Some Features of the Anatomy of the Vitaceae.¹

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With Plate XV.

THE wood structure of *Vitis*, distinguished by large vessels, broad rays, and septate tracheides, has been cited, together with that of *Aristolochia* and *Clematis*, in support of the theory that the woody cylinder of plants is derived by the coalescence of a ring of originally separate fibro-vascular bundles. The broad rays were called the 'primary' rays because they were supposed to be formed from fundamental tissue between the primary bundles. Later other rays, frequently linear, appeared in the segments of the wood, while at the same time the fascicular cambium extended across the broad rays and began to lay down secondary tissues between the primary bundles. In this manner secondary growth of the stem proceeded. According to this view, the herbaceous stem, characteristic of primitive plants, has given rise to the woody cylinder increasing by secondary growth in perennial forms. If this be the true order of development, *Vitis* is intermediate in structure between the herb and the tree.

By evidence gathered in recent investigation, this hypothesis of the origin of the woody cylinder and of the herbaceous stem has been replaced by another which seems more accurately to explain the facts. In both Lycopsida and Pteropsida, in both vascular cryptogams and seed plants, the herbaceous type of stem has proved itself to be more persistent and better adapted to modern conditions of climate.² By the work of Bailey³ and Eames,⁴ on both anatomical and palaeontological evidence, the broad ray of *Quercus* is known to have developed by aggregation and final compound-

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 54.

² Eames, A. J.: On the Origin of the Herbaceous Type in the Angiospermae. *Annals of Botany*, vol. xxv, No. xcvi, p. 215.

³ Bailey, I. W.: Reversionary Characters of Traumatic Oak Woods. *Botanical Gazette*, 1, pp. 374-80, No. 5.

⁴ Eames, A. J.: On the Origin of the Broad Ray in *Quercus*. *Botanical Gazette*, xlix, No. 3.

ing of enlarged rays originally connected with the leaf-trace. Hence, for *Quercus* at least, broad rays are secondary and uniseriate rays are primitive. Finally, Eames has explained the development of the herbaceous stem in the Dicotyledons by the localization of protoxylem and ray parenchyma with the reduction of lignified tissue and the more or less complete disappearance of the interfascicular cambium. Within the bundles, the uniseriate ray either disappears completely or is changed into a radial sheet of wood parenchyma, still appearing like a ray in cross-section, but elongate in the direction of the vertical axis of the stem.

In view of this latter explanation of the origin of the herbaceous stem, the wood structure of *Vitis* and other Vitaceae was re-examined for evidence upon the primitive condition, the mode of development, and the relation of the vine habit to the herbaceous type of Dicotyledon.

As described in detail by Strasburger,¹ the wood of *Vitis Labrusca*, L., consists of wood fibres, septate fibres, tracheides, vessels, and wood parenchyma cells. The wood parenchyma is distributed mainly about the vessels adjacent to the radial rows of tracheal elements, and beside the rays. It is sometimes scattered in radial rows through the wood.

Of chief interest in this study are the multiseriate rays, the so-called 'primary rays' of older text-books, which extend as plates of parenchyma seven to ten cells wide, continuously for a long distance vertically through the stem, although they are interrupted at intervals by the crossing over of tracheides, and less frequently of vessels. The ray cells elongate radially, are rectangular in cross and radial section, and in tangential section five or six angled. The peripheral cells along the sides vary in shape according to their location, and often are elongate in the vertical direction. Thus a sharp distinction between the ray cells and adjacent wood parenchyma cannot always be established. The rays extend from pith to cortex. Between the primary wood bundles, the ray cells are continuous with the round, narrow-lumened, thick-walled, vertically elongate, amyloiferous cells which form a sheath between the protoxylem and the broad, thin-walled cells of the pith. By gradual transition these elongate cells give place to the rectangular ray cells which become more and more elongate radially. The rays grow wider towards the cortex by the addition of adjacent fibres which gradually in the same row assume the characteristics of typical ray cells.

These multiseriate rays occur in the stem of the eleven species of *Vitis* examined. Specific differences exist in the width of the ray, the frequency of the tracheid bridges, and the number of fibres transformed into ray cells. The question now arises as to the origin of the multiseriate ray. Is it a primitive condition in *Vitis*, or has it developed secondarily, as in *Quercus*?

¹ Strasburger, E.: Histologische Beiträge, III. Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen, Jena, 1891, p. 239.

The division of the Vitaceae into two sub-families, the Vitoideae and the Leeoideae, according to Engler and Prantl, is justified on anatomical as well as systematic grounds. *Leea* differs from the other members of the family, nearly all of which are vines climbing by tendrils, in the woody stem and the shrub or tree-like habit. In the wood of *Leea* (of which a transverse section is shown in Pl. XV, Fig. 1), numerous broad rays separate narrow fibro-vascular bundles. The vessels are smaller relatively than in *V. Labrusca*, L., and are intercalated in the radial rows of woody elements. The parenchyma is vasicentric. Dividing the bundles are conspicuous linear rays (shown in detail in Fig. 2), the cells of which are smaller and less regularly rectangular than the multiseriate ray cells. Inasmuch as they are radially elongate and continue through the annual ring, they form a true uniseriate ray.

The uniseriate ray does not normally occur in the adult stem of the species of *Vitis* examined, except in *Vitis californica*, Benth. (the wood of which is shown in cross-section in Fig. 3). The vessels have reached an enormous development, often occupying nearly the entire width of the fibro-vascular bundle; the spring wood consists almost entirely of vessels, with a marked segregation of the woody elements at the end of the annual ring, and the large rays, ten cells wide, are sinuous from compression by the large vessels. Most plainly to be seen in the autumn wood (Fig. 4) are uniseriate rays which continue from ring to ring, bending about the huge vessels of the spring wood, sometimes compressed by vessels on both sides, as in the centre of Fig. 4. As in *Leea*, the cells of the uniseriate rays are small and rounded, but radially elongate. In tangential section the xylem bridges through the multiseriate rays appear sometimes two or three tracheides high. By the more frequent occurrence of these xylem bridges, the rays become elongate-fusiform, a condition somewhat like the marked compound fusiform rays of *Quercus*. In all respects, the wood structure of *V. californica*, Benth., corresponds to the conditions found in *Leea*, except for the large vessels and broader rays, which are special adaptations to the climbing habit.

The mature wood of *V. californica*, Benth. differs from *V. Labrusca*, L. and ten other species examined, in the presence of two sorts of rays, a condition strikingly similar to the ray structure of *Quercus*. The presence of the linear rays may be interpreted as the persistence of a primitive character which has disappeared in the other species, or as the result of reversion and reduction from a primitively multiseriate ray. The application of Haeckel's Law of Recapitulation to the study of plant seedlings is found to explain accurately many difficult problems of anatomy. An examination of the seedling of *Vitis* indicates the primitive structure of the wood. Seedlings of *V. Labrusca*, L., and *V. cordifolia*, Michx. (Fig. 5), exhibit in stem and root

¹ Holden, R.: Reduction and Reversion in the North American Salicales: Annals of Botany, vol. xxvi, No. ci, p. 170.

a ring of bundles separated by multiseriate rays and without intrafascicular linear rays. But below the node where the leaf-traces begin to pass out at five regions conspicuous for reduction in number and size of vessels (a cross-section of the seedling of *V. cordifolia*, Michx., is shown in Fig. 5), a departure from the adult condition is found. Within the leaf-trace segment (Fig. 7) only linear rays occur. The leaf-trace, with the reproductive axis and the root, is known to be one of the most conservative regions of the plant, where primitive structures persist long after they have disappeared in both stem and root. The fibro-vascular bundles of the petiole of *V. Labrusca*, L., cut a short distance from the branch where it is most woody, showed no vestige of uniseriate rays. The presence of the linear rays in the leaf-trace of the seedling in *Vitis* species, where all trace of them has vanished in the adult, indicates that linear rays are a primitive feature of the Vitaceae.

This interpretation of the facts is made stronger by the occurrence, even in the adult stem, of vestiges of linear rays. In *V. Coignitiae*, Pulliat, only multiseriate rays are present in the mature wood (illustrated in Fig. 8), but in the leaf-trace segments of the first year's growth (shown in detail in Fig. 9) the primitive linear rays persist. The primitive rays appear also in the leaf-trace of *V. Doaniana*, Munson (Fig. 10), the bundles of which show more abundant wood parenchyma than does *V. Labrusca*, L.; the leaf-trace segment of the first annual ring exhibits radial rows of parenchyma which appear in cross-section like linear rays. Such rows of parenchyma are to be interpreted as a transformation of ray parenchyma. In *V. arizonica* and *V. cinerea*, Noronha, the multiseriate rays within the departing leaf-trace are formed by the union of very short linear rays. In *V. cinerea*, Noronha, moreover, tannin-filled cells in the xylem of the central cylinder indicate the persistence of wood parenchyma as scattered cells. In the leaf-trace, these tannin-filled cells, arranged in uniseriate radial rows, are a last vestige of linear rays which penetrate the wood and are present in the multiseriate compound ray. In the tendril of *V. Labrusca*, L., linear rays are found in the trace of the tiny bract which subtends the longer branch of the tendril. In these forms where vestiges of linear rays still persist, there can be no doubt that primitively the structure of the wood resembled *V. californica* in the presence normally of linear rays within the fibro-vascular bundles of the central cylinder.

This conclusion is confirmed by evidence from the condition found in wounded wood of *V. Labrusca*, L. One general principle of morphology is that primitive structures which have disappeared in the normal wood are apt to reappear after a wound. The more severe the wound, the more complete is the reversion to primitive conditions. Through the wounded wood of *V. Labrusca*, L., the multiseriate rays were found to persist unchanged except by the strong development of tannin. But at a little distance from the injury, linear rays make their appearance between the multiseriate rays,

extend for some distance as linear rays, and finally become bi- or triseriate.

From the persistence of linear rays in the seedling and the leaf-trace, and the reversion to the uniseriate condition after wounds, *V. Labrusca*, L. and the other species studied may be considered as forms which have lost the linear rays by a process of reduction of ray tissue within the so-called bundle. If this be the correct interpretation of the presence of the linear ray, *V. californica*, Benth., retains the earlier condition and is the most primitive member of the genus.

In a less thorough examination of two other genera of the Vitoideae some interesting conditions were found. The wood of *Ampelopsis Veitchii*, Hort. (shown in transverse section in Fig. 11), resembles closely the structure of *Vitis* in the large vessels, the broad rays, and the absence of linear rays. The wood is reduced to a few scattered libriform fibres, and to segments terminating the annual rings. In this species, as in *V. cordifolia*, Michx., the leaf-trace segment reveals the primitive condition by the persistence of linear rays (Fig. 12). The genus *Cissus* is indigenous in tropical forests, and, according to Schenck,¹ differs from the other Vitaceae in the extreme reduction of the lignified tissues of the stem. Peculiar forms are described in which the stem is transformed by the excessive development of parenchyma and ray tissues into soft, stout 'water reservoirs'. In *Cissus nummularifolia*, the most woody of the species examined, the rays are only four or five cells broad, the wood is segregated as in *Ampelopsis*, and the vessels are large. In the leaf-trace segment of this species, vestiges of linear rays were found in the first annual ring. But in *Cissus cordata*, Roxb., and *Cissus discolor*, Blume, the reduction had progressed further. In the latter, the rays are wider than the bundles, which are reduced to a single row of large vessels surrounded by libriform fibres. Some of the fibres, particularly near the pith, are transformed into parenchyma. Here no trace of the linear rays was found. The stem might almost be taken for a woody herb.

From the study of these four genera, it seems probable that the ancestors of the Vitaceae were originally woody perennials without the climbing habit. The xylem cylinder of the stem was interrupted by both multiseriate and linear rays. For a time the two types of ray existed side by side, the broad ray serving for storage in connexion with the leaf-trace. The uniseriate rays lay within the bundles of the wood. In this condition, *Leea* still remains a tropical shrub, and is on anatomical grounds the most primitive genus in the Vitaceae.

From forms like *Leea* the other genera are probably derived. With the taking on of the twining habit came a need for mechanical strength combined with flexibility. The formation of parenchyma by the fibre ele-

¹ Schenck, Heinrich: Beiträge zur Biologie und Anatomie der Lianen, Jena, 1892-3, Part II, p. 137.

ments of the xylem is the means by which the herbaceous stem has developed as a result of the influence of the leaf-trace. In *Vitis* the development of broad rays has progressed synchronously with the reduction of radial parenchyma tissue within the bundle. So the intrafascicular rays of all the *Vitis* species investigated, with the exception of *V. californica*, Benth., have been transformed into radial wood parenchyma, or they have entirely disappeared except as vestiges in the leaf-trace segment of the first annual ring and particularly in that of the seedling. *V. californica*, Benth., is therefore the most primitive American species of *Vitis* examined, and those species which retain vestiges of the primitive rays in the adult or the seedling are more conservative of ancestral characters than those forms in which all trace of the rays has been lost.

The tendency of the bundle to a reduction of lignified tissue is shown in the increase of the broad rays at the expense of the wood fibres, and in the abundance of septate tracheides which are a stage in the transformation of xylem tissue into parenchyma. With the reduction of lignified tissue advances the elimination of radial parenchyma within the xylem. By this process the condition of *Ampelopsis* and *Cissus* is achieved. The development of the vine habit in the Vitaceae is an approach to the herbaceous type of stem. Like the herbaceous habit, it is brought about by localization of ray parenchyma and restriction of protoxylem and lignified tissue to definite xylem segments in the stem. By the loss of intrafascicular and finally of fascicular cambium, the transformation of the woody cylinder to the herbaceous stem would be complete. This mode of development is caused by the increased activity of the leaves and the need for greater storage capacity. The broad rays, the pith sheath, the elements of the phloem, all serve this purpose. The libriform fibres segregated in bundles supply the necessary tensile strength for the vine, while the broad parenchyma plates afford great flexibility.

Thus the wood structure of the Vitaceae is intermediate between that of the arboreal and fruticose types and the herbaceous stem. The course of evolution in the family constitutes another link in the chain of facts which supports the new theory of the origin of the herbaceous habit in plants.

CONCLUSIONS.

1. The ancestors of Vitaceae were shrubby or arboreal forms, in the central cylinder of which occurred interfascicular broad rays and intrafascicular linear rays. The genus *Leca* is the most primitive living representative of the family.

2. The linear rays of the mature normal wood of all species of *Vitis* examined have disappeared, except in *V. californica*, Benth., which is on these grounds the most primitive member of the genus.

3. Vestiges of the linear ray persist in other members of the Vitoideae, in the seedling, and in the leaf segments of the first annual ring. It reappears likewise after an injury.

4. From the more complete loss of the linear ray and the reduction of the xylem cylinder to separate woody bundles, *Ampelopsis* and *Cissus* appear to be less primitive than *Vitis*.

5. The vine, derived from woody ancestors, shows an approach to the herbaceous type of stem.

In conclusion, I wish to express to Dr. E. C. Jeffrey my sincere appreciation of the use of materials, and of advice and aid given in the course of this investigation. Thanks are due also to Mr. Arthur J. Eames for the use of seedling material. I am likewise indebted to the Director of the Harvard Botanical Garden for material of *Leea*, and to the Director of the Arnold Arboretum of Harvard University for numerous species of Vitaceous plants.

EXPLANATION OF PLATE XV.

Accompanying Miss Adkinson's article on Some Features of the Anatomy of the Vitaceae.

- Fig. 1. Wood of *Leea* sp. in transverse section, showing both linear and large rays. $\times 40$.
Fig. 2. The same. $\times 100$.
Fig. 3. Wood of *Vitis californica*. $\times 40$.
Fig. 4. The same. $\times 100$.
Fig. 5. Seedling stem of *V. cordifolia*. $\times 10$.
Fig. 6. Segment of the woody cylinder of the same. $\times 100$.
Fig. 7. Foliar segment of the woody cylinder of the same. $\times 100$.
Fig. 8. Section showing both foliar and non-foliar segments of the stem of *Vitis* sp. $\times 10$.
Fig. 9. Part of the same. $\times 40$.
Fig. 10. Foliar segment of the stem of *V. Coignitiae*. $\times 30$.
Fig. 11. Wood of *Ampelopsis Veitchii*. $\times 40$.
Fig. 12. Foliar segment of the stem of the same. $\times 40$.

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Adkinson, June. 1913. "Some features of the anatomy of the Vitaceae." *Annals of botany* 27, 133–139. <https://doi.org/10.1093/oxfordjournals.aob.a089446>.

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