# A CONTRIBUTION TO THE ANATOMY OF *SALVADORA PERSICA* L. WITH SPECIAL REFERENCE TO THE ORIGIN OF THE INCLUDED PHLOEM[1]

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## 1. Introduction

Little is known about the exact mode of origin of the included phloem in angiosperms. In their review of plant anatomy, Eames and MacDaniels (1925, p. 258) state that there are two methods by which groups of phloem cells become embedded in the secondary xylem. In genera like *Combretum* and *Entada*, the cambium, besides cutting off secondary phloem on its outer side, also gives rise to isolated strands of phloem towards the inside in place of xylem cells which are normally produced. After a brief period of such activity these cambium segments return to their normal function, and thus bury the inwardly formed phloem within the wood. In other forms, of which *Strychnos* is the best known example, the included phloem strands are originally formed by the cambium towards the outside as a part of the normal external phloem but later on new " extra-fascicular " cambial segments arise in the pericycle and unite with the general cambium cylinder so that each phloem strand becomes enclosed between a segment of the old or " residual " cambium and the new one. Of these the former becomes more or less inactive, but the latter produces xylem and phloem in the normal way so as to bury the included phloem deeper and deeper into the stem. This process is repeated several times at a number of places all around the circumference of the stem resulting in numerous " islands " of phloem within the xylem. Eames and MacDaniels (1925, p. 258) further remark that the behaviour of the cambium in such growth types has been studied in detail in but a few instances and add that probably only one of these methods (the *Strychnos*-type) occurs in all cases.

As regards *Salvadora persica*, which is the subject of the present study, Rosenvinge (1880) thought that the phloem islands (see Fig. 1) were cut off centripetally by the first method. Scott and Brebner (1889) and Chodat (1892) supported this view. A few years later Leisering (1899) ' from an examination of dozens of preparations

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[1] In accordance with the terminology given by Record (1933, p. 2) the term "Included phloem" is used in this paper in place of the former "Interxylary phloem".

of the stem' found that the phloem of the mature islands is not in direct contact with the xylem on its inner side (which ought to be the case if Rosenvinge's view is correct), but is separated from the latter by at least one and usually 2–3 layers of cambial cells. He therefore concluded that the development is similar to that in *Strychnos*, although he could not prove it with absolute certainty. Pfeiffer (1926) calls attention to the controversy regarding the origin of the phloem islands in *Salvadora* and suggests the need for a reinvestigation.

## 2. Material and Methods

*Salvadora persica* is a common tree in the North, West and South India. The material used in this study was collected from Agra, partly by Dr. P. Maheshwari and partly by Mr. B. L. Gupta and consisted of pieces of the root and stem preserved in formalin-acetic-alcohol. As the woody portion is very hard, short pieces of the stem and root were treated with dilute HF before embedding them in paraffin. Some sections were also cut on the sliding microtome without any embedding or pre-treatment. Safranin and Fast Green were used for staining. Some material of *Salvadora oleoides*, collected from Bharatpur, was also cut for comparison.

## 3. The Stem

*General Anatomy.*—In a t. s. of a moderately old stem the epidermis is seen to be replaced by a superficial layer of cork, whose outer cells seem to flake off at intervals (see Fig. 2). The phellogen arises sub-epidermally and cuts off centripetally a narrow zone of tangentially elongated cells composing the phelloderm.

The cortex is narrow consisting of only a few layers of thin-walled cells often containing druses or rhomboidal crystals. Due to the secondary changes in the stem these cells have a more or less flattened and distorted outline. An endodermis is not clearly differentiated, but the beginning of the pericycle is indicated by isolated groups of sclerenchymatous fibres connected to one another by means of thick-walled pitted cells.

At this stage the primary phloem is already crushed and almost indistinguishable. Even the secondary phloem is a narrow zone (Fig. 2), but this deficiency is more than made up by the intracambial phloem "islands" which are numerous and form a very conspicuous feature of the stem.

Next to the phloem is the cambium cylinder which is an actively dividing zone consisting of 4–5 layers of cells in my material. I am unable to support Leisering's statement that it forms a wide meristematic zone consisting of several layers of cells. He evidently included under the "cambium" the patches of undifferentiated parenchymatous cells cut off by it towards the inside which remain unlignified and even continue some periclinal divisions for a time (Fig. 1). It is these patches of thin-walled cells which subsequently become differentiated into the phloem islands which are dealt with in a subsequent paragraph. The wood forms the largest part of the stem. It consists of vessels, parenchyma, and fibres. At the inner end are seen more or less radial rows of the first formed xylem vessels which protrude into the pith. Some of the protoxylem vessels are seen to be distorted and crushed owing to the enlargement of the adjacent cells of the pith. In the secondary xylem the vessel elements are numerous, rather short and narrow-lumened and occurring in groups of 2 to 8. They have simple perforations and the walls bear many alternate bordered pits. The xylem fibres are numerous and thick-walled with a few reduced bordered pits having extended slit-like apertures. The xylem parenchyma cells are particularly numerous around the vessels and phloem islands. Their walls are thin and have simple oval or rounded pits. The vascular rays are 1–7 cells wide and consist of radially elongated cells often containing squarish, rhomboidal or rectangular crystals. Such portions of the rays which pass through the phloem (normal or included) are thin-walled, but the rest consist of thick-walled pitted cells.

The pith has a more or less four-sided outline in a t.s. of a young stem. Its cells are spherical with pitted walls separated by small intercellular spaces; some of them may contain solitary druses.

*Origin and Structure of the Included Phloem.*—Soon after secondary growth has commenced, the outer margin of the secondary xylem presents a more or less indented outline, which is due to the fact that at certain places the cambium cuts off towards the inside some tangentially elongated groups of thin-walled parenchyma in place of the usual lignified cells of the wood. These cells lie in perfect radial rows and differ from the cambial cells, from which they have been produced, only in having a larger radial diameter. After a short while the cambium resumes its normal activity so that the bays of thin-walled parenchyma become enclosed between the thick-walled cells of the previous and the newly formed wood. As growth proceeds some of the central cells in the islands differentiate into one or more groups of sieve tubes and companion cells (Fig. 3) but the peripheral cells still remain parenchymatous and often undergo some periclinal divisions so as to form a weak secondary cambium on the inner as well as the outer face of the phloem island (Fig. 4). In some cases the differentiation of phloem elements in the island may start even before it is actually buried into the wood, so that for a short while and at certain places phloem cells may be seen on both sides of the cambium cylinder. Only the outer of these belong to the normal phloem which is however extremely reduced in quantity, while the inner are destined to become included in the xylem. The sieve plates are usually obliquely placed. There is no special structural difference between the outer and the included phloem except that in the former some thick-walled fibres are also present. In a t.s. of a stem, about 1·3 cm. in diameter, more than 600 " islands " were counted in the wood and since *Salvadora persica* is a fairly large tree, their number must run to several thousands at the base of the stem. The inner and earlier formed phloem islands are smaller than the outer. They are further more or less circular or oval, while the outer and more recently formed groups of phloem are very much elongated tangentially, some even becoming confluent with one another at the sides.

In the older and consequently more deep-seated islands some of the central cells get degenerated and form one or more darkly staining patches in each island (Fig. 5). As regards the cause for this obliteration Pfeiffer (1926) was unable to come to a decision and suggested two possibilities, *viz.*, that this condition may either be due to a continued activity of the primary cambium enclosed in the bundle (as in *Strychnos*) or it may be caused by a division of the elements composing the island itself. My observations lead me to the conclusion that the second view is the correct one for *Salvadora*, as also for *Leptadenia* (Singh, 1943). Cell divisions accompanied by subsequent differentiation and enlargement of the elements continue to take place in the islands for a fairly long time, but being enclosed by the thick-walled cells of the wood on all sides, the phloem cells do not find enough space for outward expansion and the whole force is therefore directed inwards resulting in a crushing of the central cells. It is also observed that the thin-walled cells of the rays which happen to pass through the older islands may similarly get crushed along with the phloem elements.

As noted before, there are often seen on the margins of the older islands a few cells which have a cambial nature. A careful study revealed that this is a secondary meristem which may appear in segments on any one side, or more than one side of the island or even all round it. If it first arises on the inner side it may give the false impression that it is an embedded segment of the original cambium ring and that the development is of the *Strychnos*-type. The activity of this cambium-like layer, and the pressure caused by it towards the centre of the island, may also be partly responsible for the crushing of cells in this region.

## 4. THE LEAF

*Petiole.*—A t.s. of the petiole has a more or less circular outline with the upper side slightly flattened. The epidermis is heavily cutinised on the outside. The cortex is a broad zone of thin-walled parenchymatous cells having small intercellular spaces between them. The outer cells, forming a 2–3 layered hypodermis are polygonal, with slight thickenings at their angles and often without any intercellular spaces. There is no indication of an endodermis. The stele has an oval or flattened horse-shoe shaped form with a much greater development of the vascular tissue towards the rounded abaxial side. Small groups of fibres lie outside the isolated groups of crushed primary phloem cells. In the centre there is a very narrow flattened pith consisting of small thin-walled cells. The structure of the xylem and phloem is somewhat similar to that in the stem and it is worthy of note that the included phloem is present even in the xylem of the petiole.

*Lamina.*—The upper and the lower epidermis each consists of 1–2 layers of cells. Their outer walls are covered with a thin layer of cuticle. Stomata are present on both sides. The guard cells are small and are somewhat sunken below the general level of the epidermal cells. Subsidiary cells lying parallel to the stomatal pore are clearly seen in surface preparations. The mesophyll consists of a palisade tissue on both sides enclosing a parenchymatous region along the middle line. The palisade cells are tubular and compactly packed and contain a large number of chloroplasts whose number gradually diminishes towards the interior. Interspersed amongst them are some large pouch-like cells which are considered by Sabnis (1921) to have a water-storage function but it seems that he did not notice the large spheroidal crystal in each of these cells which usually dissolves in the process of preparation of the slides. It may be added that Sabnis also failed to observe the crystals in the inner tissues of the leaf in either *S. persica* or *S. oleoides*. The cells between the two palisade regions are horizontally elongated and contain very few or no chloroplasts. Here and there in this region occur the veins and some small groups of thick-walled pitted cells which may either serve for storage of water or merely serve to give the necessary rigidity to the leaf.

The *midrib* shows a greater convexity towards the lower side. The palisade cells are continued on the upper side, but their place is occupied on the lower by large collenchymatous cells which may or may not have any intercellular spaces between them. The included phloem continues for a certain distance in the lamina, but as the amount of secondary growth decreases, it gradually disappears towards the tip.

## 5. THE ROOT

*General Anatomy.*—The root may be diarch to tetrarch. The primary xylem strands frequently meet in the centre to form a solid xylem plate but more often a small pith is present. Secondary growth begins early and is accompanied by cork formation. The primary phloem soon becomes crushed and is unrecognisable. The secondary phloem occurs in the form of pyramidal strands composed of sieve tubes, companion cells, fibres and phloem parenchyma. In older roots it is the secondary xylem which occupies the largest proportion of the space in a t.s. Like the stem it also contains a considerable number of phloem islands scattered through it. The wood elements consist of vessels, fibres and parenchyma. There are two to four primary rays, one opposite to each primary xylem group. These are much wider than the subsequently differentiated secondary vascular rays which have the same structure as those in the stem.

*Origin and Structure of Included Phloem.*—The phloem islands arise in the same way as in the stem. The later formed islands are usually larger and more elongated than the first ones. Although they do not occupy any definite position in the wood, it appears that at least in later stages there is some kind of a periodicity in the activity of the cambium, which, roughly speaking, produces the thick-walled cells destined to form the wood and the thin-walled cells destined to form the included phloem, in more or less alternating layers.

The structure of the individual islands, the course of degeneration of the phloem cells and the differentiation of the secondary cambium show such close similarity with the stem that a detailed description seems unnecessary.

## 6. Comparison with *Strychnos nux-vomica*

While studying the origin of the phloem islands in *Salvadora*, I also cut for comparison some material of *Strychnos nux-vomica*[2] in order to gain a better insight regarding the resemblances and differences between these two forms.

My observations on *Strychnos* fully confirm those of Scott and Brebner (1889) whose account has for a long time remained the only clear exposition of the origin and nature of the phloem islands. As stated by them the islands are at first produced centrifugally as a part of the normal external phloem, but later they become bridged over by the " complementary " cambial segments, which join on to the main cambial ring (Fig. 6). These short cambial arches function normally by producing xylem towards the inside and phloem towards the outside. As a result the first formed phloem groups become buried into the wood, each having a centripetally embedded cambial segment which was once a part of the original cambium. This continues to cut off some new phloem towards the outside (but no xylem) with the result that the older phloem cells become crushed to form a sort of a cap on the outer face of each island. The islands in this species of *Strychnos* are small and circular or oval but in *Strychnos Mitscherlichii* Cockrell (1941) found that they are tangentially elongated.

It is to be noted that in *Salvadora* the condition is quite different. Unlike *Strychnos nux-vomica* the included phloem is here cut off centripetally from the normal cambial cylinder. The islands do not have any embedded cambium that can be traced back to the original cambium ring but a weak secondary cambium may occasionally arise on one or more than one side of some of the older islands. Further, the crushing of the phloem tissue takes place in the centre and not on the outside. The cap-like tissue of disorganised cells, seen in *Strychnos* is therefore not found here.

## 7. Conclusion and Summary

In conclusion, it may be said that the included phloem found in the wood of *Salvadora* (root as well as stem) is differentiated from the thin-walled parenchymatous cells cut off by the cambium on its inner side. Subsequently the cambium resumes its normal activity and the phloem becomes more and more deeply embedded into the wood.

If Leisering (1899) had made a developmental study of the included phloem and also compared the position of the crushed cells in the islands in *Strychnos* and *Salvadora*, he would not have come to the conclusion that they have a similar origin. As shown in this paper

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[2] The material of this plant was very kindly collected for me by Mr. J. Venkateswarlu (Waltair) and Mr. M. A. K. Khalil (Dehra Dun).

it is not satisfactory to rely on the presence or absence of an embedded cambial segment on the inside of an island, for such a cambium although it seems to be characteristic of the *Strychnos*-type, may differentiate secondarily in other cases.[3] It may be pointed out that the suggestion (Eames and MacDaniels, 1925, p. 258) that of the two methods of origin of included phloem, only the *Strychnos*-type occurs in all cases and the other is probably non-existent, is incorrect.

## 8. ACKNOWLEDGMENTS

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[3] Besides *Salvadora* which has been described here and *Leptadenia* (Singh, 1943), such a secondary meristem is also reported to occur around certain groups of phloem cells in the roots of some Cruciferoe (Weiss, 1883), Cucurbitaceae (Scott and Brebner, 1889), *Ipomoea batatas* (Artschwager, 1924), and *Asclepias obtusifolia* (Scott and Brebner, 1890–91).

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## 10. EXPLANATION OF FIGURES

### PLATE III

Fig. 1. *Salvadora persica.*—A cross-section of an old stem to show the distribution of the phloem islands. × 5·5.

Fig. 2. *S. persica.*—A segment of an old stem showing the origin of the included phloem. × 66.

Fig. 3. *S. persica.*—A young phloem island showing the differentiation of sieve tubes and companion cells. × 180.

### PLATE IV

Fig. 4. *S. persica.*—An included phloem island with some cambium-like cells on its outer as well as inner side. × 410.

Fig. 5. *S. persica.*—An old phloem island showing the crushing of the central cells. × 410.

Fig. 6. *Strychnos nux-vomica.*—Portion of cross-section of a stem showing the centrifugally formed phloem with an extrafascicular cambial segment on its outer side. × 290.

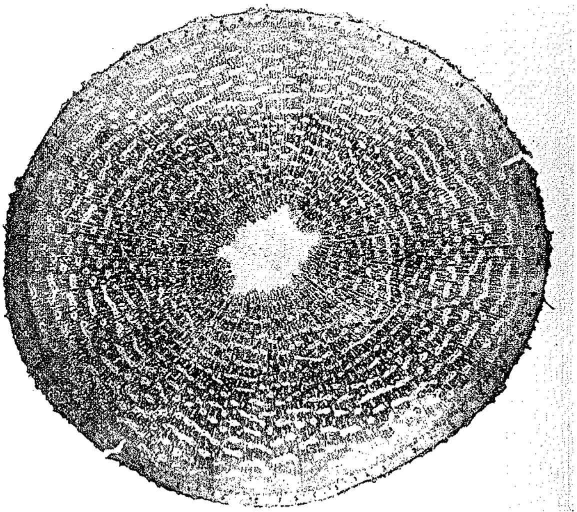

FIG. 1

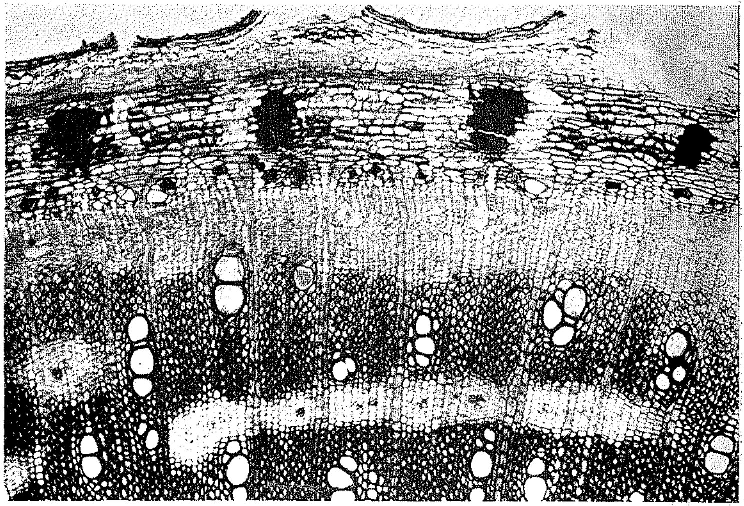

FIG. 2

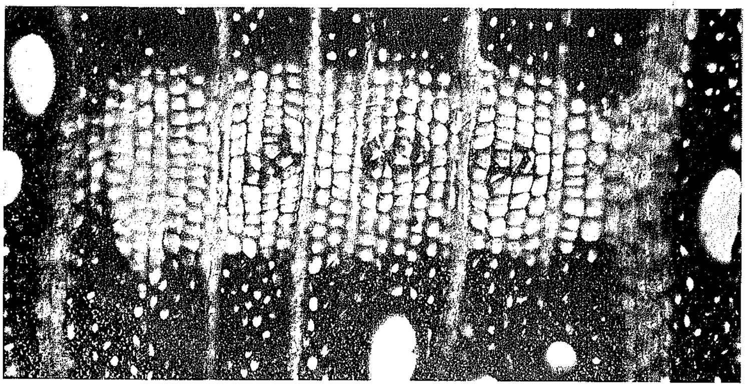

FIG. 3

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*A CONTRIBUTION TO THE ANATOMY OF* SALVADORA PERSICA *L.*

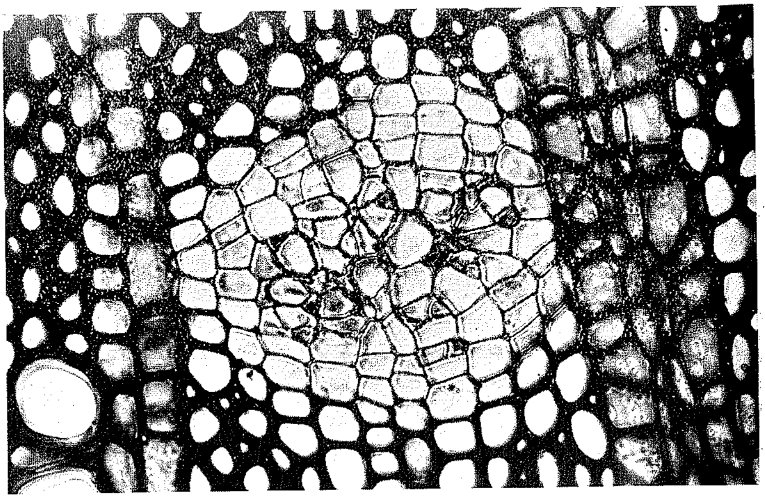

FIG. 4

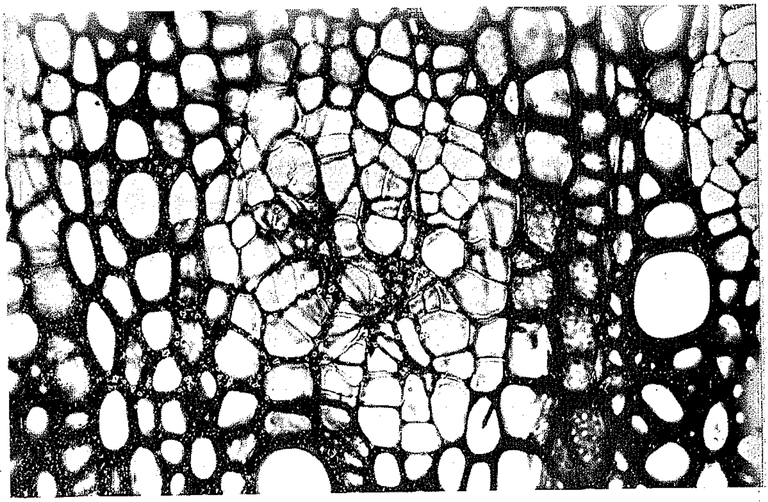

FIG. 5

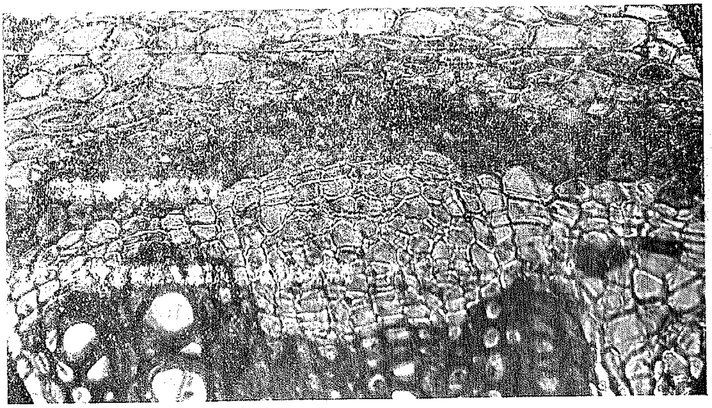

FIG. 6

BALWANT SINGH—

*A CONTRIBUTION TO THE ANATOMY OF* SALVADORA PERSICA *L.*