THE DEVELOPMENT OF HORIZONTAL CANALS IN RAYS

By M. Margaret Chattaway*

[*Manuscript received August* 23, 1950]

Summary

The development of horizontal canals has been studied by means of serial tangential sections in three genera of non-pored (gymnosperm) and six genera of pored (angiosperm) woods.

Horizontal canals, which occur in the rays of some genera of woody plants, originate as the result of changes in the cambial layer and are always developed in conjunction with vertical canals.

In the genera studied, vertical canals were found only in the xylem in non-pored timbers and only in the phloem in pored woods. They result from changes that either affect the cambial initials temporarily, or affect only the daughter cells, for subsequent divisions of the initials produce once more the normal tissue sequences of xylem or phloem.

The horizontal canals result from the same stimuli, and their origin is thus different in the two types of wood; it is in the vertical canals of the xylem of non-pored woods and in those of the phloem of pored woods. The changes that produce the horizontal canals affect the ray initials themselves permanently, for once the canals are formed they are continuous through the rays in both the xylem and the phloem that is subsequently produced.

I. Introduction

The presence of radial canals and secretory tubes in the rays of wood has, for many years, been considered a reliable diagnostic feature for purposes of identification; they are seldom traumatic, but are a normal feature of the woods of certain genera, and it is therefore strange to find that the information about them is very scanty. Their presence has been referred to time and again, but few references can be found to any work on their origin or development. Such as can be found is largely the result of investigations on young stems, leaves, and leaf traces. A resumé of the early work is given by de Bary (1884) and it appears that little has been done since, except on some genera of the Coniferae. De Bary mentions that the great majority of the Coniferae have no resin ducts in the primary tissues of the stem except those found in the cortex, and these connect only with those in the petioles and leaves. He mentions, however, that in species of *Pinus, Picea, Larix,* and *Pseudotsuga* there are also canals that are not continued into the leaf, and that these occur in the xylem of the primary bundles. It is significant that these four genera alone have resin canals in the rays. The work of Thompson and Sifton (1925) and the investigations recorded below show, however, that vertical canals are not always present in the

* Division of Forest Products, C.S.I.R.O., South Melbourne.

primary wood, or even in the innermost ring, in species of *Picea* and *Pseudotsuga*. When this occurs the horizontal canals too are absent from the primary rays and make their appearance only in connection with the innermost vertical canals.

The work that has been done on secretory passages in angiosperms is equally far back in botanical history, and has mainly been carried out on small branch material, with the greatest emphasis laid on leaf trace and petiolar bundles and the structure of the outer cortex. There are few references to any work on the mature wood. Such references, however, as are available bear out the evidence that radial canals originate in the secondary phloem of angiosperms and not in the wood.

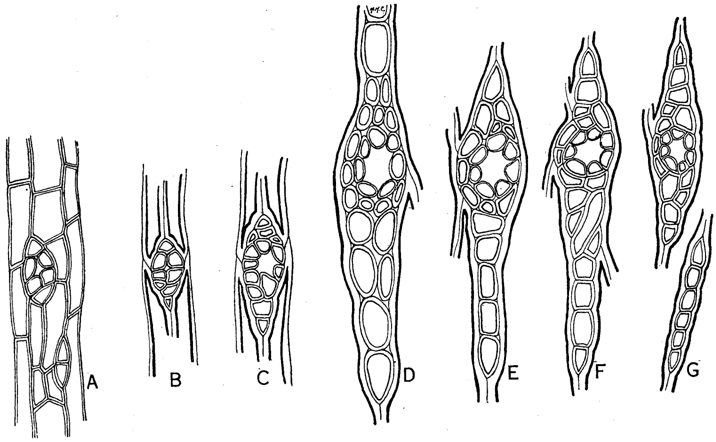


Fig. 1.—*Pinus radiata* D.Don.
A-C, tangential sections of small fusiform ray developing from primary medullary parenchyma. x120.
D-G, later stages in the development of two rays. x120.

Much of the early work was done on the predominantly herbaceous families such as the Compositae, but de Bary quotes work done by Trecul in 1886 on the Anacardiaceae. Trecul described "gum-resin-passages" in the primary and secondary phloem of genera of the Anacardiaceae, but suggested that the canals in the rays arise as "blindly ending branches which penetrate here and there horizontally into the medullary rays of the xylem." This picture of branching canals which actively grow into the fully formed rays is, of course, totally incorrect, and it can now be shown that the "blind ends" of Trecul are each the beginning of a newly developing canal. The connection of the radial canals with the vertical ones is correctly described, but the two develop simultaneously in the cambial region under some stimulus that changes the initials of the cambial layer itself. By the persistence of this change these canals must develop afterwards in the xylem as well as in the phloem, and, owing to the greater number of cambial divisions that occur towards the pith, extend a greater distance through the xylem than through the phloem.

II. Materials and Methods

The material used represents eight genera of three families of pored timbers and three genera of non-pored timbers:

Coniferae	*Pinus radiata* D.Don, *Picea smithiana* Boiss., *Pseudotsuga taxifolia* (Lamb.) Britt.
Anacardiaceae	*Euroschinus falcatus* Hook. f., *Microstemon velutina* Engl., *Pistacia lentiscus* L., *Pleiogynium cerasiferum* Domin.
Burseraceae	*Garuga floribunda* Decsne., *Protium australasicum* (F. M. Bail.) Sprague.

Sectors of wood were cut so that the same rays could be traced for several centimetres, starting if possible from the pith, and these blocks were cut into serial tangential sections of 35-40 μ thickness. By this technique the rays can be identified in the narrow sections of the young wood and then followed in successive sections of the series and their growth noted as they keep pace with the expanding circumference of the stem. This method of tracing the origin of elements from the cambium by studying their appearance in the mature wood has been used by Klinken (1914), Neef (1920), and Beijer (1927) in studies on the stratified cambium that gives rise to storeyed structure and ripple marks in wood. The technique depends on the fact that the secondary thickening of the cell wall, which occurs during the differentiation of woody tissues cut off from the cambial layer, causes a rigidity of the cells, and, as soon as it is complete, prevents any further alteration of shape. Thus the shape of the wood cells at any given point in the trunk of the tree, as seen in tangential section, gives a very fair picture of the state of the cambial layer when the cells were cut off. Extra-cambial changes may produce differences between adjacent cells in the wood — as for instance between fibres and parenchyma cells in the same radial series — but such changes are easily recognized, and the structure of the wood as seen in a series of tangential sections gives a picture from which it is easy to reconstruct the state of the cambial initials when that wood was laid down. As the rays do not grow tangentially or vertically after differentiation, this method has proved to be singularly well adapted to their study, and has been used to follow the development of the rays of the Sterculiaceae (Chattaway 1933*a*) and of the tile-cells in the rays of the Malvales (Chattaway 1933*b*). More recently it was used for a study of the vascular strands that occur in some of the rays of *Banksia* and *Dryandra* (Chattaway 1948). It has now been applied to an investigation of the origin of horizontal canals.

III. Observations

(*a*) *Resin Canals in the Rays of Primary and Secondary Wood*

(i) *Non-pored Timbers* (*Gymnosperms*)

Pinus radiata.—Tangential sections from the pith outwards showed that the primary medullary rays develop as loosely organized masses of parenchyma that gradually subdivide into smaller and more compact masses and soon become recognizable as the small uniseriate rays characteristic of the secondary wood. They are later interspersed with multiseriate rays containing radial resin canals. The origin of the radial canals is near, but not in, the pith; they are not present in the loosely organized mass of the primary medullary rays, but begin to appear very soon after the secondary rays are recognizable. Figure 1*A-C* shows a small ray containing a resin canal developing within a primary parenchymatous mass. In Figure 1*D-G*, later stages are shown in the development of two rays. The large, loosely arranged ray seen in Figure 1*D* becomes more compact in *E* and *F*, and in *G* is subdivided to form a multiseriate ray containing a resin canal and a uniseriate ray.

It is difficult to follow the origin of these large primary rays from tangential sections alone, as the loosely arranged parenchymatous tissue tears very easily under the microtome knife, but their development becomes quite clear when the tangential sections are examined in conjunction with cross and radial sections of the pith and early wood.

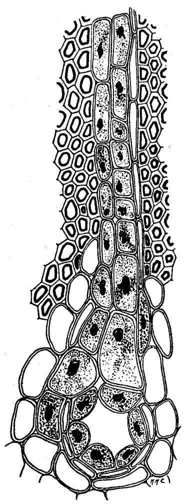


Fig. 2

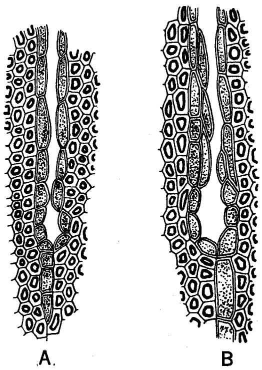


Fig. 3

Fig. 2.—*Pinus radiata* D. Don. Cross section of inner wood, showing a multiseriate ray developing in connection with a vertical resin duct. x85.

Fig. 3.—Cross sections of the secondary wood showing uniseriate rays that become multiseriate in connection with a vertical canal. x120.

A. Picea smithiana Boiss.
B. Pseudotsuga taxifolia (Lamb.) Britt.

There are no vertical resin canals in the pith of this species, but an almost complete ring of vertical canals occurs within the ring of primary wood (Plate 1, Fig. 1) and it is from these canals that the radial canals in the first annual ring originate (Fig. 2). As the rays diverge with the increasing girth of the tree, new secondary rays are formed. These are always uniseriate. The origin of new fusiform rays is always in connection with a vertical resin duct, resulting from changes in the initials of existing uniseriate rays that were contiguous with the initials from which a vertical canal was formed and were therefore subjected to the same stimulus.

Picea and *Pseudotsuga*.—The origin of the horizontal canals in *Picea smithiana* and *Pseudotsuga taxifolia* was found to be similar in detail to that observed in *Pinus radiata* (Fig. 3*A*, *B*; Plate 1, Figs. 2 and 3), though the almost complete ring of vertical canals was absent from the inner wood of both, and there were no vertical canals in the first annual ring of the specimen of *Picea* examined. This may possibly be due to the material having been a branch from a tree from the Botanic Gardens, Melbourne, for Thompson and Sifton (1925) have commented on the absence of vertical canals from the first few rings of *Picea* sp. grown under protected conditions. The descriptions and plates given by these authors show that the development of the radial canals in Canadian spruce is identical with that noted in *Picea smithiana*.

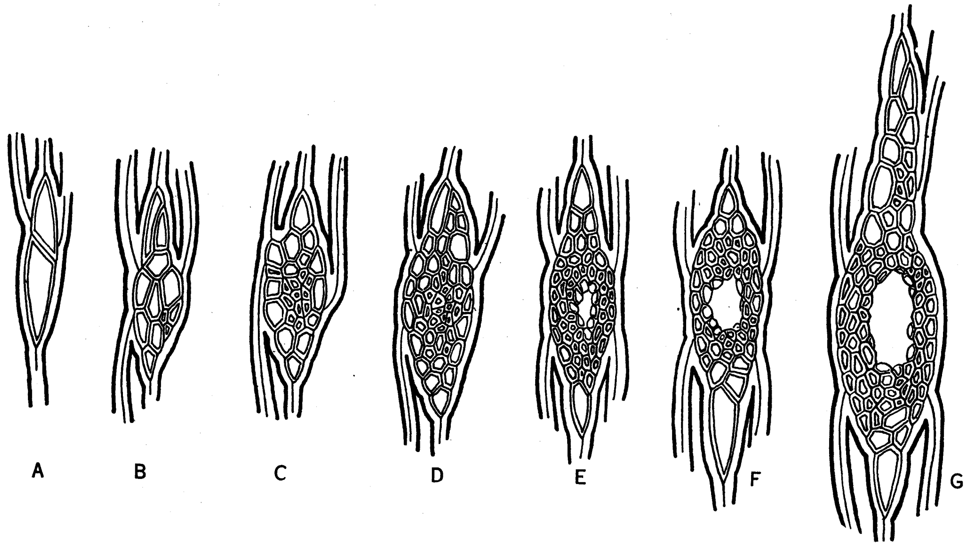


Fig. 4.—*Euroschinus falcatus* Hook f.
A-G, development of horizontal secretory canal through approximately 2.5 cm. of wood. x175.

(ii) *Pored Timbers* (*Angiosperms*)

Euroschinus falcatus (Anacardiaceae).—Material was available for study of this species from the pith outwards through several inches of wood. In the innermost sections, which were in the primary wood, all the rays observed were uniseriate, some of them very high, but all were seen to break up within about 0.5 mm. of the pith into uniseriate rays that varied from a few to about 30 cells in height. No radial canals were found in these rays. A few biseriate rays were developed in the first millimetre or so, and by about 3 mm. from the pith two radial canals were noticed; it was not possible to follow these back to their inception. At this distance from the pith most of the original rays had become biseriate and several of them were found to be developing radial canals, which could be followed in subsequent sections. Figure 4 shows details of their development. In all the rays of *Euroschinus* examined that showed resin canals in their later stages, the inception of the ray was no different from that of any other newly formed ray. However, subsequent divisions produced, not the normal biseriate, or occasionally triseriate, ray which is found throughout the mature wood, but a group of small cells the walls of which ultimately separated to produce a cavity. The details of this can be seen in Figure 4*A-G*. The actual cavity into which the secretion is poured from the surrounding cells is schizogenous in origin, the cells apparently separating along the intercellular layer. The secreting cells lining the cavity seemed little different from others of the surrounding sheath, except that their walls were somewhat thinner than those of the rest of the ray, and curved markedly into the cavity of the secretory passage. These cells are apt to tear on cutting and cannot all be observed in any single section.

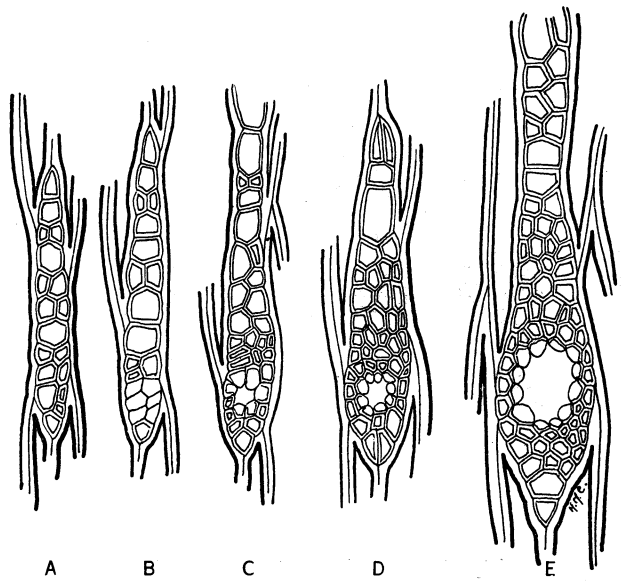


Fig. 5.—*Pleiogynium cerasiferum* Domin.
A-E, development of horizontal secretory canal through approximately 4 mm. of wood. x175.

Pleiogynium cerasiferum (Anacardiaceae).—Fresh branch material of this species was available, and it was again possible to trace the rays from the pith outwards.

The primary rays were found to be predominantly uniseriate and there were no secretory passages in the innermost millimetre of the wood. Secretory passages appeared first in the secondary wood about 1 mm. from the pith, as schizogenous passages between the cells of biseriate rays, enlarging as the rays increased in size. The course of development, which is fundamentally similar to that in *Euroschinus falcatus,* is shown in Figure 5. The main detail of difference appears to be the development of the thin-walled cells at an earlier stage in this wood. *Pistacia lentiscus* (Anacardiaceae) and *Microstemon velutina* (Anacardiaceae) showed very similar ray development. The details can be followed in Figure 6*A-G.* The small ray cells in *Pistacia* are due to the sections having been cut from rather small branch material.

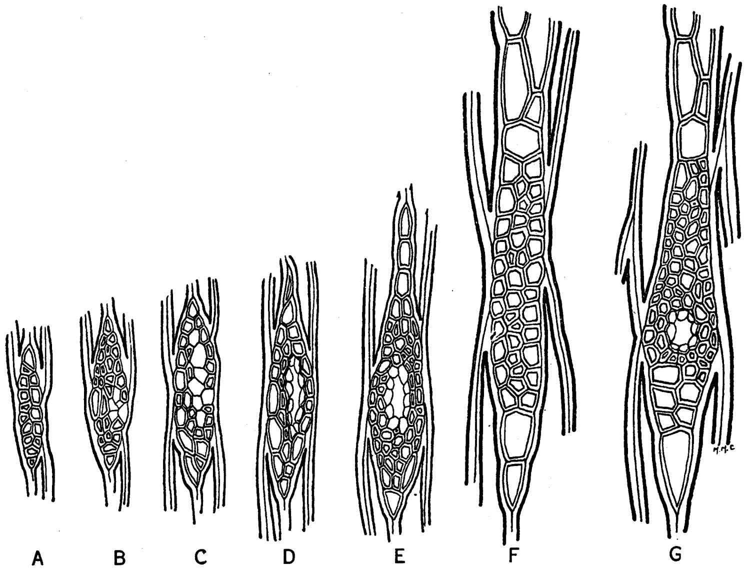


Fig. 6
A-E, Pistacia lentiscus L. Development of horizontal secretory canal through approximately 6 mm. of wood. x175.
F,G, Microstemon velutina Engl. Tangential sections before and after a horizontal secretory canal has developed. x175.

Garuga floribunda (Burseraceae).—The pattern of development in this wood followed the same general lines as that in *Euroschinus falcatus.* It was not, however, possible to procure material for studying the rays at the pith, but serial sections of the secondary wood showed that the secretary passages started through subdivisions of the existing ray initials, as in other woods studied. The stages of development are shown in Figure 7. The thin-walled tissue that occludes the cavity of the canal in the final diagram must not be confused with epithelial cells. The sections of this wood were cut in the heartwood, and the cavity of the canal has become filled with outgrowths from adjacent ray cells—tylosoids (Record 1934).

Protium australasicum (Burseraceae).—In this wood the details of development were essentially similar to those already described, the details can be seen from Figure 8*A-J.*

(b) Resin Canals in the Rays of the Primary and Secondary Phloem

Unfortunately the phloem is not such a satisfactory medium for the use of the serial tangential section method of following ray development. As the cambial initials cut off more cells towards the wood than towards the phloem the wood rays can be studied through many inches while phloem of the same age would fail to provide as much centimetres. The difficulties are further increased by a tendency of most trees to cut off successive parts of the phloem by the development of phellogen or cork cambium, and by the inevitable crushing of the soft outer tissue as the more rigid central core increases in diameter.

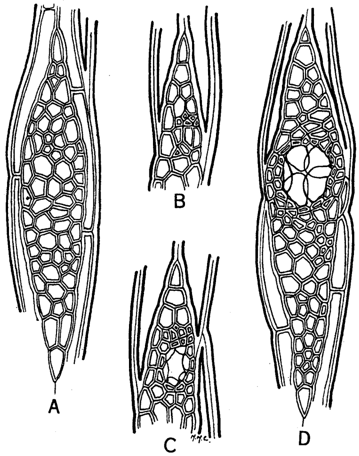


Fig. 7.—*Garuga floribunda* Decsne. Development of horizontal secretory canal through approximately 1 cm. of wood. x120.

Pinus radiata.—Serial tangential sections of the phloem were cut from the cambium outwards so that the rays were followed in a reverse direction from that taken in the wood—from the fully formed ray out towards its inception. For the reasons mentioned above it was not easy to find the earliest stages of the development of the canals, but sufficient were seen for it to be clear that they paralleled very closely those observed in the wood rays of angiosperms. The canals developed apparently spontaneously without any connection with vertical ducts. Cross sections showed that vertical ducts were absent from the phloem of *Pinus radiata*.

Pleiogynium cerasiferum and *Pistacia lentiscus*.—Transverse sections of the stem of young material showed that though vertical canals were absent from the wood of this species they were plentifully developed in the primary and secondary phloem, and that it was in connection with these vertical canals that the medullary canals in these species originated. Figure 9 shows the origin of one such radial canal in *Pleiogynium cerasiferum*. In many instances the connection of the ray and the vertical canal could be seen, though the sections did not always pass through the canal itself as is shown in the figure.

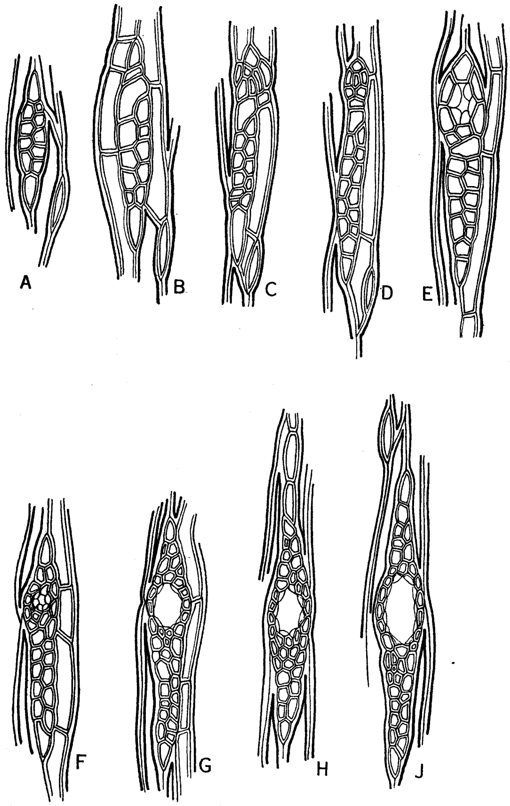


Fig. 8.—*Protium australasicum* (F.M.Bail.) T.A. Sprague. Development of horizontal secretory canal through approximately 1 cm. of wood. x120.

Tangential sections were cut from the cambium outwards in both these woods, as in the material of *Pinus,* and the resin canals in the rays traced as far as possible. Owing to the crushing and to the parenchymatous nature of the outer phloem, the rays become ill-defined and very different to follow, but the canals could be traced without any noticeable diminution in size through the phloem, and in one or two instances were observed to be in distinct connection with the vertical canals. This supports the clearer evidence of the cross sections (Plate 1, Fig. 4) that there are vertical canals in the phloem with which the radial canals in *Pleiogynium* and *Pistacia* can form a connected system.

IV. Discussion

From the foregoing observations it is clear that there is a very fundamental difference between the development of horizontal canals in pored and non-pored timbers. In each type of tree there is a system of vertical canals with which the horizontal canals are connected, but whereas in non-pored timbers this connection is found in the wood, in pored timbers it is found in the phloem.

Neither the vertical nor the horizontal canals can arise in the mature wood; they are the result of changes that have affected the cambial initials. Thompson and Sifton (1925) have stated that, in non-pored timbers, the formation of vertical canals is always the result of injury to, or irritation of, the cambium. But, whatever their cause, these vertical canals are clearly the result of some stimulus that has permanently affected the daughter cells and not the fusiform initials, for the vertical canals in non-pored timbers occur in the wood only, and the fusiform initial from which they arose subsequently produces the normal vertical elements of the wood. A horizontal canal appears to be formed when

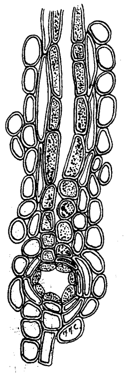
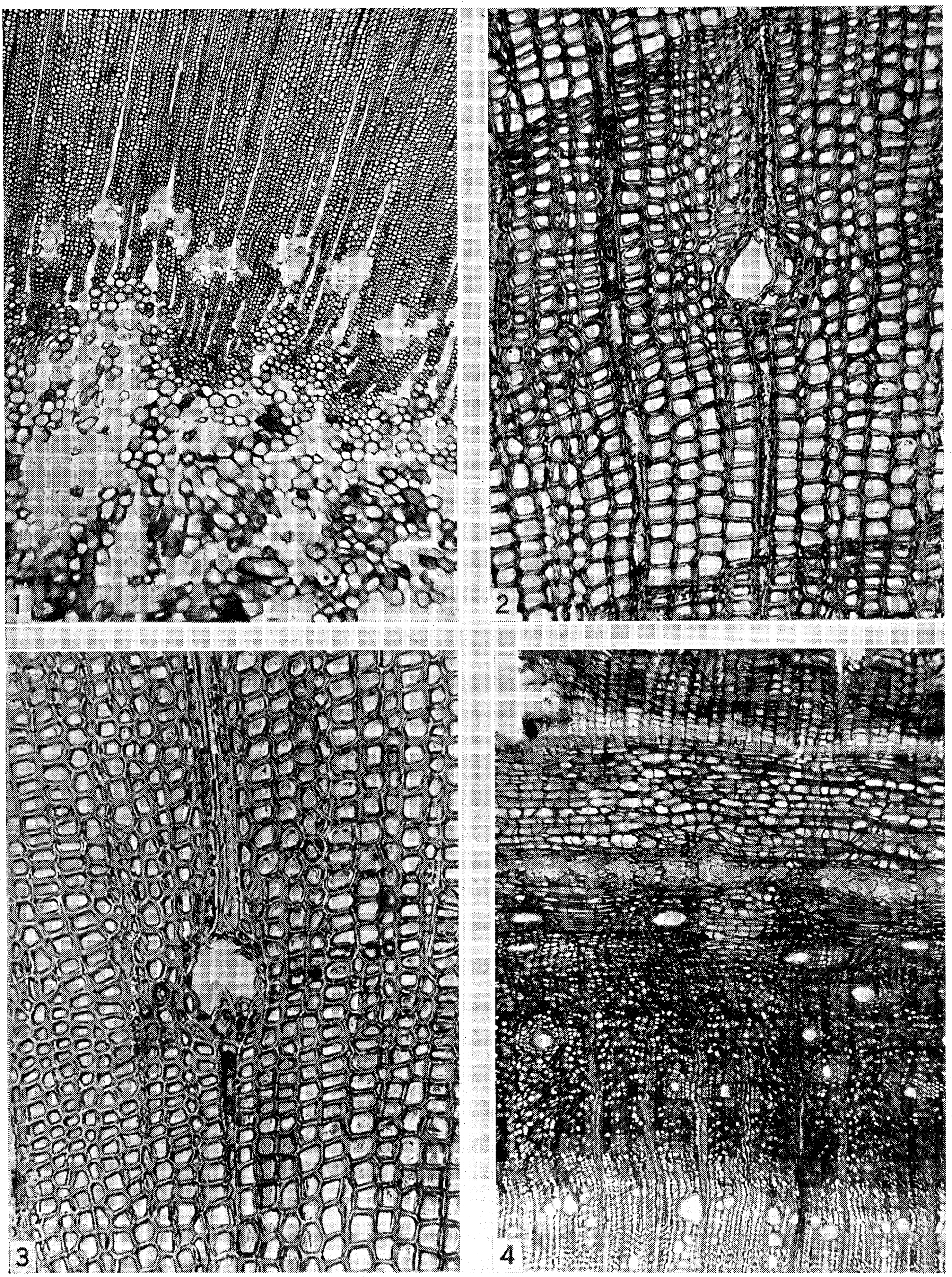


Fig. 9.—*Pleiogynium cerasiferum Domin.* Cross section of vertical secretory canal in the phloem, showing the origin of a horizontal duct from the vertical one. x120.

a ray initial occurs in the area of the cambium that is stimulated to form a vertical canal. Plate 1, Figures 2 and 3, shows uniseriate rays that have become multiseriate after they have passed around or through a vertical canal. Clearly the ray initials and fusiform initials in this area have received the same stimulus. Yet, with the fusiform initials only the daughter cells have been affected, but in the other the actual initials themselves have undergone a change. For the horizontal canal occurs in all the ray tissue subsequently produced, whether in the xylem or phloem.

In pored timbers the position is reversed. In all the material examined the vertical canals are developed in the secondary phloem and not in the xylem. The origin of the horizontal canals is again to be found in connection with the vertical ones, but the stimulus that causes production of these affects the outer daughter cells of the cambium. As in the non-pored timbers the actual ray initials are changed in the formation of the horizontal canals, which are continuous from phloem to xylem.

HORIZONTAL CANALS IN RAYS



Small vertical canals, similar to those described above, occur in relatively few genera of angiosperms, and have been found associated with horizontal canals in one genus only. They have been reported in conjunction with radial canals in one subsection on the genus *Shorea* (Desch 1941). Unfortunately it has not yet been possible to obtain material of the pith or phloem of any of these species, and the material available was not suitable for study by the serial tangential section method. However, no connections between horizontal and vertical canals could be seen in slides of the xylem. It would be interesting to know whether, in these species, as in the pored timbers investigated, canals are present in the secondary phloem.

V. Acknowledgments

The author wishes to express her thanks to Dr. H. E. Dadswell for advice and encouragement throughout the work, and to the Director of the Botanic Gardens, Melbourne, for fresh material of some of the genera studied.

VI. References

Beijer, J. J. (1927).—*Rec. Trav. Bot. Neerland.* **24**: 613.

Chattaway, M. M. (1933*a*).—*New Phytol.* **32** (4): 261.

Chattaway, M. M. (1933*b*).—*Forestry* **7** (2): 93.

Chattaway, M. M. (1948).—*J. Coun. Sci. Industr. Res. Aust.* **21** (4): 275.

de Bary, A. (1884).—"Comparative Anatomy of the Phanerogams and Ferns." (Eng. Trans.). (Oxford University Press.)

Desch, H. E. (1941).—Dipterocarp Timbers of the Malay Peninsula. *Malay. For. Rec.* **14**.

Klinken, J. (1914).—*Bibl. Bot. Stuttgart.* **84**: 1.

Neef, F. (1920).—*Z. Bot.* **12**: 225.

Record, S. J. (1934).—"Identification of the Timbers of Temperate North America." (John Wiley and Co.: New York.)

Thompson, R. B., and Sifton, H. B. (1925).—*Philos. Trans.* B **214**: 63.

Explanation of Plate 1

Fig. 1.—*Pinus radiata* D.Don. Cross section of pith and inner wood. x 20.

Fig. 2.—*Picea smithiana* Boiss. Cross section of secondary wood. A uniseriate ray becomes fusiform after passing through a vertical resin canal. x 180.

Fig. 3.—*Pseudotsuga taxifolia* (Lamb.) Britt. Cross section of secondary wood. A uniseriate ray becomes fusiform after passing through a vertical resin canal. x 180.

Fig. 4.—*Pleiogynium cerasiferum* Domin. Cross section of phloem showing vertical secretory canals. x 65.