The Development of 'Sanio's Bars' in *Pinus Inops*.

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With four Figures in the Text.

THE 'bars of Sanio' are the short rods or bars found stretching, in most cases, from the two tangential walls of the tracheides, cambial cells, and phloem elements, in many Conifers and protruding as small rod-like projections into the lumen of the tracheides in the veins of the leaves of *Juniperus*. In many cases the bars in the wood of Conifers occur as a series of radial rods extending throughout several annual rings. In the xylem region these bars have lignified walls, and in the cambium and phloem walls of cellulose.

The history of their investigation dates back to Sanio (1), and reference to them is occasionally found in the works of later investigators down to the present time. Sanio in his work records what he termed at first a false cell-wall crossing the cell cavities of the tracheides in *Hippophae rhamnoides* and in *Pinus sylvestris*. In radial section these appear as rods crossing from the inner to outer walls, and in tangential section as spots on the tracheide walls. Sanio regarded these at first as possibly being the end walls of tracheides, but abandoned this idea later. He further stated that in radial sections of wood the bars sometimes appear as little sprouts on each tangential wall of the tracheides. Sanio's suggestion as to the origin of the bars is that they arise by a bending in of the two tangential walls of the tracheides, but he failed to find a corresponding depression of the outer contour of the tracheide, and further suggested that this may be due to some optical effect caused by some chemical alteration of the tracheide wall at that point. It was Sanio who first demonstrated that in the xylem region the walls are lignified and in other regions cellulose.¹

Independent of Sanio, von Mohl (2), on investigating the leaf structure of *Sciadopitys*, found bars present in the vascular elements, and further

¹ Confusion was introduced as to these bars by Miss Gerry (Ann. Bot., 1902), by reference to the clear areas above and below the bordered pits of coniferous wood as being the 'bars of Sanio', and further by stating these bars were of a cellulose nature.

records bars occurring in the xylem of the leaves of *Juniperus communis*, *J. Oxycedrus*, *J. oblonga*, and *J. macropoda*, but in this case mostly occurring as projections which end blindly in the lumen of the tracheide.

About the same time C. Winkler (3) recorded the occurrence of bars in *Araucaria brasiliensis*.

The following year Russow (4) observed Sanio's bars in the wood of tracheides of *Abies Pichta* and *Pinus sylvestris*, and found them crossing ten successive annual rings and passing through the cambium and young bast elements: he further records their presence in *Pinus nigra*, *P. Pinea*, *P. Strobus*, *P. Laricio*, and *P. anachuite*.

Mention is also made of rod-like outgrowths by de Bary (5), under the head of 'Tracheides with Transverse Bars', who records them as occupying the corners of the vascular bundles of the stems of *Lycopodium* and in the margins of the vascular bundles of *Juniperus* leaves. de Bary stated that they are somewhat flattened, cylindrical rods branching irregularly on all sides, the branches fusing with one another to form a network through the cavity in some cases, and in others forming thickenings on the walls of the tracheides. In the leaves of *Juniperus* their points of attachment and origin are especially the margins of the bordered pits, in *Lycopodium* the margins of the spiral or reticulate thickenings of the lateral walls. In *Biota orientalis* in the vascular bundles of the leaves the swollen margins of the bordered pits are often elongated into blunt cones, which protrude into the cavity, but end blindly without coalescing with one another or with the opposite wall. With these facts before us, the projections found on the inner walls of the ray tracheides of *Pinus* might also be compared with Sanio's bars, for they project into the lumen of the tracheides, as do the ingrowths in the leaves of *Juniperus*.

In 1890 C. Müller (6) pointed out the wide distribution of these bars, and he gave them the name of 'Sanio's bars', indicating that they occur in the four groups of Coniferae (Abietineae, Cupressineae, Podocarpeae, and Taxineae). Müller further indicated their possible mode of development, and discusses three possible modes of origin as follows:

1. The bars are secretion products of special protoplasmic accumulations in the cambium cells.
2. The bars are produced by partial reabsorption of the transverse walls of tracheides.
3. The bars are formed by an infolding of the tangential walls of the tracheides.

In support of (1) he compared the formation of a cell-wall in cell-division where the new wall is formed from the protoplasm, the formation of a cell-wall in a *Vaucheria* filament when injured in any way, and the formation of cell pegs or bars in *Caulerpa*. His objection to (1) is that if the bars are produced in this way it is not easy to see why they should not

fill the whole lumen of the tracheide, i. e. be a complete transverse wall; and it is difficult to explain their occurrence in radial rows at the same height in the cambium cell, as the protoplasm is constantly streaming. The strand of protoplasm would therefore be stationary, and further the vertical radial plate-like nature of the bars is not possible on this hypothesis. Müller alleges that the bar form, stretching from wall to wall, is not shown in the cambium cell; the bars are free at both ends. (As will be shown later, this statement is not correct.)

2. In support of Müller's second possible mode of origin, that the bars are produced by partial reabsorption of the transverse tracheide walls, he stated that the presence of square ends to tracheides is not uncommon in *Ginkgo*: in some cases rows of tracheides occur, each tracheide having a square end wall. Against this view, however, Müller points out that square end walls are rather the exception than the rule, and that a partial solution of transverse walls is otherwise not known in coniferous wood; and he further points out that if reabsorption took place in tangential sections the bars would appear elongated in the transverse direction, whereas they are elongated in the long direction of the tracheide.

3. In support of his third suggestion, that the bars are formed by folding of the tangential tracheide walls, he points out the infolding of the cell-walls in the mesophyll of Pine leaves, also the folding of the walls of transfusion tissue and the occasional folding over of a tracheide when it comes in contact with a medullary ray.

The view finally adopted by Müller is:

'Sanio's bars' arise from folds of the radial walls of the cambium cells, and the transition from plate to bar form depends on partial reabsorption, which results in the setting free of the bar as a consequence of the total reabsorption of the bar groundwork in the cambium cell.

In 1892 W. Raatz (7), working independently at the same time as Müller, published at a later date his observations on 'Sanio's bars', and added to the list of species in which the bars occur, including the xylem of the veins of the leaves of *Hippophae rhamnoides*, root, stem, and secondary wood of *Salix fragilis*, and *Casuarina equisetifolia*. Raatz pointed out that the bars are not universal phenomena and not structures to be relied on as always occurring, and further stated that in *Abies pectinata* frequently little projections occur on the middle of the bar.

Raatz summarizes the development of the bars in the following way:

1. The bars are more or less abnormalities, not arising in any regular order and not having any definite function.

2. The bars are formed by the tangential walls of the cambium cell coming in contact, and as this cambium cell gives rise to a tracheide and the walls become lignified, so the walls of this bar becomes lignified.

From the various theories as to the origin of 'Sanio's bars' and the

confusion arising therefrom it appeared desirable to reinvestigate their development. Specimens from about twenty-five species of *Pinus* were obtained in May, 1914, and fixed in watery picric acid.

Amongst the species collected was *Pinus Inops*, which, on examination, showed the bars most frequent, and so appeared most suitable for investigation.

Transverse, radial, and tangential sections were taken; for transverse and radial hand sections were found most suitable, but for tangential the

FIG. 1. Transverse section of *Pinus Inops*, showing 'Sanio's bars' crossing xylem (x), cambium (c), and phloem (ph). $\times 520$.

microtome was used after embedding the wood in paraffin wax of 52° C. melting-point.

In transverse sections the bars were found to cross the lumina of the tracheides as relatively thick lignified rods, and in the cambium to be merely fine thread-like structures with cellulose walls, these threads sometimes widening out again in the bast or retaining their thread-like character, but still with cellulose walls. The way in which the bars cross the cambium and phloem could be more easily seen in radial than transverse sections, where, in addition to crossing the sieve tubes, the thread-like bars could be demonstrated crossing the phloem parenchyma (Figs. 1 and 2).

FIG. 2. Radial section of *Pinus Inops*, showing bar of Sanio crossing xylem (x), cambium (c), and phloem (ph). $\times 415$.

The most interesting part of the investigation came out in the serial microtome-cut tangential sections, where whole series of sections could be obtained, tracing the bar outwards from the xylem through the cambium and into the phloem, the bar appearing in section throughout.

In the xylem region the bar appears as a hollow tube varying in out-

line from circular to oval, sometimes the opening being obliterated owing to its lateral walls coming together (Fig. 3, D to F).

An attempt was made to find out whether any substance was present in the cavity of the bar ; protoplasm, cellulose, and fungal hyphae stains

FIG. 3. Series of tangential sections passing from cambium through the tracheides, showing change of shape and variations of thickness in the bar whilst passing through various parts A-F. $\times 390$. A, in cambial region ; B and C, in tracheides near cambium ; D-F, in successively more remote tracheides.

were used respectively, but in no case was it found possible to demonstrate any substance present.

Tracing the bar outwards from a distance of two or three tracheides from the cambium, it was noticeable that, as the neighbourhood of the cambium was reached, the bar became slender with a smaller lumen and

FIG. 4. Series of tangential sections, showing bar in section in cambium and through the two tracheides nearest to cambium. $\times 390$. A and B, in xylem elements ; C, D, E, in cambial elements.

thinner walls, and frequently in the tracheides nearest to the cambium small masses of protoplasm were often found attached to the bar laterally (Fig. 3, B ; Fig. 4, C).

Passing through the cambium with the bar in section, the bar becomes reduced to a small dot showing no hollow in its centre ; if a hollow is present

it is too small to demonstrate. Frequently this dot-like structure is completely enveloped in protoplasm (Fig. 3, A and B), or has small masses of protoplasm attached to it laterally. The thread-like bar continues through the cambium radially and often widens out again in the phloem region.

In all these tangential sections the bar rarely occurs near the transverse end walls of a tracheide, but most frequently about half-way between the end walls. From the evidence obtained by the presence of protoplasmic masses around the bars in the cambium region, it would appear that once started in *P. Inops* the bars continue their existence by means of these protoplasmic masses, but exactly what starts them could not be demonstrated. That they are formed by partial reabsorption of the end walls of tracheides, as suggested by Raatz and Müller, does not seem to hold for this species, as the end walls of the tracheides where they are flattened frequently have bars present a short distance above or below this end wall. The view put forth that these bars are formed by tangential walls of the cambium cells bending in, until they come in contact, did not appear to be the case in *P. Inops*, as throughout the whole radial width of the cambial cells they did not vary in diameter, which would be the case if a folding of the wall took place, as they would appear smallest in diameter in the middle of the cell and gradually increasing towards the outer or inner tangential walls. The following would appear to be the probable explanation of the observations recorded in this paper:

In its first stage as yet revealed a 'Sanio's bar' is a very delicate cylindrical rod stretching radially and freely across a cambium cell in a transverse plane. As the cambium cell grows in a radial direction, the rod keeps pace with it by stretching along its main axis. The cambium cell eventually cuts off a daughter-cell, which in turn grows radially and directly or indirectly, after a further division, gives rise to a tracheide (or sieve tube), with whose radial increase of width the bar keeps pace. At the same time surface growth of the tangential walls of the growing daughter-cell or cells takes place in longitudinal transverse and intermediate directions. The bar, firmly fixed into the primary walls, is at its ends exposed to tension at right angles to its long axis in all directions, and the natural result is a rupture in the centre of the rod, which now becomes hollow. At first it would appear that there is no disparity in rate of growth in surface of the tangential walls in the longitudinal and transverse directions, so that the hollow in the centre of the axis itself is cylindrical in form; but when, as is the case later, growth in length of the cell greatly predominates, the rod is exposed at its ends mainly to tensions at right angles to its main axis in the radial longitudinal plane of the cambium cell, with the consequence that the bar and its central cavity are stretched in a corresponding manner, and the appearance in cross-section is that shown in Fig. 3, F. The bar is thus from a very early stage a solid elastic body, since the tension in

a direction at right angles to its main axis is transmitted from the two ends to the middle, so that the rod becomes hollow along its whole length.

At the same time the rod becomes thicker by means of deposits on it of layers of wall-substance (which in tracheides assumes the form of lignified material and in phloem cellulose). Such a deposit recalls the mode of centripetal thickening of pegs and the like projecting in from the walls of *Caulerpa*, and the projections in the mesophyll of Pine needles and other plants, also the deposit of cellulose on hyphae of a parasitic fungus traversing a living cell whose protoplasm is responsible for the cellulose in question. This explanation explains the continuity of the Sanio bars throughout successive tracheides and sieve tubes, the growth in thickness, the origin of the central hollow, and the final shape of the mature bar, but there is no clue to the original inception of the bar in the cambium cell.

SUMMARY.

1. Sanio's bars are small rods crossing the tracheides, cambium, and phloem elements in many Conifers.
2. In phloem and cambium the walls are of cellulose, whilst in the xylem region they are lignified.
3. In cambium the bars exist as thin solid rods, and in the xylem and phloem as more or less hollow rods.
4. Small masses of protoplasm frequently surround the rods in the cambium cells and suggest a possible mode of origin.

In conclusion, I wish to convey my best thanks to Professor Percy Groom, of the Imperial College, for his help and profitable suggestions during the progress of the investigation, and to Mr. A. W. Hill, Assistant Director of the Royal Botanic Gardens, Kew, for allowing me to have specimens of Pine woods from the Kew Collection.

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