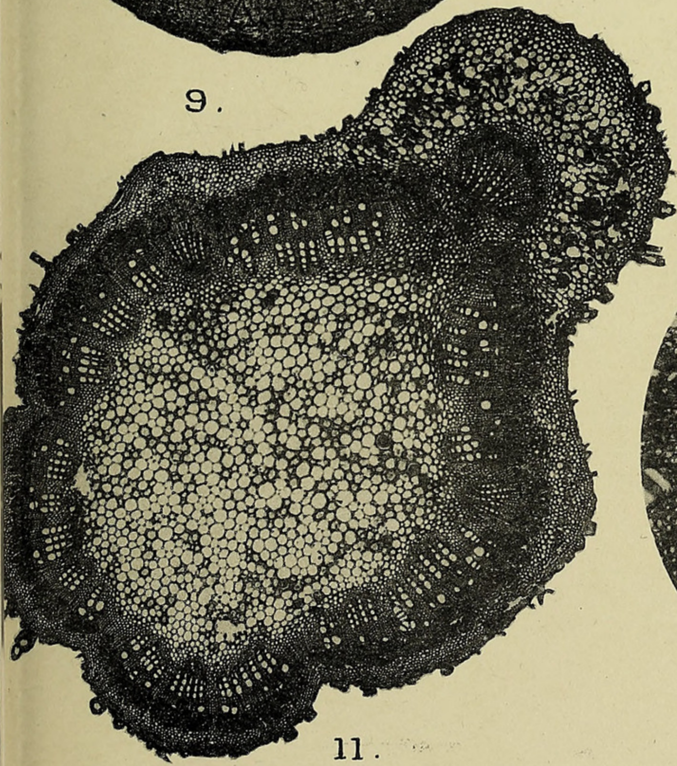


8.

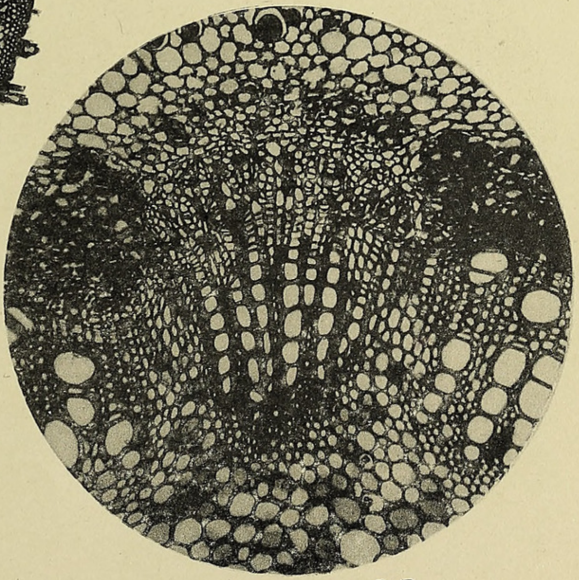
9.



10.

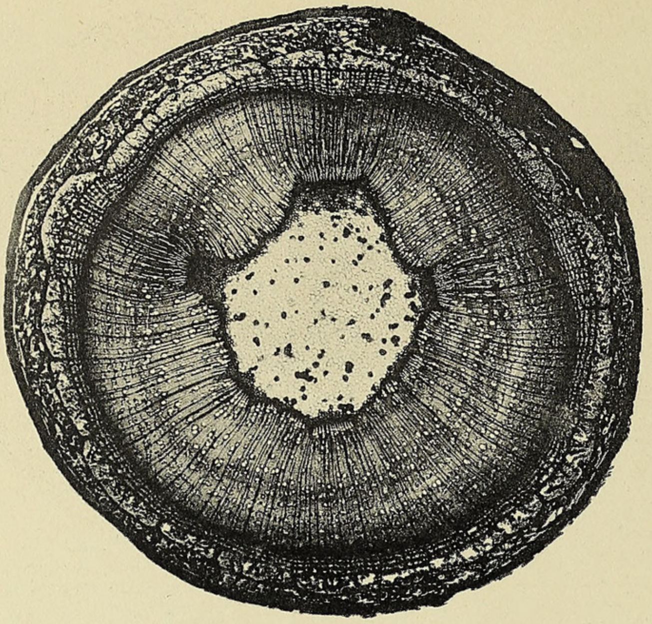


11.

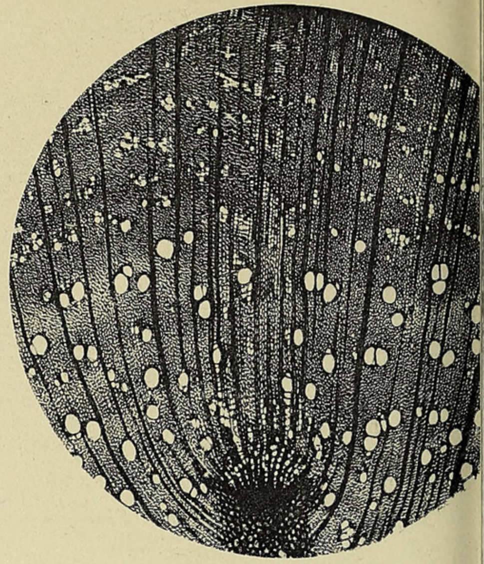


12.

Huth coll.

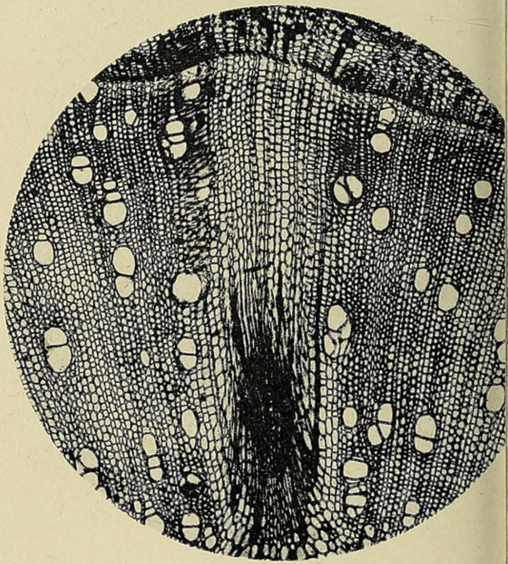


13.

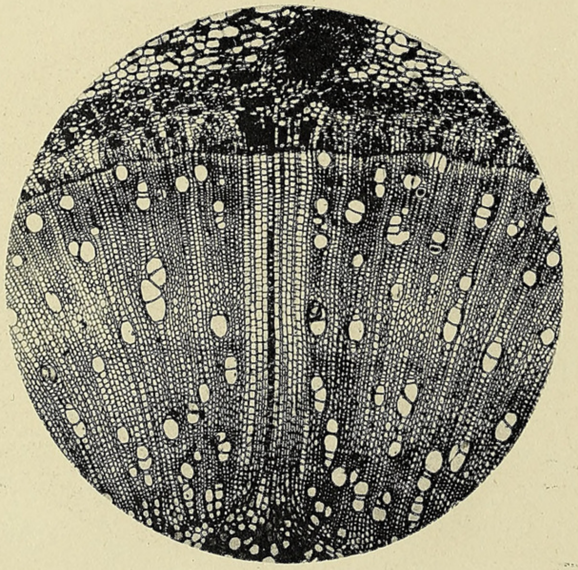


14.

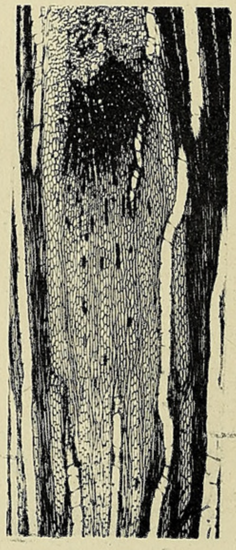
15.



16.



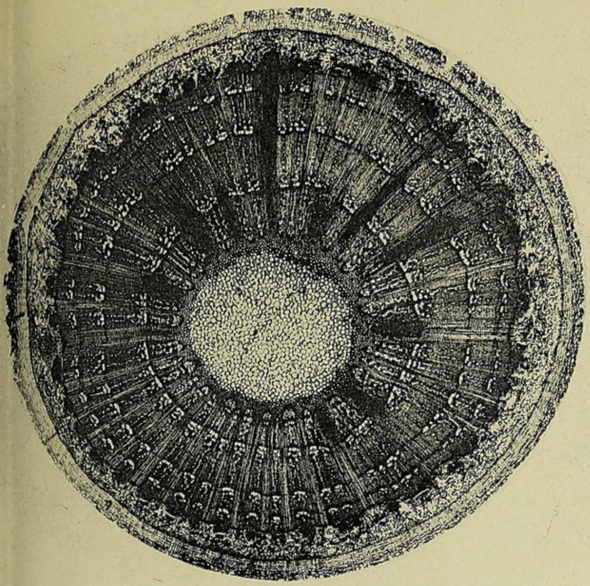
17.



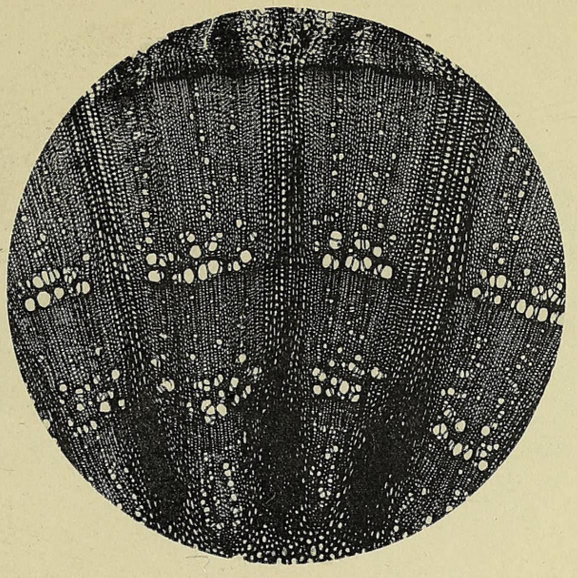
18.

19.

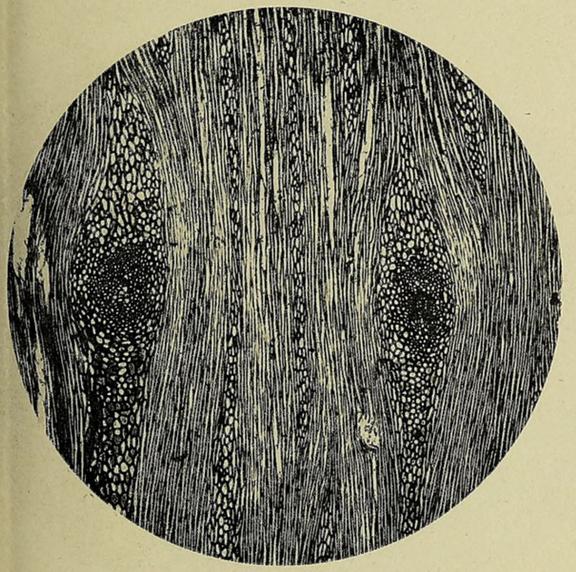
JEFFREY — HERBACEOUS DICOTYLEDONS.



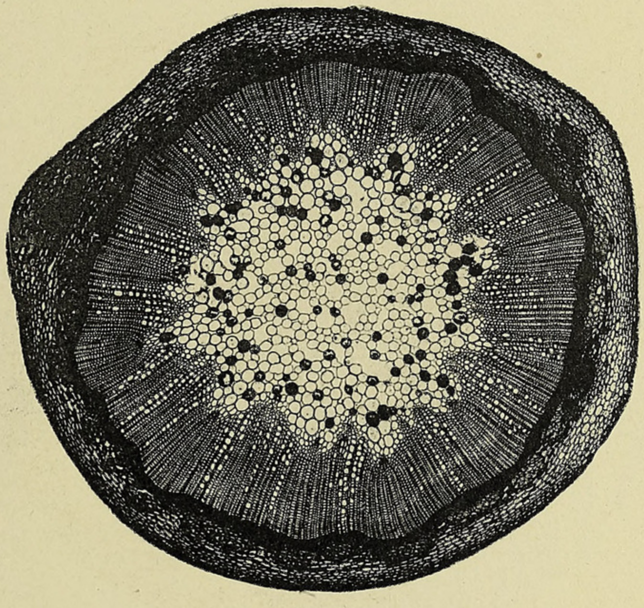
20.



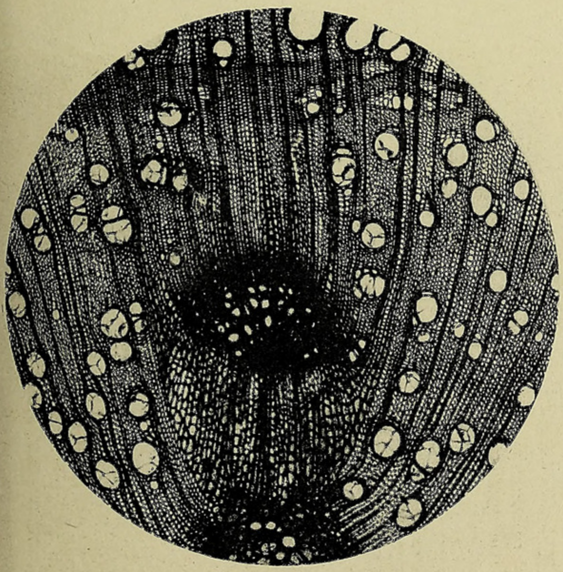
21.



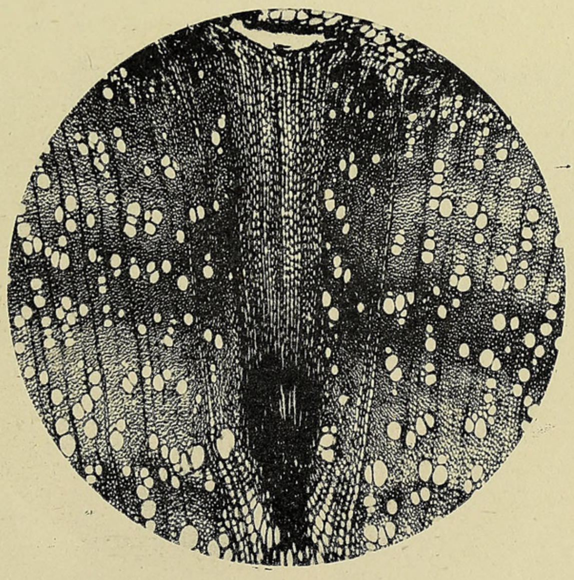
22.



23.

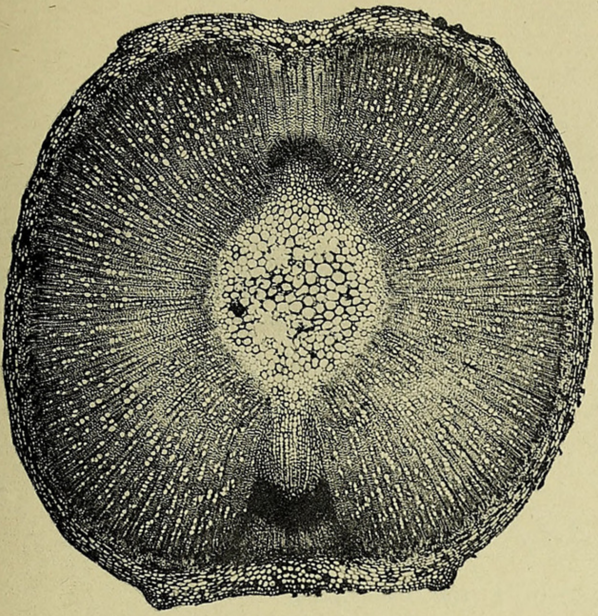


24.

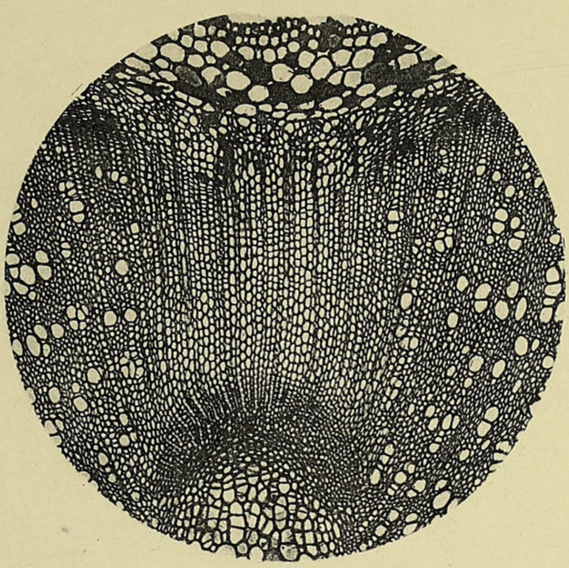


25.

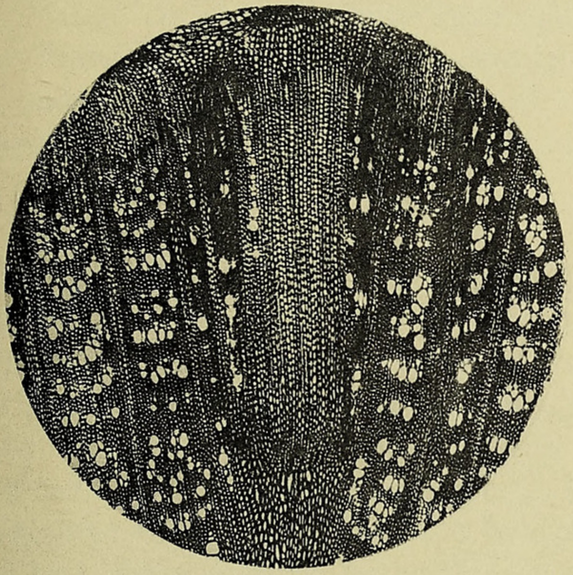
Huth coll.



26.

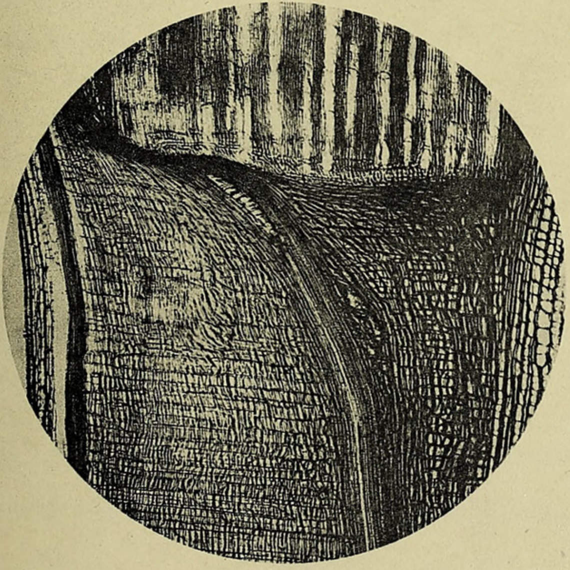


27.



28.

29.



30.

31.

32.

Huth coll.

JEFFREY — HERBACEOUS DICOTYLEDONS.