Secondary Thickening in *Kendrickia Walkeri*, Hook. f.

BY

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With Plate XXXI.

IT was suggested to me by Professor Bower that the secondary thickening in the stem of *Kendrickia Walkeri* might afford an interesting field for investigation. For the material on which my observations were made, and for much valuable assistance during the course of the investigation, I am indebted to Professor Bower.

Kendrickia Walkeri, Hook. f., a member of the family of Melastomaceae, is an epiphytic climbing shrub, which, like the ivy, climbs by adventitious roots. It is found growing on the Anamallay Hills, S. India, and in Ceylon 'in the forests of the lower Montane zone, and extending down to 2,000 ft. in the Kukul Korale.'¹ The lower parts of the stems are said to be flattened with distichous leaves, but at the summit they are spreading, pendent, bearing leaves on all sides.²

Upon preparing sections of the stem, it was found that even the finest twigs showed a slight development of secondary thickening, which, to all appearance, had taken place in a perfectly normal manner.

The arrangement of tissues in this early stage corresponds with the type (c) described by De Bary.³ Here the vascular bundles form a continuous ring, which 'assumes the structure of a vascular bundle', no primary medullary rays being present. Other members of the Melastomaceae also possess this same arrangement. Pl. XXXI, Fig. 1, represents a transverse section of a sector of a stem at this stage. In the centre of the stem is the somewhat large pith, containing an occasional ill-developed cauline bundle, which is not shown in the figure, and, projecting into the pith, are a number of prominent, completely separated, internal phloem-groups. A complete cambium ring is present with secondary xylem to its inner

¹ H. Trimen, Handbook of Flora of Ceylon, vol. xi, p. 200.

² Hooker, Flora British India, vol. ii, p. 526.

³ De Bary, Comp. Anat., Engl. ed., p. 457.

side, and secondary phloem to its outer side. The xylem is composed mainly of short, square-ended tracheids, with but few vessels. Many of these xylem-cells present rather a curious appearance, due to the shrinking and curling up in the cell-cavity of the separated inner layer of the thickened cell-wall. This layer is presumably cellulose, from the fact that it stains blue with Schulze's Solution. The xylem of *Medinilla*, another member of the Melastomaceae, also shows this same feature. At this stage neither primary nor secondary medullary rays, nor even isolated groups of parenchyma cells, are to be seen.

In slightly older stems, small patches of thin-walled parenchyma cells, with large intercellular spaces, are found situated at irregular intervals throughout the xylem-ring. These patches are, in all probability, equivalent to medullary spots.¹ They are developed from the inner side of the cambium ring, and consist of cells, identical in size and form with the xylem-cells, from which they differ solely by the absence of thick walls (Figs. 2, 3, and 4). The large intercellular spaces might be considered as another point of difference, but this is not so, because patches of thick-walled xylem-cells with similar spaces are also met with at irregular intervals in the xylem-ring (Fig. 5). In addition to these patches there are a number of large areas of parenchymatous tissue, forming wedges which project radially inwards; they are opposite the slight indentations of the stem surface, and are seen to have developed from the inner side of the cambium-ring. These wedges are never, in stems of this age, continuous with the parenchyma of the pith, nor do they communicate with the parenchymatous patches. The cambium opposite each wedge is slightly deflected towards the centre, in correspondence with the surface indentation, but it is always external to the area of xylem-parenchyma forming the wedge. These wedges are not merely radial spokes in the xylem, but are continuous as broad plates or wedges throughout a considerable length of the stem. The fact that there is no equivalent development on the phloem side of the cambium seems to differentiate these structures from ordinary, secondary medullary rays. The parenchymatous cells of the wedge are identical in appearance with those of the patches (Figs. 2, 3, and 4). In transverse section, in many instances, the cells have rounded-off edges with intercellular spaces so exceedingly well marked that the whole tissue presents somewhat the appearance of being composed of marbles, arranged in a series of regular rows (Fig. 7). At somewhat rare intervals, one or perhaps a small group of three to four thick-walled xylem-cells may be seen enclosed in the parenchymatous wedge. This in no wise disturbs the regularity of the tissue-arrangement, as the xylem-cell is identical in size with its parenchymatous neighbours. This regularity of arrangement, which is also

¹ De Bary, Comp. Anat., Engl. ed., p. 492.

characteristic of other Melastomaceae,¹ is a most striking feature, both in the parenchyma and in the thick-walled xylem, of the secondary thickening in *Kendrickia*.

In stems of about this same age the formation of tylosis is of exceedingly common occurrence. It takes place not into old or damaged xylem-elements, but through the pit-membranes of normal, often newly formed tracheids and vessels (Fig. 6). Occasionally in stems of this age the tylosed cells may develop into sclerotic cells. Although thickening of the cell-wall, with pit-formation, is of fairly common occurrence in tylosed cells, yet actual development into sclerotic cells is somewhat rare. Haberlandt² cites a few cases in which such a development occurs.

The fact that tyloses are thus prominent features in the still comparatively young stem is of considerable interest, when viewed in the light of the changes which take place in the older stems to be described later.

In most instances this wedge-formation goes on coincidentally with the rest of the secondary thickening, and no further changes are observable until the stem has gained considerably in thickness. The size of the stem, however, is not always an indication of the extent of the internal changes. Occasionally a stem of small diameter may have a much more complicated internal structure than one of much greater diameter.

It is after the stem has acquired the structure above described that the apparently mature cells of the secondary zone of thickening begin to show a rather abnormal development, which takes origin in one or several cells, at the central margin of the parenchymatous wedges. These cells take upon themselves new growth, and enlarge or dilate laterally and in a central direction. This enlargement is accompanied by cell-division, and the resulting cells then proceed to encroach upon the hard xylem area, and, as is evident from the figures, this may take place in either of two ways. In Fig. 7 the process has been one of penetration of parenchymatous projections, between the contiguous walls of xylem-elements, by means of which adjoining rows of tracheids have been split apart. In this figure it is found by counting from left to right that there are ten rows of parenchymatous cells and ten rows of tracheids. The new growth from the cells of the third row of the wedge, which is shaded in the figure, has penetrated between the third and fourth rows of tracheids, in the first instance to the extent of three cells deep, then, having separated the second and third tracheids of this fourth row, has proceeded to interpolate the product of its division, between the fourth and fifth rows, until there is a direct parenchymatous connexion between the wedge (*a*) and the patch (*b*). In this case tylosis has played no part whatever, and, as is evident from the figure, not a single tracheid is missing.

¹ Voechting, in Hanstein's Botanische Abhandlungen, iii, p. 1, 1875.

² Physiologische Pflanzenanatomie, p. 283.

In Fig. 8 the ingrowth has taken place mainly from the cell (*d*), and here the tracheid (*e*) is the only one of its row which has escaped destruction. From comparison with other examples of similar cases, it is highly probable that tylosis into the missing tracheids first took place, and that these tylosed cells, partly by their own expansive force and possibly partly by absorption, caused the complete disappearance of the row of tracheids, of which (*e*) is the sole representative. No trace of the lost tracheids is to be seen, with the exception perhaps of an occasional slightly pronounced thickening of a wall of one of the cells of the new ingrowth. This, however, may also be present, in cases where there is no suspicion of tylosis having occurred.

In Fig. 9 the processes seem to be coexistent. The cell marked (*a*) in the figure has evidently been a tracheid into which tylosis has taken place, and subsequently its contents have overstepped their bounds and penetrated between two adjoining rows of tracheids. In Fig. 10 rather a good example of this process is seen in a somewhat earlier stage. The two cells (*a*) are probably parenchymatous cells; cells (*b*) and (*c*) seem to be tracheids, into which tylosis has taken place, and which have undergone a slight expansion. A small process from cell (*c*) indicates the point at which penetration between the two neighbouring tracheids is about to take place. In Fig. 11, where the process has advanced somewhat farther, a solitary row of tracheids is represented, completely separated by parenchymatous ingrowths from the rows adjoining.

It is rather remarkable that many of these newly formed parenchyma cells develop farther into sclerotic cells, with peculiarly well-marked lines of stratification and pit-formation. As a general rule these sclerotic cells seem to be dotted about haphazard through the new growth; sometimes surrounded by parenchyma-cells, as in Fig. 11, and sometimes inside tracheids or vessels, as in Fig. 13. These cells may possibly be of some use in the splitting process, by acting as blocks, holding apart the separated masses of xylem, and thus assist in relieving the pressure on the ingrowing parenchyma, which must of necessity be very great. This suggestion, however, will not hold good in every instance, as is obvious from the position of many of the cells.

The ingrowth, as a general rule, starts from the two oldest, diametrically opposed wedges, and proceeds towards the pith (Fig. 15), but later the younger, less deep wedges, and even many of the isolated parenchyma patches follow suit.

The result of the process is the division of the axial woody ring into a varying number of small portions, which lie embedded in a mass of large-celled parenchyma (Fig. 14). The arrangement of the separate portions is by no means regular, and varies in different parts of the stem. Occasionally very small fragments of wood, containing only a few tracheids, are found

occupying an oblique position, surrounded by a mass of parenchyma-cells. These have evidently been separated from their neighbours, twisted out of position, surrounded, and then left behind by the cells of the advance guard of the new ingrowth.

The material at my disposal contained only one portion of a comparatively old stem (Fig. 17), but from an examination of this it was quite evident that the changes in *Kendrickia* were by no means at an end when the parenchymatous communications between the wedges and the pith were effected. No formation of secondary cambium in the large-celled parenchyma of the ingrowth was ever observed, but it seemed as if the quiescent cambium, lying between the original internal phloem-groups and the axial woody ring, had, stimulated apparently by the arrival of the cells of the ingrowth, become active once again, and cut off xylem on the one side and phloem on the other. Only four such groups were noted, but from lack of mature material further developments could not be observed.

GENERAL COMPARISONS.

From the naked-eye appearance (Figs. 15, 16, and 17) the stem of *Kendrickia* would seem to resemble rather closely the stem of a climbing *Bignonia*, or one of the Malpighiaceae. In reality, however, the cases are very dissimilar. In these plants, at the stage which would resemble Figs. 15 and 16, the areas of soft tissue, the so-called furrows of Schenck, consist of bast-plates with cambium at their central margins, and result from a decreased formation of secondary xylem, with increased production of secondary phloem at these several points. Very different is it with *Kendrickia*, where the cambium ring remains complete, is never broken up, nor more than slightly deflected towards the pith, and where the appearance of furrowing of the wood is due entirely to the difference in thickening of the cell-wall in adjoining areas of the secondary xylem-elements. The furrow in the one case contains bast, and in the other xylem-parenchyma.

A comparison of the later changes is of great interest. In *Tetrapteris*, one of the Malpighiaceae, the cambium at the inner margin of the furrow, after a period of quiescence, again becomes active, and cuts off xylem and phloem at the sides of the furrow. The medullary rays of the axial woody ring, lying in the prolongation of the furrow, then proceed to stretch and divide, and form broad bands of dilated parenchyma-cells, which split the woody ring into a definite number of segments.¹ A somewhat similar process takes place in the stems of many of the Bignoniaceae.

Hill² points out that in the tuberous portions of the roots of *Bignonia*

¹ Schenck, Beiträge z. Biol. u. Anat. d. Lianen, Pt. ii, p. 115.

² Ann. Bot., vol. xii (1898), p. 323.

Unguis there is a 'breaking up of the xylem into separate masses, often by a certain amount of dilatation-parenchyma'. Unfortunately he does not state the origin of the dilatation-parenchyma, nor the mode of breaking up of the xylem, so that a further comparison of this root with the *Kendrickia* stem cannot be made.

In the stems described above, the splitting which takes place is not, strictly speaking, an entirely new formation. The medullary rays contained in the axial woody ring connect the furrows with the pith, and therefore from the first actually map out the wood by fine lines of divisions into its various segments. Thus by the dilatation and new growth of apparently mature parenchyma a microscopic line of separation is converted into a large conspicuous split.

In *Kendrickia* the axial woody ring contains no medullary rays, therefore there are no existing lines of separation of which to make use. Yet in both cases, though by widely different methods, the same result is reached, viz. large parenchymatous communications between the internal and the external soft tissues.

Schenck¹ discusses the causation of this new growth, and advances as probable the theory that the continued renewal of the bast-plates causes a tangential or radial tension in the axial woody ring, which acts as a stimulus, leading to a dilatation of the lines of least resistance, viz. the primary medullary rays and the pith. In *Kendrickia*, however, the first evidence of the change about to occur is the dilatation and division of one or more cells of the wedge, therefore there is nothing in the nature of preliminary anatomical changes which could constitute a stimulus, tangential or otherwise.

Farther, in the stems mentioned above, the woody ring is divided into a definite number of segments, each with a distinct portion of pith attached to its inner margin; and immediately succeeding the splitting, isolated secondary cambiums become evident at varying intervals in the dilatation-parenchyma. In *Kendrickia*, on the other hand, the separated portions of wood are so small in many cases that they by no means deserve the name of segments; also the pith, if attached, is not always recognizable as such; and lastly, isolated, secondary cambiums are never developed in the dilatation-parenchyma, even in stems at the age of that in Fig. 17. It is quite possible, however, that they may develop in still more mature stems.

Thus it is seen that, although the splitting of the axial woody ring is by no means a rare phenomenon in plants, yet the details of the process in *Kendrickia* are in some ways quite unique. The part which tylosis plays in the process, by utilizing the space contained in the lumen of the tracheids and vessels, with the subsequent destruction of the identity of these cells,

¹ Loc. cit., p. 231.

together with the separation of the rows of tracheids by the parenchyma-cells cutting a path for themselves, seem to be without parallel in the, as yet, described Anatomy of Plants.

EXPLANATION OF FIGURES IN PLATE XXXI.

Illustrating Miss Clark's paper on *Kendrickia Walkeri*.

Fig. 1. Transverse section of a young stem of *Kendrickia Walkeri*. *M* = pith; *int. ph.* = internal phloem; *xy* = xylem; *c* = cambium; *ext. ph.* = external phloem; *K* = cortex; *P* = commencing periderm formation. $\times 180$.

Fig. 2. Transverse section of a slightly older stem showing commencing wedge formation. $\times 120$.

Fig. 3. Longitudinal radial section at the margin of a wedge. $\times 120$.

Fig. 4. Tangential section of the same. $\times 120$.

Fig. 5. Patch of xylem-cells with large intercellular spaces. $\times 180$.

Fig. 6. Beginning of tylosis. *a* = parenchyma-cell; *b* = vessel. $\times 180$.

Fig. 7. Transverse section showing early stage of splitting of the axial woody ring. *a* = central margin of wedge; *b* = parenchymatous patch. $\times 120$.

Fig. 8. Ditto, at a slightly older stage. *a* = wedge; *b* = patch; *c* = pith; *d* = cell from which the ingrowth has mainly taken place; *e* = only tracheid of a row which has escaped destruction. $\times 120$.

Fig. 9. Ditto, at the margin of the ingrowth. *a* = parenchymatous cell. $\times 120$.

Fig. 10. Ditto. *a-a* = parenchymatous cells; *b* and *c* = tracheids filled with tylosed cells. $\times 120$.

Fig. 11. Ditto, at a fairly old stage. *a* = wedge; *b* = isolated tracheid; *c* = pith; *d* = a split or gap in the tissue; *T* = isolated row of tracheids. $\times 120$.

Fig. 12. Ditto. *a* = wedge; *b* = sclerotic cells; *c* = pith; *d* = vessel filled with tylosed cells. $\times 120$.

Fig. 13. Longitudinal radial section at the margin of the ingrowth. *a* = cells at the margin of the wedge; *b* = cavity of a vessel; *c* = a tylosed cell which has developed into a sclerotic cell; *d* = a tylosed parenchyma-cell. $\times 120$.

Fig. 14. Transverse section of the old stem showing a separated portion of the axial woody ring embedded in dilatation-parenchyma. The arrow represents the direction taken by the ingrowth. *a* = wedge side; *c* = pith side. $\times 80$.

Fig. 15. Photograph of the cut surface of the stem. The faint shading connecting two of the wedges through the pith indicates the position of the first ingrowth. $\times \frac{1}{3}$.

Fig. 16. Ditto. Showing slightly different configuration of the wood. $\times \frac{1}{3}$.

Fig. 17. Ditto, of old stem. $\times \frac{1}{3}$.

Clark, A. M. 1907. "Secondary thickening in *Kendrickia walkeri*, Hook.f." *Annals of botany* 21, 361–368. <https://doi.org/10.1093/oxfordjournals.aob.a089140>.

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