

# The parenchymo-vascular cambium and its derivative tissues in stems and roots of *Bougainvillaea glabra* Choisy (*Nyctaginaceae*)

Z. PUŁAWSKA

Institute of Botany University of Wrocław, Kanonia 6/8, Wrocław, Poland

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## Abstract

In the shoots and roots of *Bougainvillaea*, the parenchymo-vascular cambium produces thinwalled secondary parenchyma to one side and the secondary vascular bundles embedded in the "conjunctive tissue" to the other. Periclinal division of a single cambial cell in one radial row brings about periclinal divisions of the adjacent cells of the neighbouring rows. Anticlinal division of a single cambial cell at one level, on the other hand, causes anticlinal divisions of the adjacent cells of the overlying and underlying tiers.

## INTRODUCTION

In *Nyctaginaceae* secondary vascular tissues form collateral bundles embedded in fibres and parenchyma ("conjunctive tissue"). The meristematic tissue giving rise to the bundles lies outside them and forms the peripheral cylinder.

In several-year-old *Bougainvillaea* branches the border between primary cortex and secondary tissues is marked out by the fibres arising from the outermost cells of the meristematic cylinder. So far only such branches have been described in which, between the outer fibre ring and the youngest bundles, there are at most several layers of undifferentiated cells. Balfour (1965) and Studholme and Philipson (1966) believe that in *Bougainvillaea* and *Heimeliodendron* secondary thickening is due to one permanently acting meristematic zone which produces xylem to its inner side and phloem within itself. This interpretation is not accepted by Esau and Cheadle (1969), who consider that in *Nyctaginaceae* the secondary growth is due to successive cambia arising in the phloem or outside it. Each of these produces xylem and phloem in the normal direction.

One permanently-acting meristematic zone, producing secondary tissues unidirectionally, or successive cambia, each producing xylem and phloem in the normal direction? The present paper endeavours to find an answer to these questions by investigating stems much older than those studied by the above named authors. It appeared that the older and thicker the branch the more it contains secondary tissues, not only inside but outside the zone of dividing meristematic cells. On the latter side exclusively thinwalled parenchyma is formed, and on the inner side vascular bundles together with the surrounding fibres and parenchyma. The radial cell rows of common origin include meristematic cells, and the secondary tissues lying on their outer and inner sides. Disturbances in the regular formation of radial files are due to elongation growth of the fibres, extension of the vessels and divisions connected with differentiation of the sieve tube elements and companion cells. These disturbances are of the same nature and by no means more pronounced than in other plants in which cambium forms phloem and xylem on opposite sides.

The extravascular cylinder of meristematic tissue characteristic for *Bougainvillea* may, therefore, be referred to as cambium in the sense of any meristematic tissue giving rise to secondary tissues on opposite sides. In the present paper the tissue giving rise to secondary tissues in *Bougainvillea* is referred to as the parenchymo-vascular cambium in contradistinction to the vascular cambium of most plants. The term cambium denotes here all the meristematic cells, and not exclusively their initial layer.

#### MATERIAL AND METHODS

As object of investigations served the 20-year-old specimen of *Bougainvillea glabra* Choisy growing in the glasshouse of the Institute of Botany and Biochemistry, Wrocław University. Several centimeter long segments of annual and several-year-old stems were fixed in 70 per cent alcohol and free-hand cross sections were prepared from them. From thick several-year-old branches longitudinal slices were cut including epidermis, primary cortex, outer secondary parenchyma, cambium and some of the inner secondary tissues. These slices were fixed by the routine method in 0,5—0,5—20 CrAF, embedded in paraffin, cut on a microtome transversally and longitudinally in radial and tangential plane. The sections were stained with safranin O and fast green or tannic acid and embedded in Canada balsam. Preparations of old roots from a specimen in hydroponic culture were similarly made. Besides, cross sections were prepared from fresh material and inspected and photographed without staining.

Cambium and the formation of secondary tissues are described on the basis of thick sprout and compared with the thin lateral branches and roots. The descriptions are illustrated by photographs.

### OBSERVATIONS AND RESULTS

Cambium initiation. General characteristic of secondary tissues.

In young stems still undergoing elongation growth, outside the bundles scattered in parenchyma, the peripheral meristematic tissue cylinder with the embedded youngest bundles is already visible (Plate I, photo A, Plate II, photos A, B). The cells of this cylinder are identical with the procambial cells of the inner bundles (Plate III, photos A, B and C, D).

The meristematic cylinder develops in the peripheral parts of the shoot at the site where in gymnosperms and most dicotyledonous plants the only cylinder, eventually the only ring of bundles differentiates. In gymnosperms and most dicotyledones all the bundles on the entire length of their longitudinal course run in one circle so that next to one another lie the upper segments of the older bundles and the lower ones of the younger bundles. Procambium lies then between the phloem and xylem of the radially extending bundles and between the bundles extending laterally. In *Bougainvillea*, however, the bundles run at various distances from the stem centre, the older ones being situated to the centre and further from the meristematic cylinder, and the youngest ones touching the cylinder (Longitudinal course of primary vascular bundles in *Bougainvillea* shoots, Puławska 1972). The procambium is in bundles between the phloem and xylem, and it also forms outside them the peripheral cylinder.

In the parts of the stem which have ended elongation, however, still before production of secondary tissues has started, the procambium of the inner bundles dividing periclinally gives regularly arranged cells resembling cambium (Plate IV, photos B, C, D). Whether from these cells only metaxylem and metaphloem elements differentiate, or also secondary elements is a matter of conjecture. A definite criterion is, namely, lacking which would make possible distinction between the pitted vessels of the metaxylem and similar vessels of secondary xylem. One thing is certain, the younger the bundle (the closer to the meristematic cylinder) the more it contains meta elements and secondary elements, and the less proto elements or even none (Plate I, photo B, Plate II, photo C).

The outermost cells of the procambial cylinder, adjacent to the primary cortex parenchyma in still elongating parts of the stem are

several times longer than the remaining procambial cells (Plate III, photos A, C). This means that they elongate and do not divide, or divide transversally less frequently than the remaining procambial cells. In older stems which have ended elongation growth these outer long cells differentiate to fibres which delimit the border between primary cortex and the meristematic cylinder together with the tissues originating from it (Plate III, photo E).

In stems which have ceased to elongate, the procambial cells lying immediately under the outer fibre ring at first do not divide periclinally, whereas those lying deeper undergo periclinal division giving rise to the first population of cambial cells (Plate II, photos C, D). These cells form a ring connecting all the youngest bundles (Plate V, photo A). Therefore, the further development of these bundles is interrelated and also depends on the activity of the cylinder. This activity is maintained by cells situated immediately under the outer ring of fibres, that is outside the youngest bundles. The cells of this zone — a remnant of the procambial cylinder — become the initial cells of the next population of periclinally dividing cells (Plate V, photos B, C).

From each parenchymo-vascular cambium population, collateral bundles, fibres and parenchyma arise inwards, and on the outer side only parenchyma. In this way from one year to another the number of secondary tissues increases not only inside the cambial cylinder but also outside it. It is easy to notice this when comparing cross sections of the stem in the stage of initiation of secondary growth (Plate V, photo A) with several-year-old (Plate VI) and many-year-old branches (Plate VII).

As the circumference of the stem increases, the continuous outer fibre ring is gradually disrupted to smaller and smaller fragments separated by parenchyma (Plate VI, photo A), and finally it presents single fibres distant from one another (Plate VII, photos A, B, C). The border between primary cortex, and the secondary tissues is easily noticed even when there are no fibres on the cross section. The radial rows of secondary parenchyma end, namely, at the border of the primary cortex. The primary cortex cells are stretched further in tangential direction than the adjacent cells of secondary parenchyma. The border between primary cortex and the secondary tissues is also clearly seen on longitudinal radial sections (Plate III, photo E). In the outer secondary parenchyma numerous raphid idioblasts differentiate which grow in width, and slightly also in length (Plate III, photo F).

The anatomy of a several-year-old stem shows the following picture on the cross section: under the peridermis there is a several-layered primary cortex separated from the secondary tissues by singly scattered fibres. Deeper there is a multilayered zone of secondary thinwalled



parenchyma with scattered raphid idioblasts. Adjacent to this parenchyma is the cambial cylinder which encompasses the bundles and the fibres and parenchyma surrounding them (Plate VII, photos A, B, C). The first vessels and first sieve tubes of the given bundle differentiate within the meristematic cylinder (Plate VIII photos A, B, D; Plate IX, photo C). However, since the initial cells of the successive population of cambial cells are outside the youngest differentiating bundles (Plate IX, photo C), therefore after some time the full grown bundles are completely to the inner side of the meristematic cylinder.

In each bundle there is one to several vessels of strikingly large diameter ( $100-200\mu$ ), and a varying number of smaller vessels (Plate VI, photo B, Plate VII, photo B, Plate X, photos A, C).

The phloem consists of sieve tubes and companion cells. The phloem part of the bundles is surrounded by parenchyma cells, and the xylem part by fibres. In this way tangential layers of thinwalled parenchyma arise with embedded phloem in them — opposite the phloem — vessels. Between the fibres radial rows of parenchyma run; these rows vary in length and their width is equal to one, two or more cells (Plate VI, photo B).

### Characteristic of cambium

#### Periclinal divisions

In stem several years old, the parenchymo-vascular cambium consists of fusiform cells exclusively ( $200\mu$  long) which on tangential section are arranged in tiers (Plate XV, photos A, B).

The nondividing cambial cells do not differ on cross sections from the youngest cells of the outer parenchyma, and the border between these tissues cannot be distinguished (Plate IX, photo A).

It is easier to delimitate this border on longitudinal radial sections since the cells of the outer parenchyma, owing to transversal divisions, are shorter than those of the meristematic cylinder (Plate III, photo E). On the other hand, the border of the meristematic cylinder from inside is sharply outlined both on cross and on longitudinal radial sections, because the thinwalled meristematic cells adhere here either to the thickwalled lignified cells or to the phloem tissue.

On cross sections the tangential walls of cambial cells from neighbouring radial files are as a rule shifted in relation to each other so that to each radial wall of the cell of one row falls one tangential wall of the neighbouring row (Plate X, photo B, Plate XI, photo A). On cross sections the cambium cells therefore have the shape of rectangular hexagons. When a single cell in some file divides periclinally so that the newly formed wall is shifted in respect to the existing ones (what

is most frequent) then the two daughter cells are fivesided (Fig. 1a, cells b), or one is four- and the other sixsided (Fig. 1b, cells a, c). Which of these variants occurs depends probably on the shift of the cells in the neighbouring rows in respect to one another.

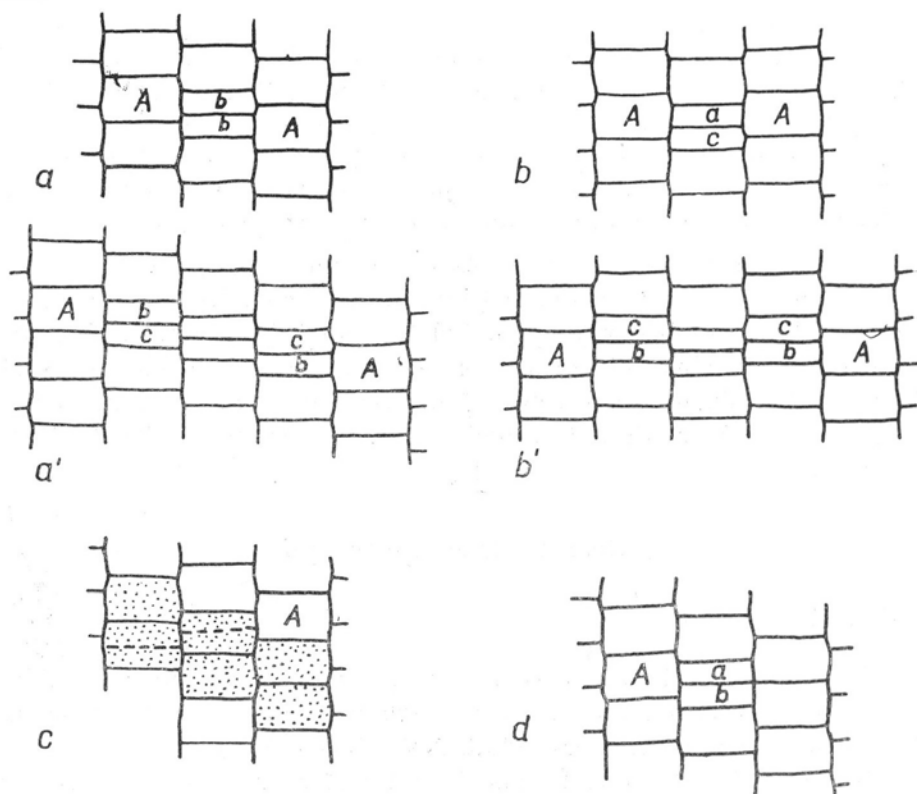


Fig. 1. Periclinal divisions of cambium cells on cross sections: illustration of the principle of disturbance and returning to the basic shape and basic number of contacts. Daughter cells: *a* — foursided, *b* — fivesided, *c* — sixsided, *A* — heptagonal cells before the division. Fig. 1c — the daughter cells of the first division dotted; periclinal wall arising after division of one of the daughter cell marked by interrupted line.

For instance the cell pattern in Fig. 1a favours the formation of fivesided cells, whereas the cell shift in Fig. 1b gives rise to one four and another fivesided cell. In both cases, in the adjacent files heptagonal cells appear (Fig. 1a, 1b, cells *A*). The newly formed pattern is labile, two tangential walls on one radial are an exceptional and transient phenomenon. The heptagonal cells, namely, divide tangentially so that both the fivesided daughter cells from the first division become sixsided again and in the new division one daughter cell becomes sixsided (Fig. 1a', cells *c*), and the other fivesided (cells *b*).

Besides, in the adjacent files, in which so far no division took place, there appear heptagonal cells (cells A).

If after the first division one of the daughter cells is four and the other sixsided, then the division of the neighbouring heptagonal cells changes the foursided one into a hexagonal cell (Fig. 1b'). One of the cells from this new division is hexagonal (Fig. 1b', cells c), and the other pentagonal (Fig. 1b', cells b), whereas in the adjacent files there appear heptagonal cells (Fig. 1b', cells A). The above variants appear when all the tangential walls are shifted in relation to one another. When the newly formed tangential wall does not meet the tangential wall only on one side, and meets on the other, then one of the two daughter cells is foursided (Fig. 1d, cell a), and the other fivesided (cell b), and only one heptagonal cell (cell A) is formed on the side where the tangential walls did not meet. The result is always the same: periclinal division of a single cell in one radial row causes periclinal divisions in the adjacent cells of both neighbouring files, or at least in one of them.

Owing to the principle of disturbance and return to the basic shape and basic number of contacts, in each radial file one cell becomes the initial one, rather because of its situation than for its exceptional properties. It is only division that makes this cell different from the remaining ones. The greater number of cells capable of taking on the function of an initial cell is only a necessary reserve.

The heptagonal cambium cells with two tangential walls on one radial wall, or less frequently octagonal cells with two tangential walls on both radial ones are, in view of their situation and size not yet dividing cells. They frequently lead the periclinal divisions spreading to the sides (Plate XIII, photos A, B) or they stand in the rows in which periclinal divisions are distinctly delayed as compared to the neighbouring files (Plate XII, photo A).

Periclinal divisions rapidly spread to the sides, and before the second division starts in the particular rows, there forms on the cross section a cambium layer two daughter cells thick (Plate IX, photo D; Plate X, photos A, C).

The succession of the following divisions in the particular rows is not identical. Namely, if — as shown in Fig. 1c — the upper one of the two daughter cells in the middle row divides so that it fails to meet the tangential walls of the neighbouring rows, then, in the row on left the heptagonal cell should divide, that is the lower daughter cell from the first division, whereas in the row on the right side neither of daughter cells from the first division is the heptagonal cell, but a cell which did not divide previously (Fig. 1c, cell A). The periclinal divisions do not spread beyond the initial cells, probably because some of the tangential walls of the neighbouring files meet. In the case discussed,

the newly formed wall in the middle row would meet the tangential wall on the right. In this situation division of the upper daughter cell in the middle row would not bring about any division in the file on the right, but would cause division of the lower of the two daughter cells in the row on the left.

On cross sections, the tangential walls of the neighbouring rows actually meet sometimes on one or on both sides (Plate XI, photos B, D).

After the second division which one of the daughter cells undergoes — in some files the lower, and in others the upper one — cambium three cells thick forms (Plate X, photo B). In dependence whether the upper or lower daughter cell divides, two different arrangements of the three cells are possible. By way of division of one of these three cells, a population of four cells may arise in six different patterns. The distribution of thick and thinner tangential walls is different in each of these six patterns (Fig. 2).

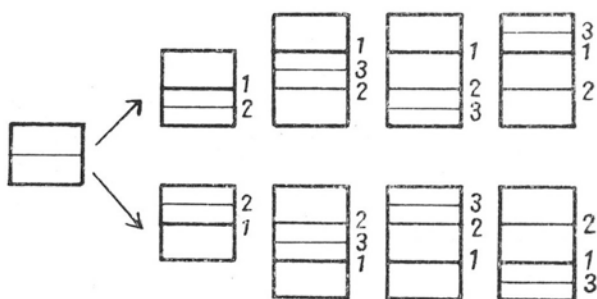


Fig. 2. Periclinal divisions of cambium cells on cross sections: the formation of cambium population three and four cells thick. Numbers 1, 2, 3 denote the succession of periclinal walls.

If we take into account the fact that periclinal divisions in the neighbouring rows are interconnected, and try to find guidance in the unequal thickness of the tangential walls, the genesis of definite cambium patterns may be deduced with quite a high probability. For instance in photo A (Plate XI) the cell in row IV (Fig. 3) must have divided

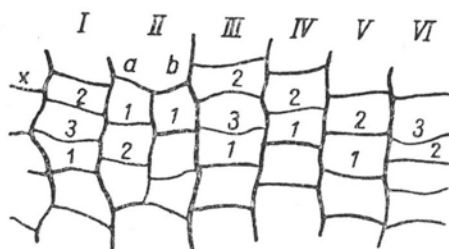
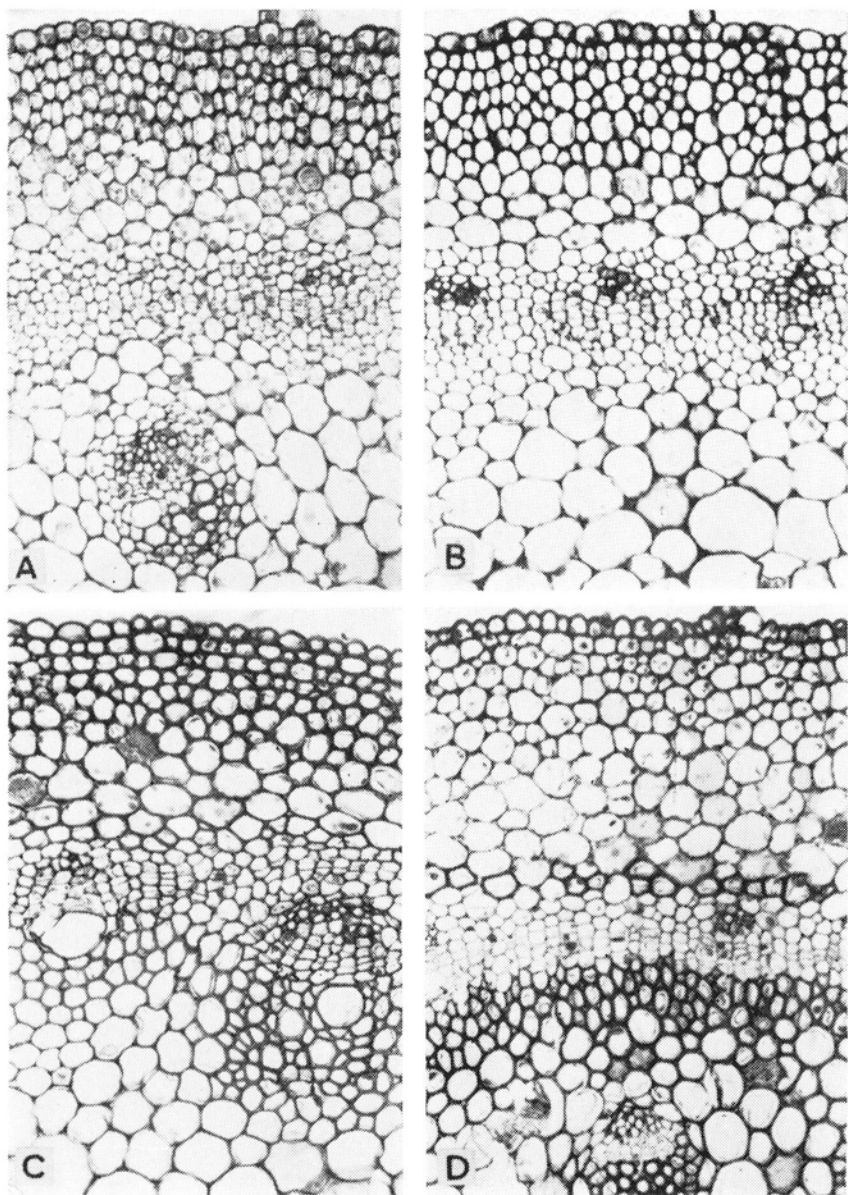


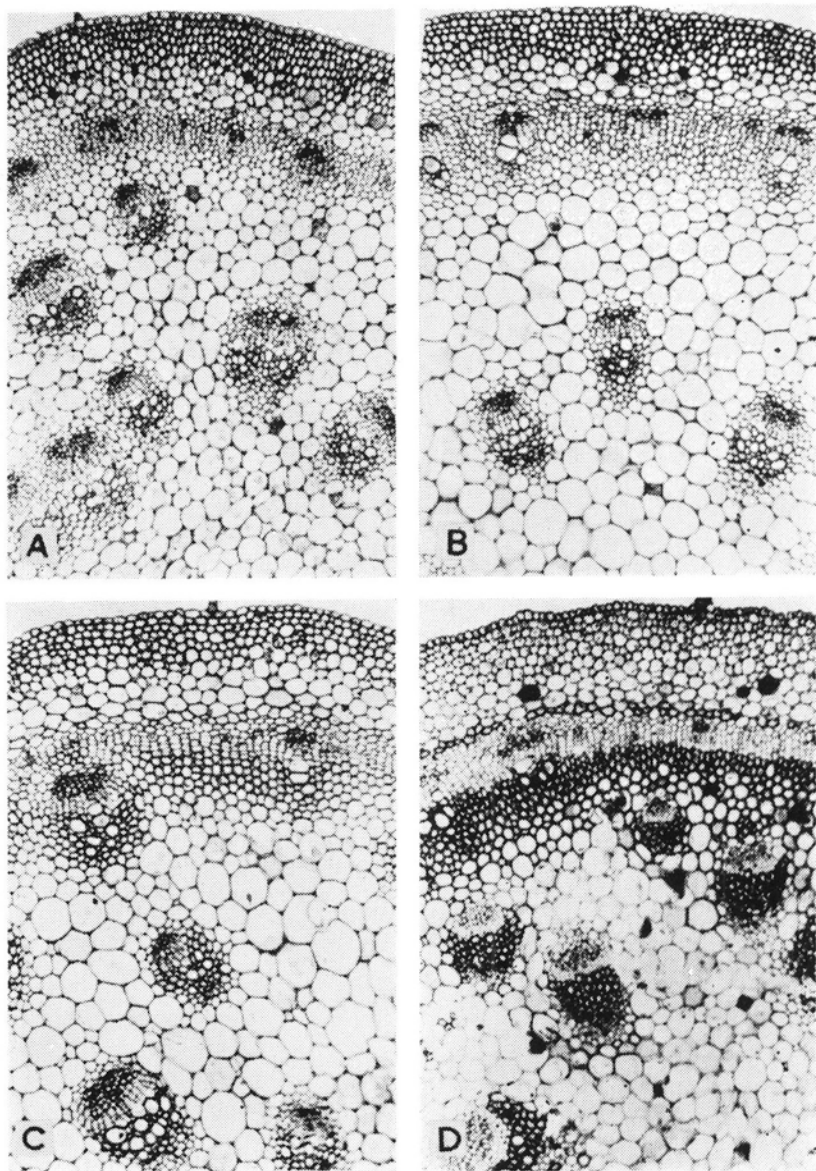
Fig. 3. The genesis of cambium pattern from photo A Plate XI. The correlation of periclinal divisions in the neighbouring radial rows. Numbers 1, 2, 3 denote the succession of the formation of periclinal walls in rows, numbered I—VI.



Cross sections through the stems of one-year-old thick sprouts of *Bougainvillea globra* Choisy.

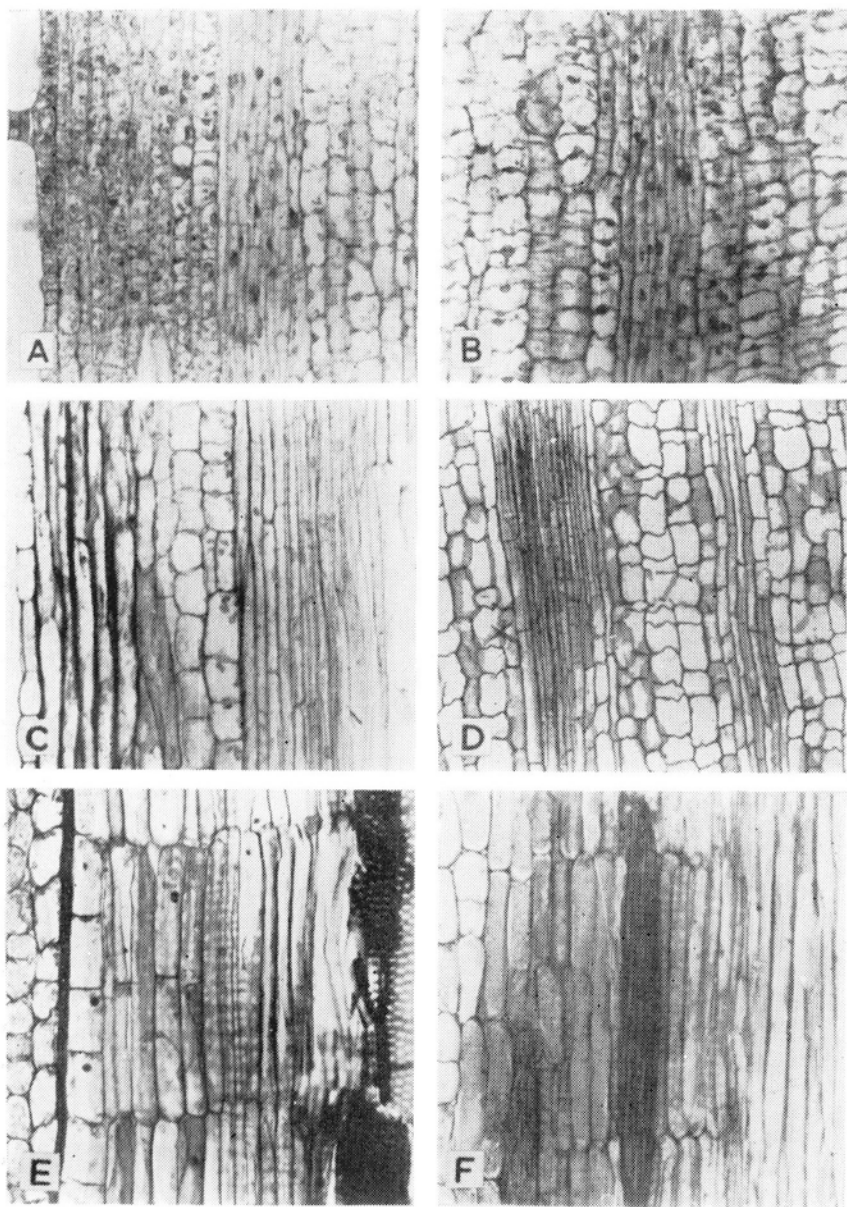
A — the internode from the region of elongation, B — the internode at the border of the region of elongation, C, D — the internodes at the beginning of secondary growth. X 74.

# Plate II



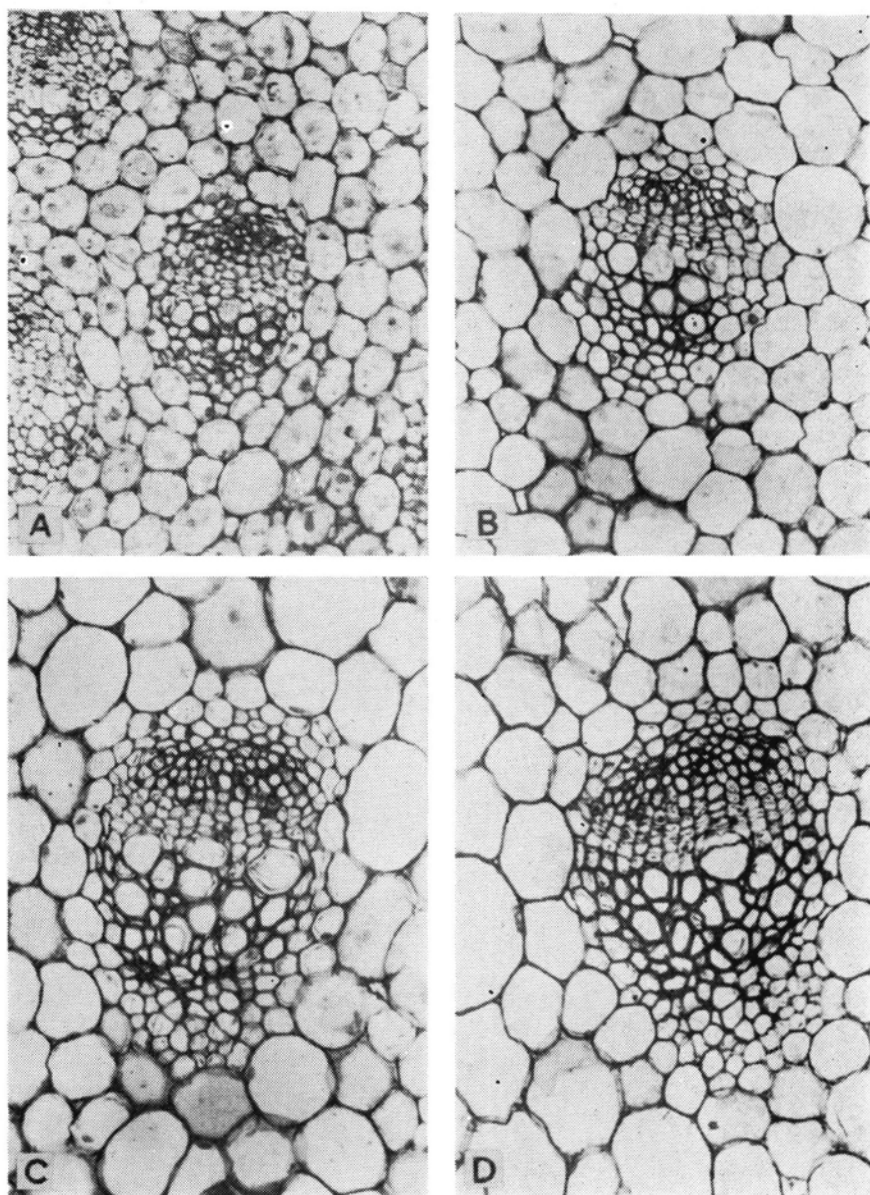
Cross sections through the stems of one-year-old thick sprouts of *Bougainvillea*  
 A, B — the internodes from the region of elongation, C — the internode at the  
 border of the region of elongation; the formation of the first cambium population,  
 D — the internode at the beginning of secondary growth. X 190.





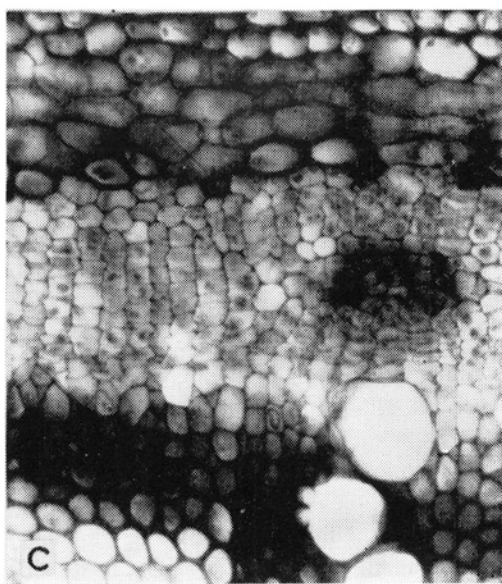
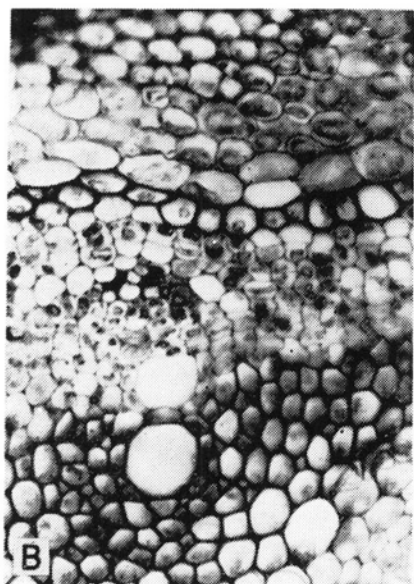
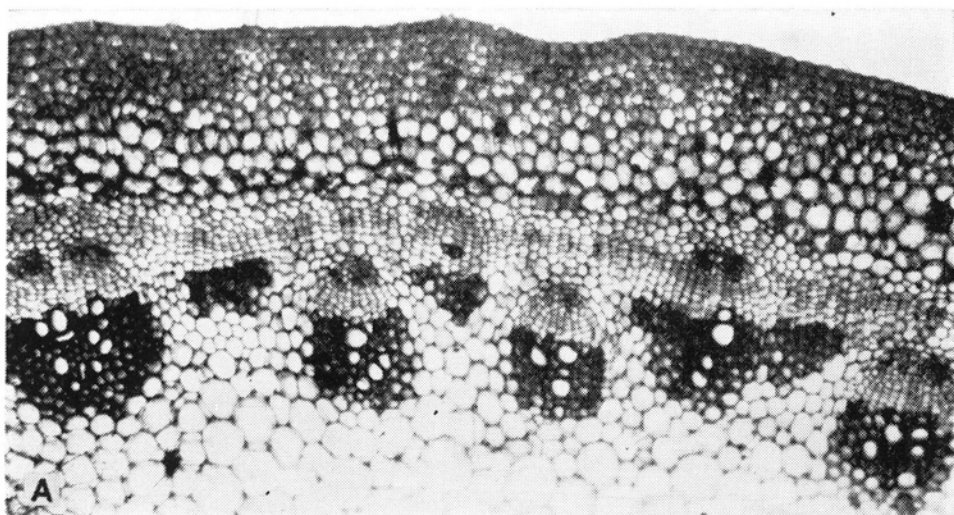
Median longitudinal sections through the stems of thick sprouts of *Bougainvillea*  
 A, B — the internode from the region of elongation, C, D — the internode at the  
 border of the region of elongation, E, F — the inner bundles, E, F — meristematic  
 cylinder with adjacent tissues in several-year-old stems. X 170

Plate IV

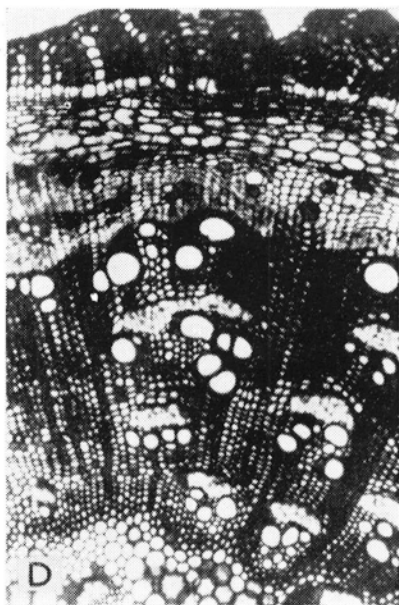
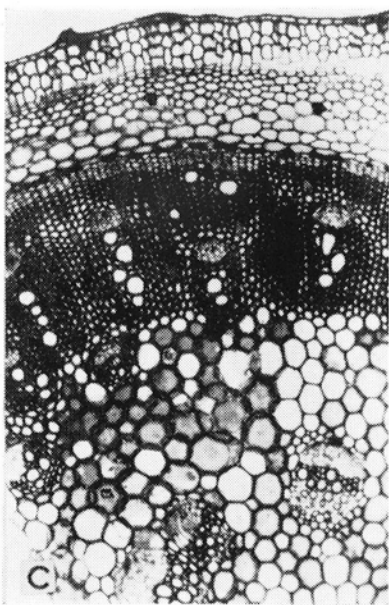
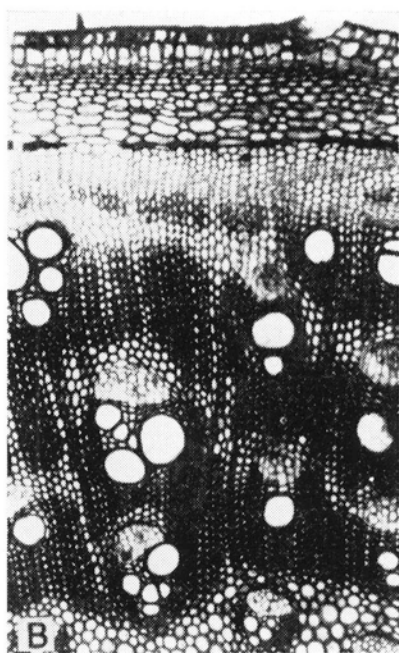
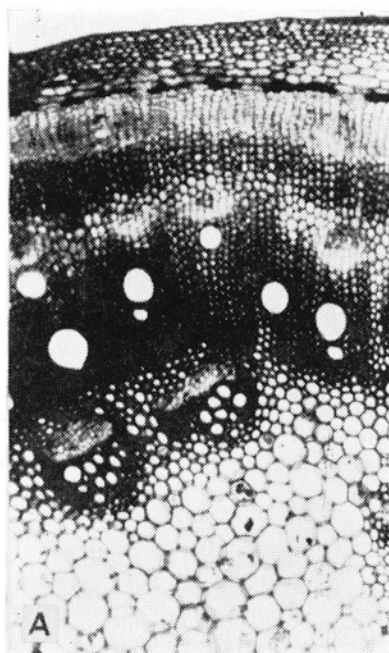


Cross sections through inner bundles from the stem of *Bougainvillea* thick sprouts  
 A, B — the internodes from the region of elongation, C — the internode at the  
 border of the region of elongation, D — the internode at the beginning of secondary  
 growth. X 190

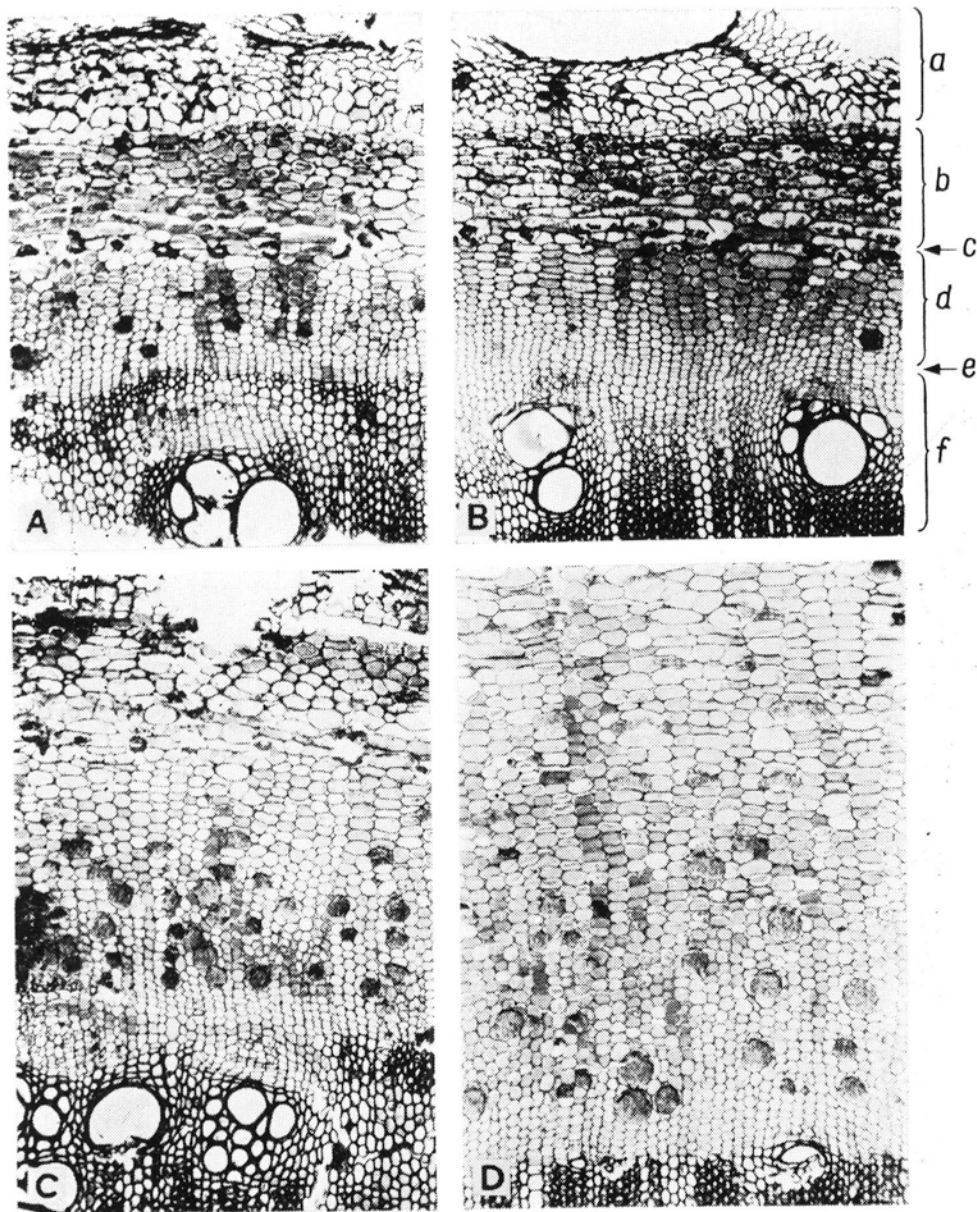




Cross sections through peripheral part of the stems of *Bougainvillea* thick sprouts  
 A — the first population of the parenchymo-vascular cambium. X 100, B, C —  
 the formation of the second cambium population. X 250



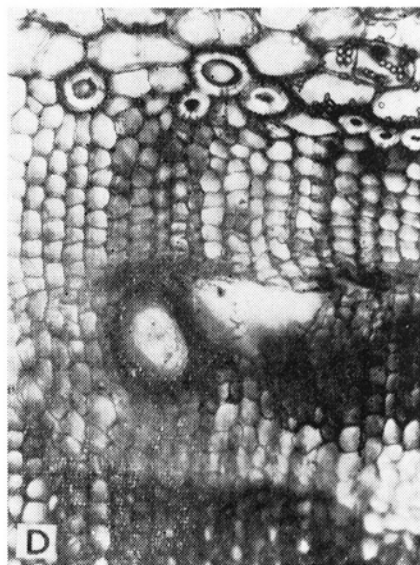
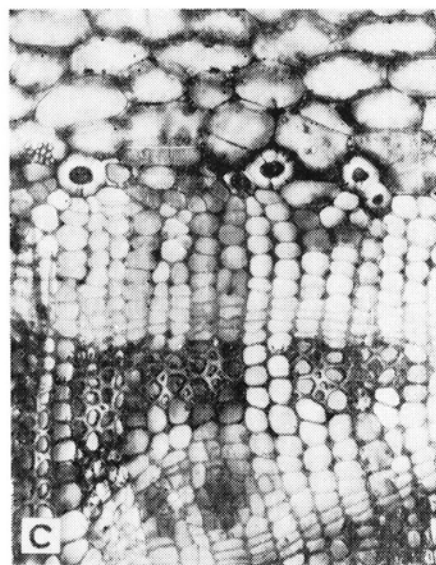
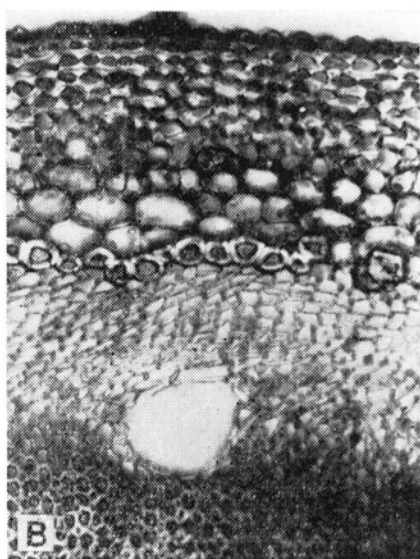
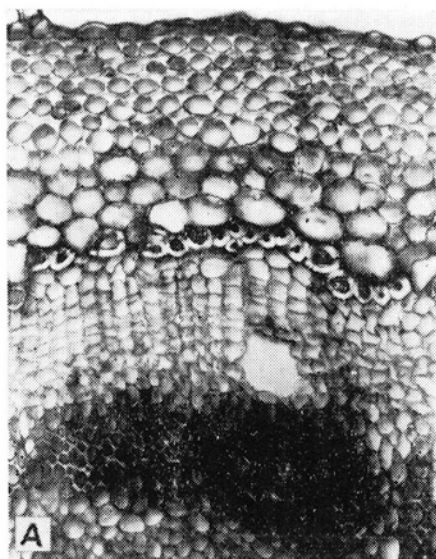
Cross sections through several-year-old *Bougainvillea* stems. A, B — the stems of thick sprouts, C, D — the stems of thin lateral shoots.  $\times 69$



Cross sections through peripheral tissues of thick, many-year-old *Bougainvillea* stems.

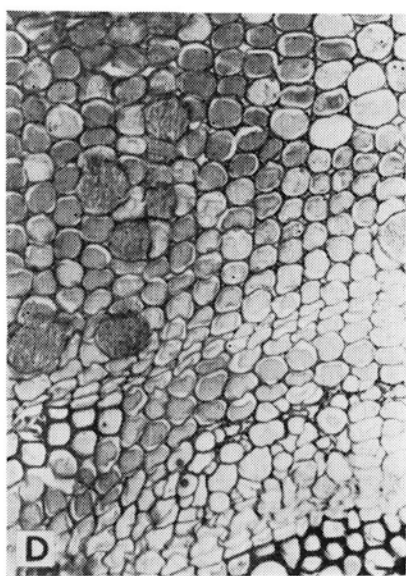
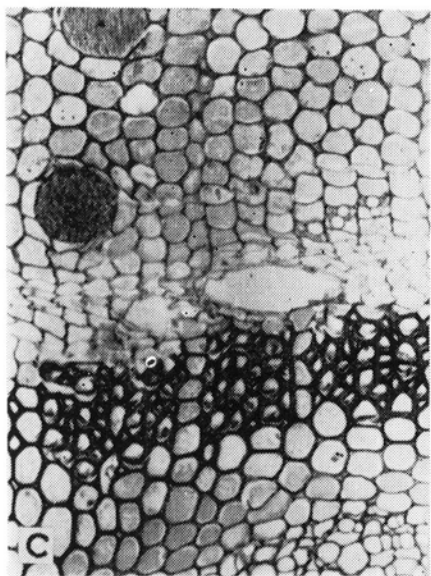
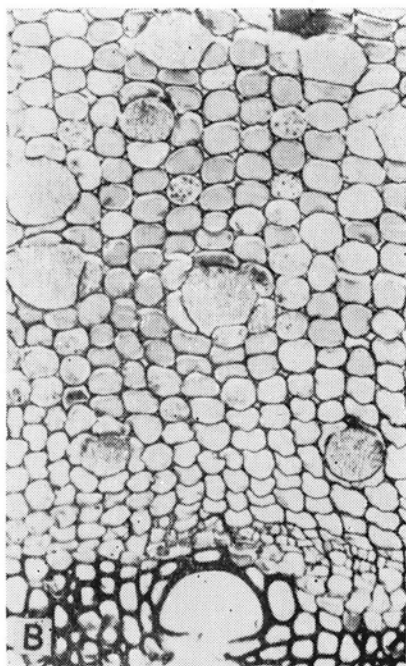
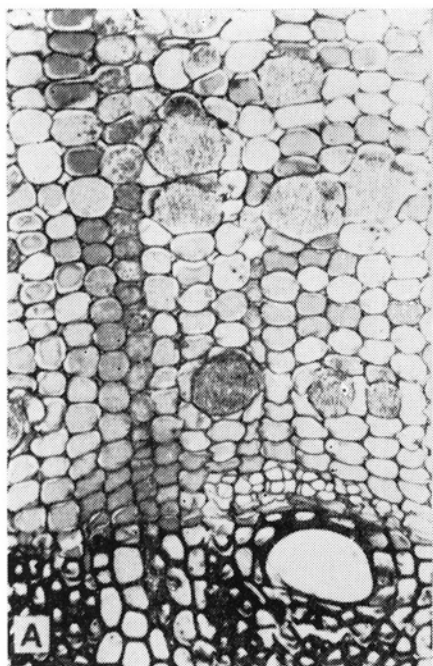
A — stem four-year-old, B — stem six-year-old: a — peridermis, b — primary cortex, c — external fibers, d — secondary external parenchyma, e — cambium, f — secondary vascular tissues, C stem  $\pm$  10-year-old, D — stem  $\pm$  20-year-old.

Plate VIII



Cross sections through peripheral tissues of thick one-year-old (A, B) and several-year-old (C, D) *Bougainvillea* stems. Photos of free-hand sections from fresh and not stained material. A, B —  $\times 150$ , C, D —  $\times 170$

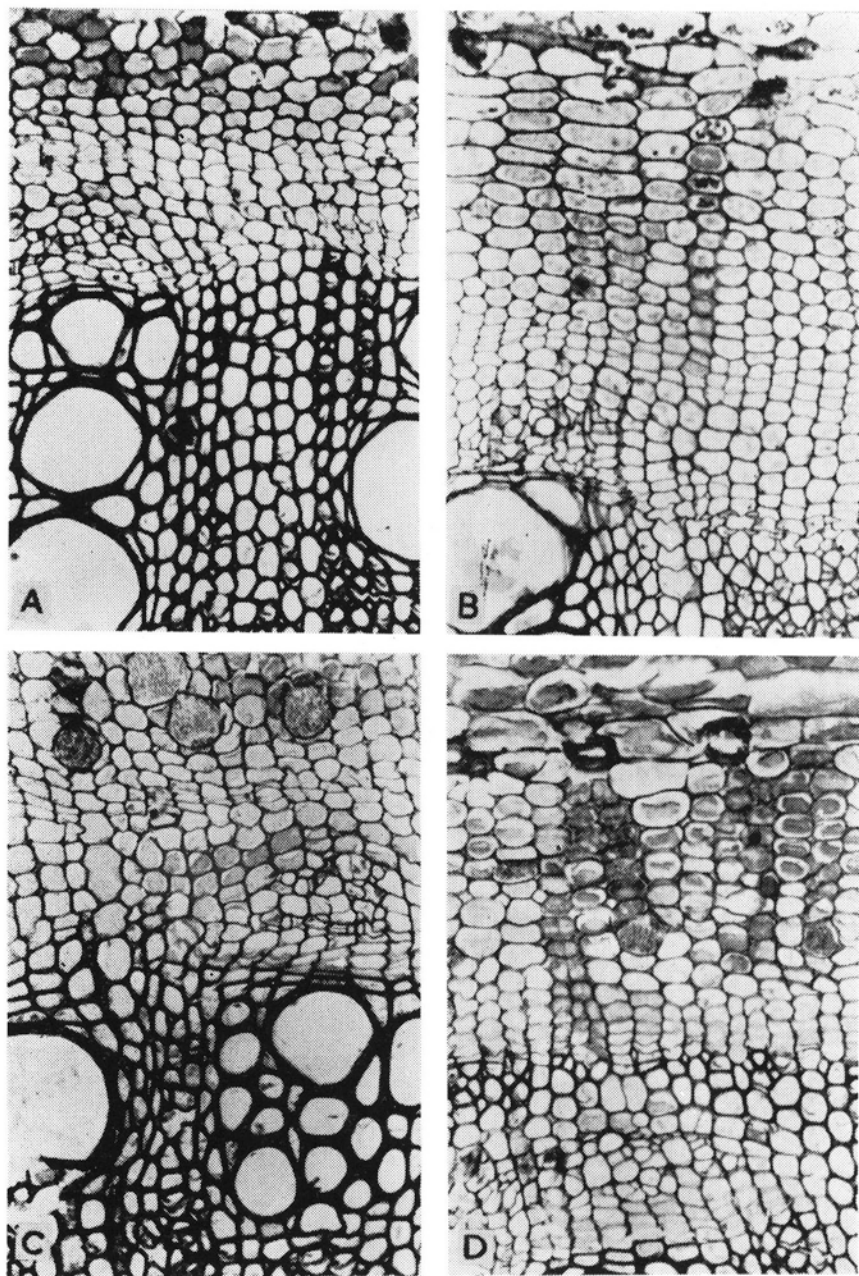




Cross sections through peripheral secondary tissues of thick many-year-old *Bougainvillaea* stems.

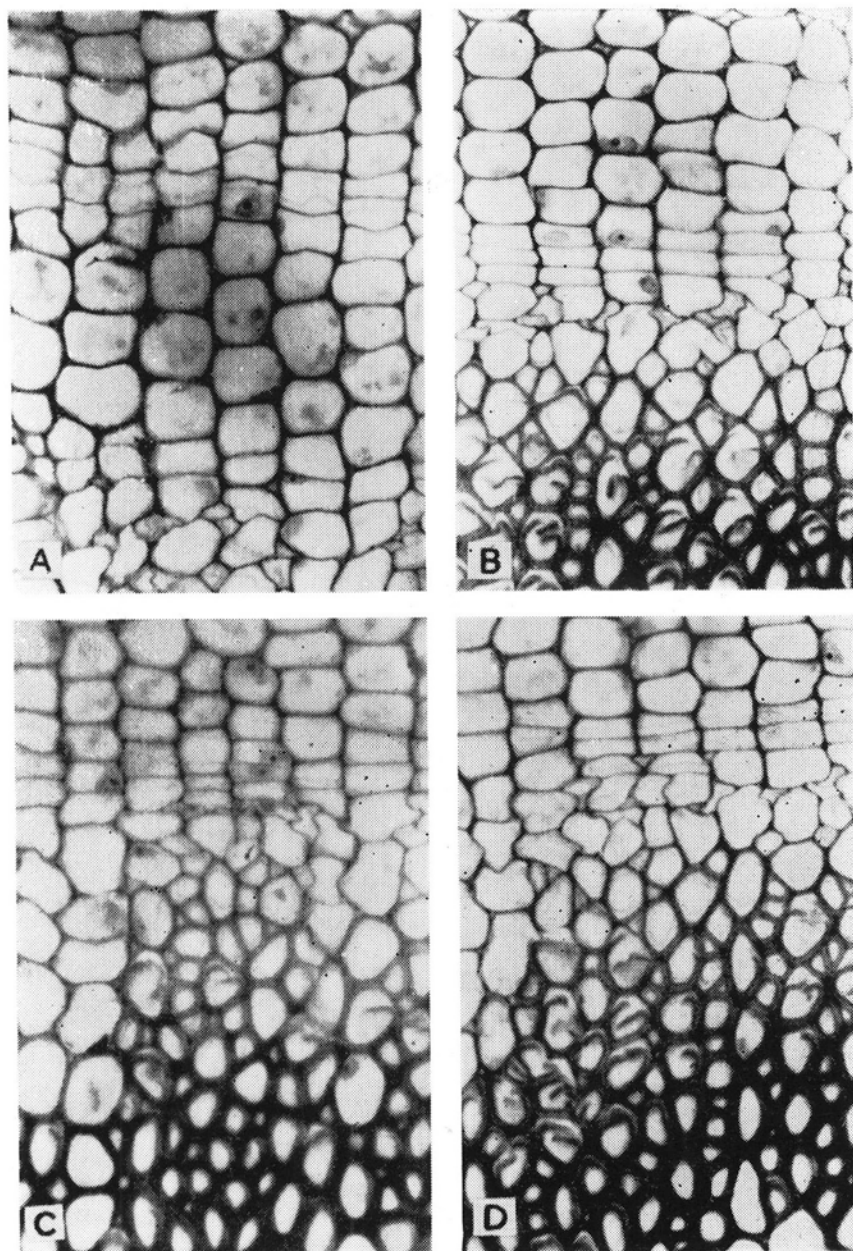
A, B — before the formation of a new cambium population, C, D — the first periclinal divisions initiating the new cambium population.  $\times 170$

Plate X



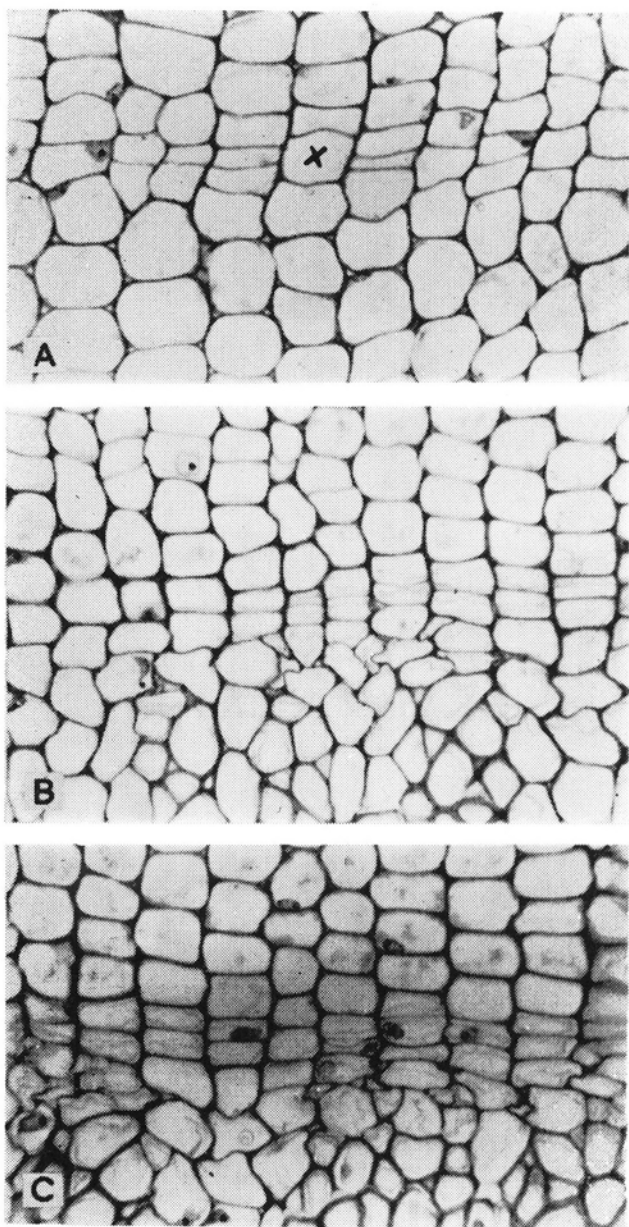
Cross sections through peripheral secondary tissues of thick several-year-old and many-year-old *Bougainvillea* stems. The formations of a new cambium population.

× 170



Cross sections through a cambium zone and adjacent tissues from thick five-year-old *Bougainvillea* stems. The periclinal divisions of cambium cells.  $\times 432$

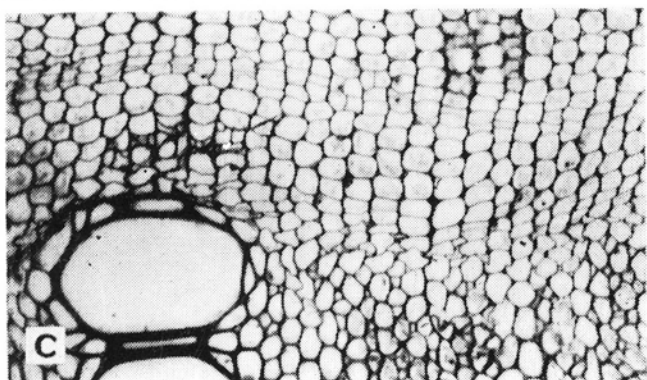
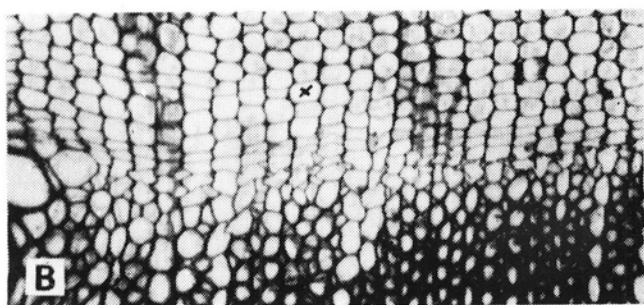
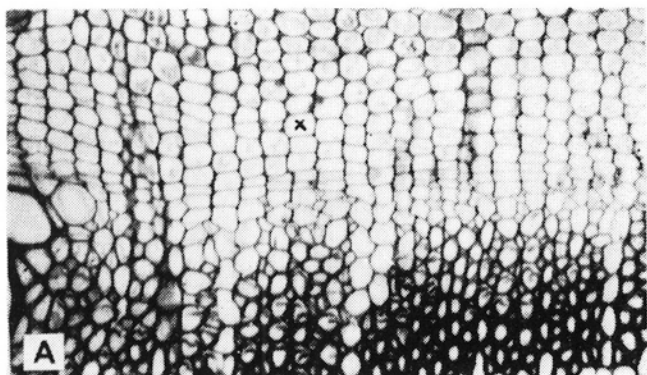
Plate XII



Cross sections through a cambium zone and adjacent tissues in the thick five-year-old *Bougainvillea* stem. The periclinal divisions of cambium cells. A — the octagonal cell marked with a cross.

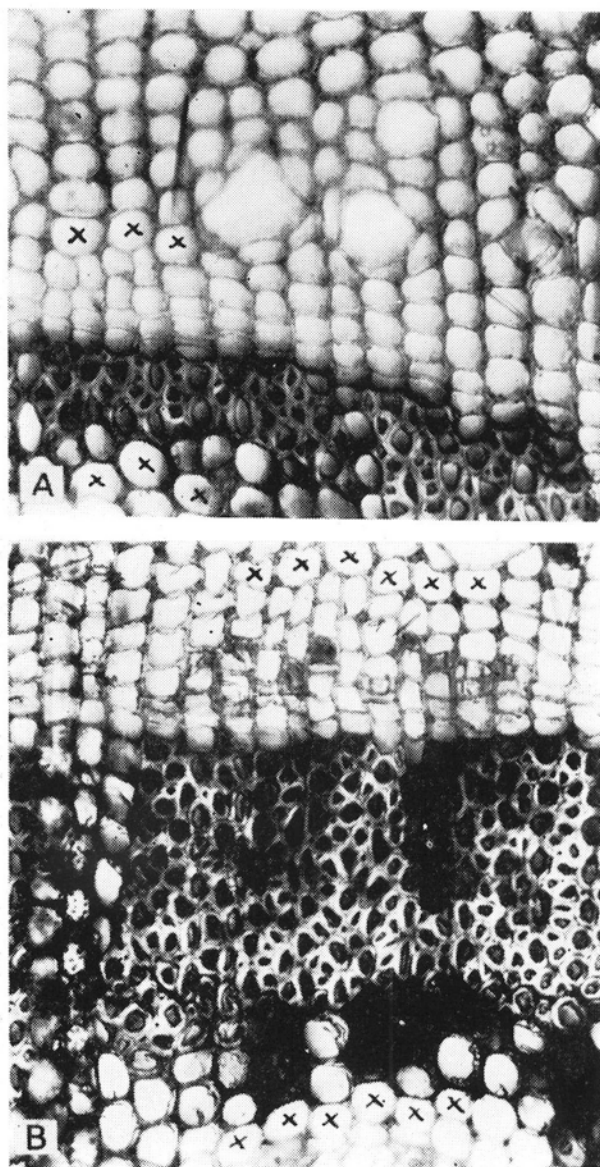


Plate XIII



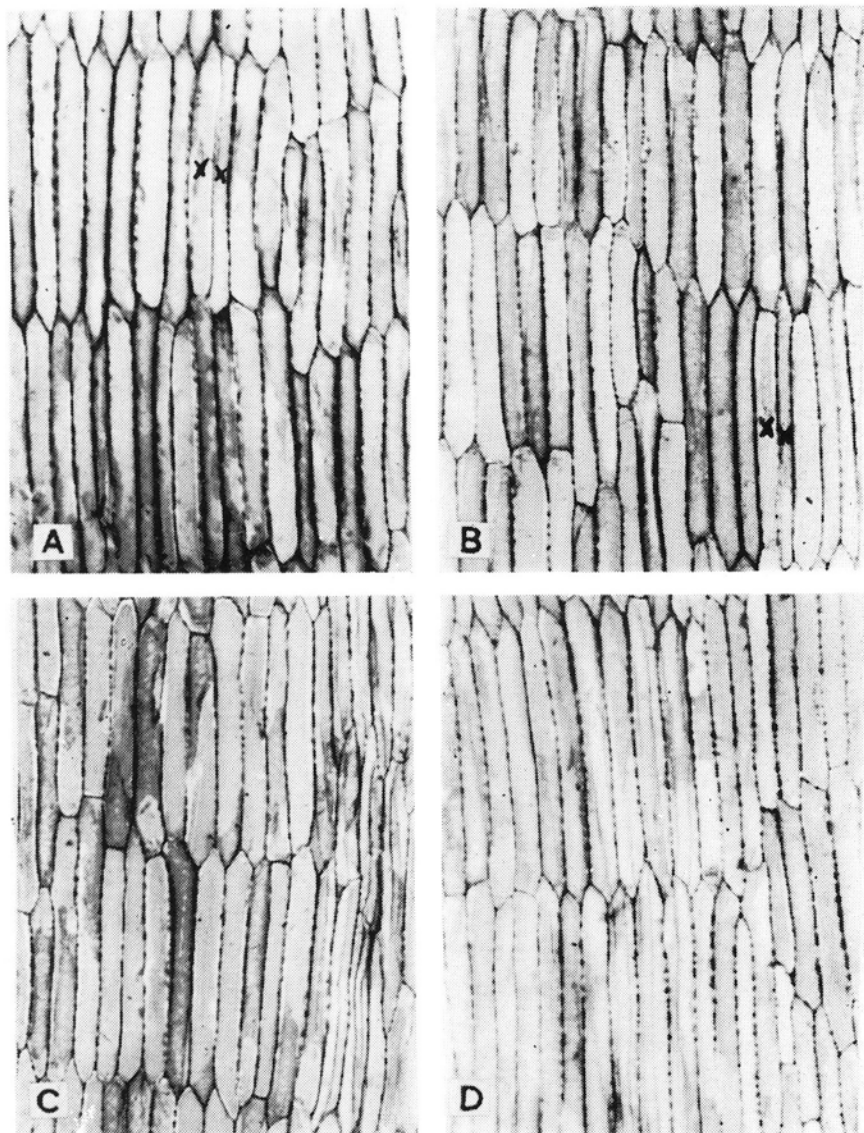
Cross sections through peripheral secondary tissues in thick five-year-old *Bougainvillea* stem.

*A, B* — different levels of the sections through the same sector of the stem; spreading of periclinal divisions initiating a new population of the parenchymo-vascular cambium. The cells of the precedential population divide also. Heptagonal cells marked with crosses, *C* — another part of the same stem. The finish of the activity of the precedential cambium population and the beginning of the activity of a new one.  $\times 170$



Cross sections through a cambium zone with adjacent tissues from the several-year-old *Bougainvillea* stem.

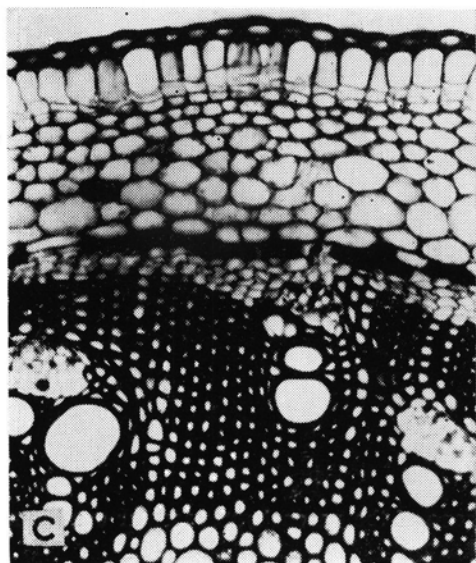
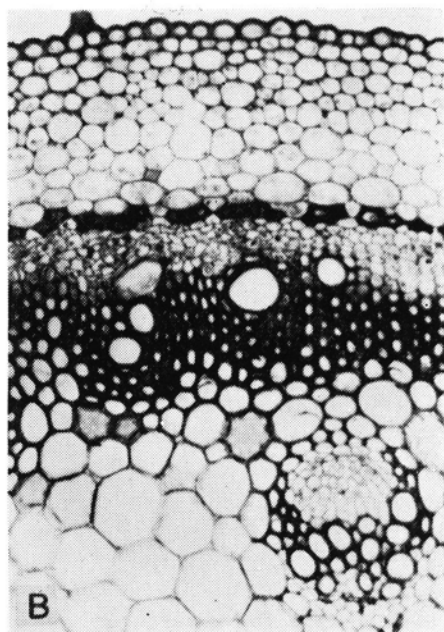
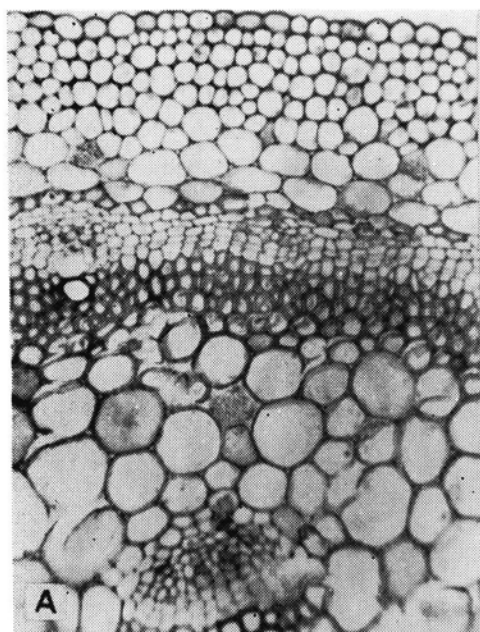
Anticlinal divisions: on both sides of the fibers the corresponding rows marked with the crosses.  $\times 250$



Longitudinal tangential sections through a zone of the parenchymovascular cambium from the 10-year-old thick branch of *Bougainvillea*.

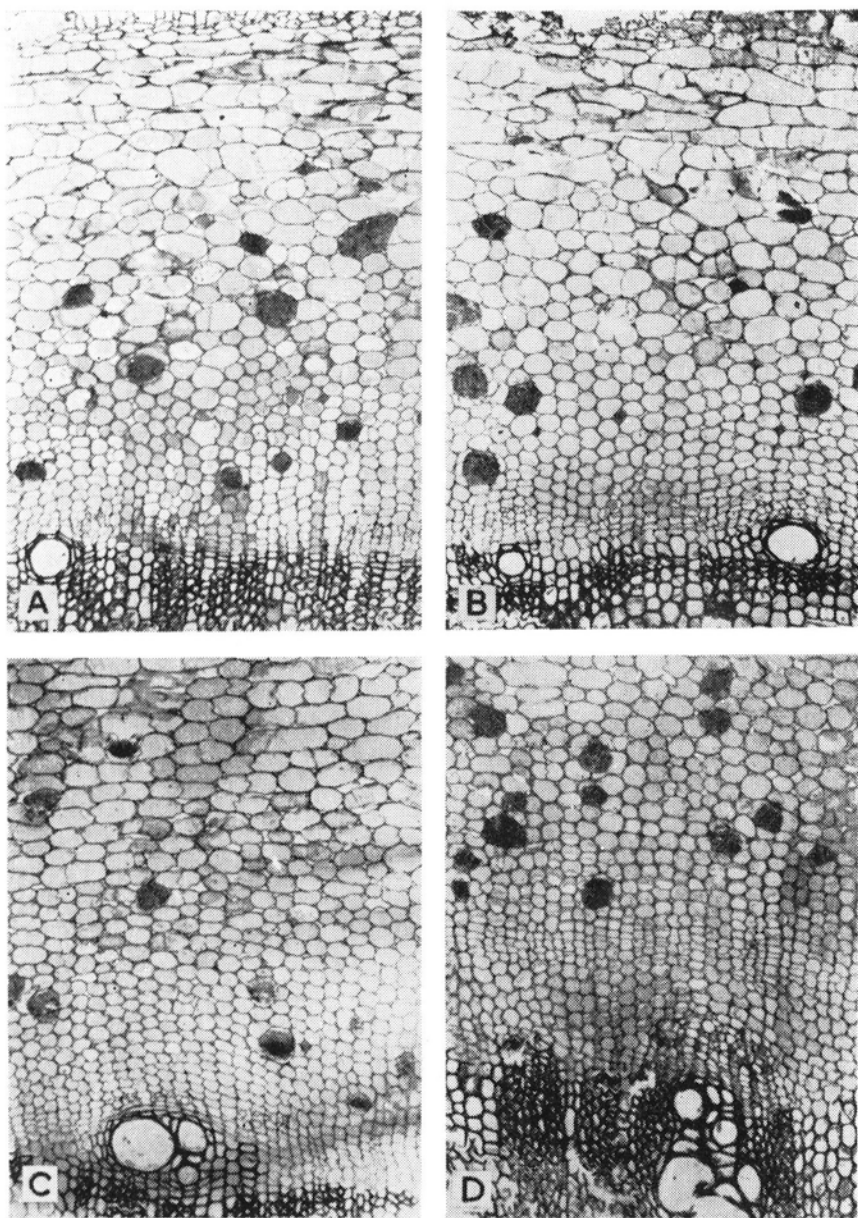
A, B — the daughter cells after anticlinal division marked with the crosses, C, D — anticlinal divisions of the mother cells of the sieve tubes.  $\times 170$

Plate XVI



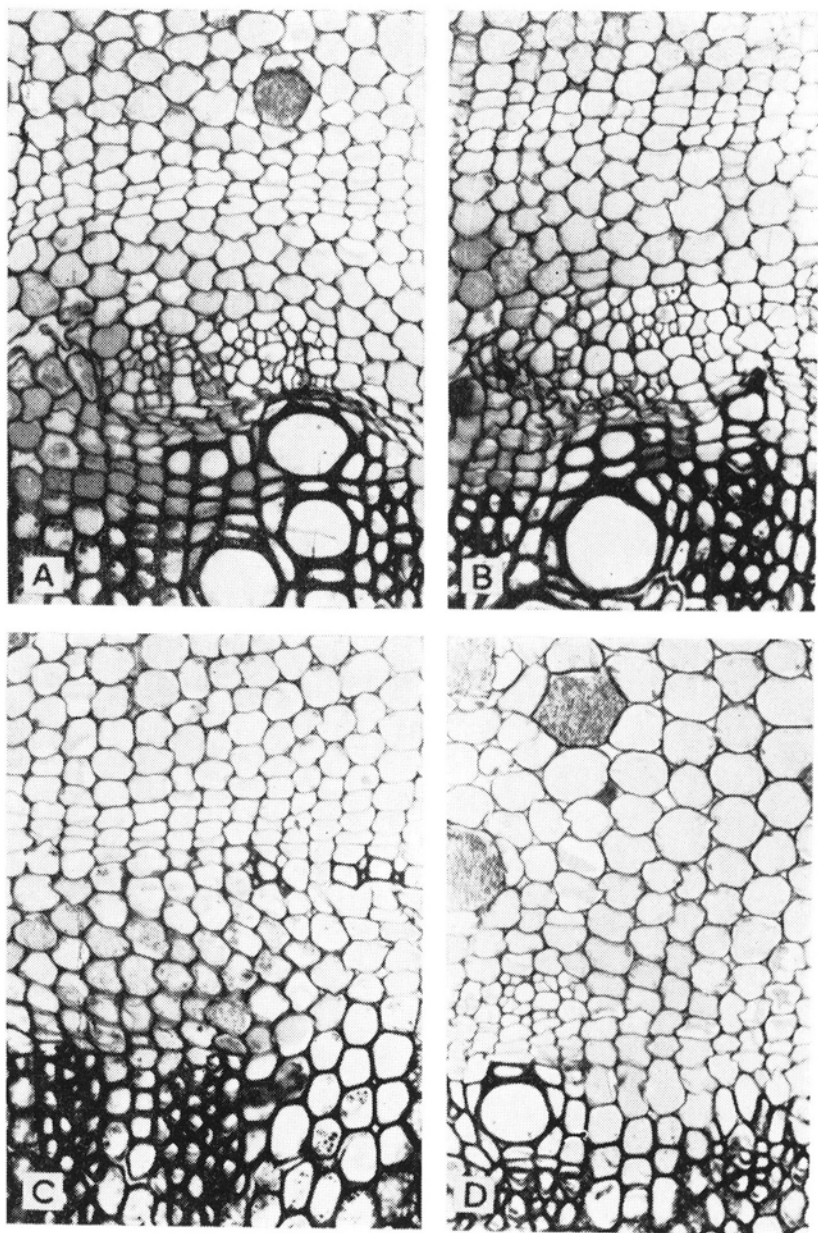
Cross sections through peripheral tissues in thin lateral *Bougainvillea* shoots. A, B — one-year-old stems, C — two-year-old stem, D — five-year-old stem.  $\times 170$

Plate XVII



Cross sections through the peripheral tissues of the many-year-old roots of *Bougainvillea* specimen in hydroponic culture.  $\times 69$





Cross sections through a cambium zone and adjacent tissues from the many-year-old *Bougainvillea* roots.

A, B, C — the formation of a new cambium population.  $\times 170$

first most probably. The formation of wall 1 in this row caused the formation of walls 1 and 2 in row III, and of wall 1 in row V. The formation of walls 1 and 2 in row III conditioned in turn the appearance of wall 1 in row IIb, whereas the arising of wall 1 in row IIa was probably the consequence of formation of wall 1 in row I. Walls 2 and 3 in row I are more or less of equal thickness, and it cannot be concluded with certainty which of them is older. Both, however, are surely younger than walls 1 and 2 in row IIa, and the formation of wall 3 in row I must have been conditioned by formation of walls 2 in row IIa. On the other hand, the formation of wall 2 in row I was conditioned by the appearance of wall X in the neighbouring row of the left which is not visible on the photograph. Formation of wall 2 in row IV produced wall 3 in row III as the second tangential wall on the radial wall of the upper cell of row IIb. It may be supposed on this basis that, in further sequence this cell will divide periclinally into two new ones. Formation of wall 2 in row IV caused wall 2 to arise in row V, and formation of wall 2 in row V resulted in the formation of wall 2 in row VI. In row VI wall 3 formed owing to the division in the neighbouring row on the right which is invisible on the photograph.

### Anticlinal divisions

The older the branch the more secondary parenchyma it contains outside the cambium. The number of cells increases, namely in the radial row and so does the number of rows. The number of rows increases by their doubling. All new rows — formed by splitting of the older ones — extend to the cambium (Plate VII). On the inner side of the cambium, owing to disturbances caused by elongation of the fibres and growth of the vessels, the radial files are not so well delineated everywhere as in the outer parenchyma. Nevertheless on both sides of the cambium, corresponding older, and younger rows arising by the splitting of the former can be distinguished (Plate VIII, photo C, Plate XIV). This would mean that it is the initial cells (Plate X, photos B, C; Plate XI, photo A. Plate XII, photo A), and not its derivatives that divide anticlinally. It would also indicate that the initial cells do not divide in excess, are not eliminated from the cambium by transforming to adult tissues.

The cambial cells of *Bougainvillea* divide anticlinally according to the scheme described in detail for storeyed cambium by Beijer (1927) on the example of *Herminiera elaphroxylon*. Anticlinal divisions disturb the zigzag pattern of the end walls characteristic for storeyed cambium. The new anticlinal wall runs more or less from the middle of one of the two end walls of the cell to a similar wall at the other end. The new anticlinal wall may in this case unite two end walls

which lie on the same side of the cell axis or on its opposite side (Beijer, 1927, Fig. 12). The zigzag pattern is restored since division of a cell in one storey results in division of definite cells in the neighbouring stories.

If the new anticlinal wall unites two end walls on the same side of the cell axis, a foursided and a sixsided cell arise (Plate XV, photo B). The end walls of the foursided cell are horizontal, therefore the cells adjacent to this cell from above and below are sevensided. Anticlinal division of these sevensided cell restores the typical sixsided shape of the foursided cell and changes the shape of one or both the daughter cells from this new division. When the anticlinal wall unites two end walls lying on opposite sides of the cell axis, then both the daughter cells are fivesided, and each has one horizontal end wall (Plate XV, photo A).

According to the arrangement of the end walls it is possible to foresee which cell will be the first to divide anticlinally. The sevensided cells are those which will divide. They are also broader than others.

Thus, anticlinal divisions of cells from superposed storeys are interconnected as do the periclinal divisions of neighbouring cells in the radial files. Anticlinal divisions spread in vertical direction, and the periclinal ones along the periphery.

The mother cells of the sieve tubes (Plate XV, photos C, D) also divide anticlinally. Their division results in formation of member of the sieve tube and of companion cells.

#### Differentiation of secondary tissues.

Essential differences between thick sprouts and thin lateral branches.

When the cambium zone reaches a thickness of 4—6 cells formed in successive periclinal divisions, the outermost of these cells probably cease to divide, the innermost one differentiate to fibres, and the cells adjacent on the outside to the differentiating fibres continue to divide (Plate X, photo D).

On cross sections there are more rows of fibres than of cambium cells (Plate VIII, photo C; Plate XI, photos B, C, D). It is however, easy to distinguish the fibres derived from the cambium files visible in the photographs from those originating from cambium cells not comprised in the cross section. Fibres derived from neighbouring cambium files from the same storey are separated from one another on their whole or almost whole length by the ends of fibres which originate from the cambium of two other stories — the upper and the lower one.



In thin lateral branches several years old on the cross section the number of cambium rows is equal to that of fibre rows (Plate XVI, photos B, C).

Outside the fibres, in the places where bundles do not differentiate, the layer of periclinally dividing cambium cells on the average 4—6 cells thick — is not disturbed. Only in some places, close to the fibres the first vessel members of the given bundle at the given site differentiate (Plate VIII, photos A, B, D; Plate IX, photo C). The sieve tube elements and the companion cells arise in the outer part of the cambium zone (Plate IX, photo C).

Between the phloem and xylem elements there remain undifferentiated cells which become the short-lived vascular cambium. Owing to this cambium of secondary origin the initiated bundles continue to extend. Their growth ceases when the tissues derived from the parenchymo-vascular cambium lying on the sides of the woody part of the bundle, differentiate to fibres or to lignified parenchyma, and those which are situated on the sides of the phloem differentiate to thinwalled parenchyma.

Outside the phloem of the youngest bundles, from the moment of initiation of the latter, undividing cambium cells belonging to the same population from which the fibres and bundles derive is present. These cells cease to divide when the innermost cells of the same population began to differentiate to fibres. Among the outermost cells of each population there are initial cells of the subsequent population (Plate IX, photo C). In each radial file, there remain outside the initial cell one or two cells which differentiate to the outer parenchyma. The meristematic cells situated on the opposite side of the initial ones differentiate to the inner parenchyma. Thus, for each population, those cells are initial which divided but seldom in the preceding population.

From each cambium population (counting from outside), the following tissue layers arise: the outer parenchyma layer one or two cells thick, a single layer of initial cells of the subsequent population, a layer of inner parenchyma varying in thickness, with groups of phloem embedded in it, and a fibre layer of varying thickness with embedded vessels of the particular bundles on the same rays as the phloem.

New populations of the parenchymo-vascular cambium are initiated concurrently with the development of new bundles. In the thin lateral branches the number of bundles increases every year less than in the thick sprouts, at the same time in the lateral branches the particular bundles continue to extend in thickness — owing to the secondary vascular cambium — longer than in the thick sprouts. Therefore, a thin five-year-old lateral branch for instance (Plate XVI, photo D) has less outer parenchyma than an even-aged sprout (Plate VII, photo A).

The roots of *Bougainvillea glabra* Choisy were also studied. Cross sections of roots of various ages were prepared from the specimen in hydroponic culture. No significant differences were found between the roots and stems as regards the mode of secondary tissue formation. Cross section through the peripheral tissues of a root more than ten years old are very similar to those of a stem of the same age (Plates XVII, XVIII).

## DISCUSSION

### Opinions of various authors concerning the formation of secondary tissues in *Nyctaginaceae*

The secondary growth in *Nyctaginaceae* has been investigated in the last ten years by Balfour (1965), Studholme and Philipson (1966), Esau and Cheadle (1969). Philipson and Ward (1965) discuss in a review paper on the ontogenesis of cambium in the shoots of seed plants all the earlier publications on this subject. After persuing this literature one has the impression that the views of the particular authors regarding the formation of secondary tissues in *Nyctaginaceae* differ so widely that no agreement between them can be found, the more so since the authors themselves stress the divergences in their views.

Balfour as well as Studholme and Esau and Cheadle based their conclusions on investigations of several-year-old stems. Both Balfour (1965) and Esau and Cheadle (1969) describe and show on their illustrations *Bougainvillea* stems in which between the phloem of the youngest bundles, and the outer perivascular fibres there are two to three layers of parenchyma cells. In the present work, owing to the study of various-aged stems, it has been demonstrated that the older and thicker the stem the more it contains of this parenchyma, and the meristematic cells lie between this thinwalled outer parenchyma and the bundles with the conjunctive tissue surrounding them.

According to Balfour (1965) and Studholme and Philipson (1966), in the stems of *Nyctaginaceae* all the secondary tissues with the exception of phloem form inwards of the meristematic cylinder, and phloem arises within the meristematic zone. Esau and Cheadle (1969), on the other hand, believe that *Nyctaginaceae* have a successive cambia, each of which produces phloem and xylem in the normal direction. At first sight it would seem that both these opinions are completely discrepant. The difference would, however, exist only if Balfour would claim that the initial cells of the meristematic zone

remain the whole time on its outer border and produce secondary tissues only on one side. Although Balfour does not mention initial cells, it results from her description that in *Bougainvillea* the initial cells dividing periclinally produce derivative cells on either side. In this way a broad zone arises which Balfour refers to in general as the meristematic zone. She considers that the term cambium is not suitable for denoting this specific for *Nyctaginaceae* secondary meristematic tissue.

Studholme and Philipson (1966) refer to the views of Balfour and speak of initial cells. They investigated the stem of *Heimeliodendron*, another representative of *Nyctaginaceae*, and consider that the essential difference between the cambium typical for dicotyledones and that of *Nyctaginaceae* consists in that the latter do not have a permanent layer of initial cells.

Esau and Cheadle (1969) use the term cambium to denote the initial layer, whereas Studholme and Philipson (1966) apply it to the entire zone of meristematic cells. Esau and Cheadle affirm that the cambium produces secondary tissues on both sides. Studholme and Philipson do not describe the action of initial cells, they only say that the innermost cells of the meristematic zone (cambium) differentiate to fibres and vessels, whereas phloem arises within meristematic zone. The outermost cells of this zone prolong its duration. It would results therefrom that there is no essential difference between the concepts of Balfour (1965), Studholme and Philipson (1966) on the one hand, and those of Esau and Cheadle on the other (1969). The seeming discrepancies are the consequence of insufficiently clear language and different use of the same terminology.

Philipson and Ward (1965) introduce the notion of bidirectional and unidirectional cambium. They call unidirectional such cambium which produces phloem on the same side as xylem, notwithstanding whether parenchyma is formed on the opposite side of the cambium. According to this terminology, *Bougainvillea* has unidirectional cambium. This defination, however, may suggest that secondary tissues arise exclusively in one direction, whereas the term parenchymo-vascular cambium is unequivocal.

#### Comparison of parenchymo-vascular cambium of *Bougainvillea* with the vascular cambium of other plants

Morphologically *Bougainvillea* cambium differs from that of most other plants in that it consists only of fusiform cells. The functional difference lies in that only thinwalled parenchyma is produced outwards, and inwards phloem and xylem, as well as the conjunctive tissue. The second of the characters mentioned does not actually concern the

cambium itself. It cannot be, namely, claimed that in *Bougainvillea* phloem and xylem are formed on the same side of the cambium because the properties of cambium of this plant are different than in the plants in which phloem and xylem are formed on opposite sides of the cambium. The course of differentiation of the cells produced by the cambium probably does not depend on its properties.

The cambium cells of *Bougainvillea* have an average length of 200—250  $\mu$ . On longitudinal tangential sections they are arranged in tiers. As regards the length of the fusiform cells and the degree of specialisation of the vessels correlated with this length, Bailey (1923) distinguishes three groups among dicotyledones. According to this classification, *Bougainvillea* should belong to the most highly specialised group in which the cambium cells are shortest and arranged on tangential section in tiers. The vessels are also correspondingly specialised. The elements of the *Bougainvillea* vessels have a simple perforation plate, and the largest among them have a diameter equal or greater than their length. The length of the vessel elements is equal to that of the cambium cell.

In *Bougainvillea*, like in all other plants, the cambium cells of the neighbouring radial files are as a rule shifted in relation to one another. On cross sections each cell from one row contacts two others from the neighbouring rows on each side. To both the tapering ends also two cells are adjacent on each side. The fusiform cell of *Bougainvillea* exhibits thus — like the cells of storeyed cambium in other plants and those of many other meristematic tissues — 14 contacts.

This fundamental spacial shape of meristematic cells has been described in connection with their division and growth by Lewis (1923, 1930, 1935), Sinnot and Bloch (1939, 1941) and Meeuse (1942). The latter author called attention to the similarity between cambium and rib meristem and the tunica. In all the tissues mentioned new walls form perpendicularly to the direction of growth. If the new walls arise in the plane to the elongation this means that they do not undergo surface growth since only walls parallel to the elongation show such growth. In the cambium, after periclinal division, only the radial walls increase in area, and in the rib meristem after transversal divisions the longitudinal walls undergo surface growth. In rib meristem, the newly forming transverse walls in one file alternate with those of the neighbouring ones (Sinnot and Bloch, 1939), like newly formed tangential walls in one row of cambium are shifted in relation with tangential walls of the neighbouring rows.

In the rib meristem, beside the walls perpendicular to the elongation, new walls parallel to this direction are also formed, this leading to the splitting of one file into two new ones. Similarly, in storeyed cambium the number of rows increases owing to anticlinal divisions.

When the cell divides parallelly to the direction of growth, neither the newly formed wall nor the wall of the mother cell extend immediately after this division. It is only division in the plane perpendicular to the direction of growth that "triggers" surface growth of the walls parallel to the elongation. Probably the new walls do not undergo surface growth in any tissue immediately after their formation. If they arise in the plane perpendicular to the direction of growth, they induce surface growth of the walls perpendicular to them, and if they are formed in the plane parallel to the direction of growth, the newly formed cells do not grow before dividing in the plane perpendicular to the direction of growth.

Priestley (1930, part II), in his work dealing with sliding growth includes drawings (text — Fig. 2) which illustrate the changes in shape of the dividing meristematic cells. From the sixsided cell after division two fivesided ones arise which, owing to the division of the neighbouring cells, become sixsided again. These changes are possible because the newly forming walls do not undergo surface growth. In the fivesided cells, owing to stretching of the walls of the mother cell, and lack of stretching of the newly formed wall, the two strait angles formed after division gradually change to angles of almost  $120^{\circ}$ .

Divisions, growth and differentiation of the particular cells are inseparably bound with the development of tissue as a whole. According to this concept Priestly (1930) formulated the principles of symplastic growth of the walls in plant tissues, and Sinnott and Bloch (1939, 1945) developed his concept and enriched it with new observations. In developing tissues division of some cells is inseparably associated with that of others. Evidence of this may be found in the investigations of Yeoman and Evans (1967) on the development of callus. These authors established that in early phases of callus growth, a greater number of cells divide simultaneously or almost so. Pairs of daughter cells form first, and then four-cell groups. In all meristematic tissues, when the cells are tightly packed after each division, the number of contacts of the dividing and neighbouring cells changes. Subsequently, however, such cells divide and in such plane that the previously divided cells return to their basic shape and basic number of contacts, while the dividing and not yet divided cells change. The first to observe this and describe it in detail was Lewis on the example of parenchyma cells (1923) and epidermal cells (1930). It has been demonstrated in the present study that the rules of cell division formulated by Lewis may be fully applied to the cambium. On tangential sections, the cells of storeyed cambium are sixsided, and, after anticlinal division of one of these cells, two fivesided ones arise, or one foursided and one sixsided one. Owing to the division of neighbouring cells of the upper and lower tier, the changed cells return to their sixsided shape. Anti-

clinal division of the cells of storeyed cambium and the changes in shape associated with it on tangential sections have been described by Beijer (1927). In the present work it has been demonstrated that the conclusions of this author based on investigation of storeyed cambium in roots of *Herminiera elaphroxylon* are also valid for the cambium of *Bougainvillaea*. It has also been found that, similarly as anticlinal divisions of cells of the superposed tiers are interconnected, so are the periclinal divisions of neighbouring cells of the radial files.

From the beginning of investigations on cambium, the views concerning initial cells were controversial, and to date no concordance has been reached, in the first place because the particular authors use the term initial cell in various senses. Newman for instance (1956) shares the opinion of Sanio (1875) and considers that in each radial row there is such a cell in the cambium, from which after division into two, one cell after a greater or smaller number of divisions will differentiate to a phloem or a xylem cell, and the second one will preserve its meristematic properties. Newman came to this conclusion after analysing the arrangement of cells on cross sections through the cambium of *Pinus radiata* D. Don. One cannot, however, conclude solely on the basis of analysis of cell arrangement as to whether the initial cell differs in some way from its derivatives dividing yet. Catesson (1964) after exhaustive investigation of the cambium in *Acer pseudoplatanus* reached the conclusion that it contains no initial cells, since in each radial file there exist other identical cells which divide with the same frequency and have identical histochemical and cytological characters. Neither did Srivastava (1966) and Srivastava and O'Brien (1966) did not detect any characters while investigating cambium in the electron microscope, which would help to distinguish the initial cells in the meristem. Thus, these investigators believe that the initial cells must differ in some respect from their daughter cells which continue to divide. This assumption results directly from the definition of an initial cell. Since, namely, after division of the initial cell, from the very beginning one is destined for differentiation to a adult type, and the other preserves meristematic properties, it is to be expected that both these cells should differ by some noticeable characters.

When both daughter cells, after division of the initial cell preserve their meristematic properties and are equal in all respects, this does not mean that their future fates will be the same. Both the identical cells after dividing may produce two pairs of cells differing from one another. One of these pairs for instance may be determined towards development into xylem cells, and the other may retain meristematic properties. In this case the fate of both the daughter cells is not

determined at the moment of their formation, but only when they themselves start to divide.

Probably in the cambium there are no such initial cells, in which, after division into two, only one would preserve unlimited possibilities of development, and the second would lose them at the moment when it arises. The potentialities of both the daughter cells are most probably equal, and only the derivatives of one of them gradually or suddenly lose the unlimited possibilities of development. Fosket (1970) and Fosket and Torrey (1969) after culturing plant tissues with the application of growth regulators believe that the hormonal medium in which cell division occurs is the decisive factor initiating differentiation of a specific cell type. There are numerous data supporting this suggestion, and it would seem that a cell with unlimited development possibilities — that means an initial cell, will give after division two cells with the same ability. However, if one of these cells divides in a different hormonal medium than the other, there will arise two new cells, the developmental possibilities of which are limited. As the result of further divisions cells will form with more and more limited possibilities, thus with a more and more definite direction of differentiation. If this is true, the initial cell cannot be expected differ noticeably from its derivatives which partly are meristematic cells.

Studholme and Philipson (1966) consider that the essential difference between typical vascular cambium of other dicotyledones and that of *Nyctaginaceae* consists in that in the latter there is no permanent initial layer. So far, however, no one seems to have proved that such a layer represents typical cambium. All models represent only initial cells of some population periclinally dividing cells. It is probable that in all plants, like *Bougainvillea*, the initial cells of each subsequent population are derived from those of the preceding population.

Since there is no method which would allow direct observation of cambium growth the sequence of cell division cannot be established with certainty (Murmānis 1971). Conclusions in this respect result in the first place from analysis of the cell groupings in cambium on cross sections. On the basis of the unequal thickness of the tangential walls, the sequence of cell division in the radial file may be determined, and in this way the initial cells of the analysed group can be indicated. These cell groups are composed, however, of a small number of cells which arose as the result of several successive divisions. Therefore the conclusions as to the sequence in division and differentiation of the cells in the radial rows on larger segments are not reliable.

Mahmood (1968) investigated from the point of view of thickness and structure of the cell wall, groups of cells on transverse sections through the cambium of *Pinus patula* and established a theoretical model of the succession in division and differentiation of cells in a radial file.



A model of the succession in cell's division and differentiation is also given by Wilson (1964). Both these models differ by many details, but in both the cells preserving unlimited possibilities of development — that is the initial cells — divide less frequently than the derivative cells differentiating to adult cell types.

The above mentioned investigators analysed the succession in cells division in single radial files as if the cells divided independently in each row. In the present paper it was attempted to analyse the cell arrangement in cambium on cross sections taking into account the fact that periclinal divisions in neighbouring rows are interconnected. It has been demonstrated that periclinal cell division in one radial row brings about such divisions in the cells of the neighbouring rows, and owing to this the divisions spread to the entire periphery of the organ, probably simultaneously from a number of foci. Anticlinal division of cambium cells, on the other hand, spreads along the long axis of the given organ.

It was found in the present study that in *Bougainvillea* initial cells divide anticlinally not in excess and are not removed from the cambium. Cumbe (1963) suppose that, in the woody dicotyledones in which the cambium cells are short, there is no elimination, similarly as in *Hibiscus lasiocarpus* investigated by this author as representative of herbaceous dicotyledones.

#### SUMMARY

The paper describes the distribution and formation of secondary tissues and the arrangement and division of cambium cells in various-aged *Bougainvillea glabra* Choisy stems. The roots were also compared with the stems and it was found that both organs are similar as regards the essential characters of secondary tissue. The cylinder of secondary meristematic tissue called parenchymo-vascular cambium outwards produces only thinwalled parenchyma. This fact has so far not been described. On the inner side the cambium produces secondary vascular bundles and „conjunctive tissue”. The older the stem the more bundles are present in it inwards from the cambium, and the more thinwalled parenchyma on the outer side. Parallely with the development of new bundles, new populations of parenchymo-vascular cambium develop successively.

The division and arrangement of the cambium cells were studied in the light of general regularities. Attention is called to the fact that the shape and basic number of contacts of the cambium cells is preserved because the periclinal division of cells in one radial row is associated with similar divisions of the adjacent cells of neighbouring rows. According to the same rules anticlinal division of a cell at one tier brings about similar divisions in the upper and lower tiers.

In the discussion of results it is attempted to draw uniform conclusions from the seemingly controversial concepts of various authors concerning the mode of formation of secondary tissues in *Nyctaginaceae*. The parenchymo-vascular cambium of *Bougainvillea* is compared with the typical vascular cambium found in most dicotyledonous plants and with other meristematic tissues. This comparison leads to the conclusion that the cells of all meristematic tissues divide according to the



same general principles. In all developing tissues, division of every cell neutralises on the one hand the consequences of earlier divisions as regards the shape and contact of the cell, and on the other, induces further divisions. In all developing tissues the successive divisions are causally related and the all divisions together constitute a chain of causes and results.

Attention is also called to the problem of initial cells in the cambium, and the causes of lack of uniformity in the views of various authors on this subject are discussed.

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*Parenchymo-waskularne kambium i jego pochodne tkanki  
w łodygach Bougainvillea glabra (Nyctaginaceae)*

Streszczenie

W niniejszej publikacji opisano rozmieszczenie i powstawanie wtórnych tkanek, oraz układ i dzielenie się komórek kambium w różnego wieku łodygach *Bougainvillea glabra* Choisy. Z łodygami porównano korzenie wykazując, że oba organy są do siebie podobne co do zasadniczych cech wtórnej budowy. Stwierdzono, że z cylindra wtórnej tkanki twórczej — nazwanej kambium parenchymatyczno-waskularnym — na zewnątrz różnicuje się wyłącznie cienkościenny miękisz — czego dotąd nie opisywano — a do wewnątrz tkanki waskularne, zebrane w kolateralne wiązki lyko-drzewne, oraz otaczające te wiązki włókna i miękisz. Im starsza łodyga, tym więcej w niej wiązek do wewnątrz od kambium, a cienkościennego miękiszu na zewnątrz. Równolegle z rozwojem nowych wiązek rozwijają się kolejno coraz nowe populacje parenchymatyczno-waskularnego kambium.

Podziały i układ komórek kambium rozpatrzono w świetle ogólnych prawidłowości. Zwrócono uwagę na to, że podstawowy kształt i podstawowa ilość kontaktów komórek kambium zachowuje się dzięki temu, że styczny podział komórek w jednym promienistym rzędzie pociąga za sobą styczne podziały przylegających

komórek z sąsiednich rzędów. Wg tych samych prawideł antyklinalny podział komórki z jednego piętra pociąga za sobą antyklinalne podziały komórek z górnego i dolnego piętra.

W części omawiającej wyniki próbowano uzgodnić rozbieżne na pozór poglądy różnych autorów co do sposobu powstawania wtórnych tkanek u *Nyctaginaceae*, oraz porównano parenchymatyczno-waskularne kambium *Bougainvilleae* z typowym waskularnym kambium większości dwuliściennych, oraz z innymi tkankami merystematycznymi. Z porównania tego wysnuto wniosek, że komórki wszystkich merystematycznych tkanek dzielą się wg tych samych ogólnych prawidłowości. We wszystkich rozwijających się tkankach — biorąc pod uwagę kształt i kontakty komórek — podział każdej komórki z jednej strony niweczy skutki wcześniejszych podziałów, a z drugiej strony wywołuje dalsze podziały. We wszystkich rozwijających się tkankach następujące po sobie podziały pozostają między sobą w związku przyczynowym i suma wszystkich podziałów stanowi łańcuch przyczyn i skutków.

Zwrócono ponadto uwagę na problem inicjalnych komórek w kambium próbując wskazać na przyczyny braku jednomyślności na ten temat.

Profesorowi Doktorowi Henrykowi Teleżyńskiemu autorka dziękuje za krytyczną dyskusję nad rękopisem.

*Instytut Botaniki i Biochemii  
Uniwersytetu Wrocławskiego  
Wrocław, Kanonia 6/8*