Radial secondary growth and formation of successive cambia and their products in *Ipomoea hederifolia* L. (Convolvulaceae)

KISHORE S. RAJPUT*, VINAY M. RAOLE and DHARA GANDHI

Department of Botany, Faculty of Science, The Maharaja Sayajirao University of Baroda, Vadodara – 390 002, India

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*Corresponding author. E-mail: ks.rajput15@yahoo.com

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**INTRODUCTION**

During the course of evolution, plants have evolved different modes of secondary thickening for mechanical support and safety of vessels for hydraulic conductivity. From an evolutionary viewpoint, it has been accepted that normal cambium is ancestral in dicotyledons and that the origin of variant types has very probably been phylogenetic, as they represent an alternative solution to the production of secondary tissues (Carlquist, 1988). Of these, the formation of successive cambia is most common and is usually found in climbing species, whereas, in trees, it is either rare or almost non-existent. Although its occurrence has been reported in some species (Schenck, 1893; Pfeiffer, 1926; Chalk & Chattaway, 1937; Metcalfe & Chalk, 1950; Philipson & Ward, 1965; Philipson, Ward & Butterfield, 1971; Carlquist, 1988; Rajput & Rao, 1998, 1999; Rao & Rajput, 1998, 2000) these species are restricted to only a fraction of dicotyledonous taxa. In all the reported cases, the development of successive cambia varies in its origin from species to species. Successive cambia usually form secondary xylem centripetally (towards the centre of the stem) and secondary phloem centrifugally (towards the periphery of the stem). In *Ipomoea hederifolia*, however, the development of successive cambia occurs from the parenchyma cells located four
to six cells away from the phloem produced by previous cambium. However, cambia developing from conjunctive tissues show a functionally reverse nature, which has not been reported so far in any of the plants showing variant secondary growth.

The formation of successive cambia has been known for a long time and tends to occur in different members of Convolvulaceae (Metcalfe & Chalk, 1950; Pant & Bhatnagar, 1975; Lowell & Lucansky, 1986; Carlquist & Hanson, 1991). Various workers have studied the stem and wood anatomy of Convolvulaceae, the most important contributions being those of Metcalfe & Chalk (1950), Mennega (1969), Lowell & Lucansky (1986), and Carlquist & Hanson (1991). However, most of these studies are based on dried wood samples, with fewer studies on wet preserved samples. D’Almeida & Patil (1945, 1946) described the xylem structure of some of the species of Convolvulaceae, but did not pay much attention to variant secondary growth. Similarly, Pant & Bhatnagar (1975: 64) concentrated their studies on the development of medullary bundles (interxylary phloem) in two species of Argyreia, but paid little attention to the pattern of secondary growth.

Ipomoea is the largest and most diverse genus of the family, comprising about 500 species (Angiosperm Phylogeny Group website, version 8, June 2007, http://www.mobot.org/MOBOT/research/APweb), generally characterized by a vine growth habit (McDonald, 1992). Ipomoea hederifolia L. has been introduced worldwide by cultivation because it has ornamental flowers, and is naturalized in the palaeotropics (Lowell & Lucansky, 1986: 382), but most wild and escaped cultivated species are noxious weeds (Lowell & Lucansky, 1990: 232). Although the vegetative anatomy and morphology of I. hederifolia have been studied previously (Lowell & Lucansky, 1986), most attention has been paid to the structural details of the xylem and phloem. In the present study, we report certain additional features which have not been described previously for this species. These data contribute to a better understanding of the taxonomy of I. hederifolia, add to the existing knowledge of vine anatomy, and reveal a new type of cambial variant that has not been reported previously in any species of Ipomoea.

MATERIAL AND METHODS

Ten to 15 segments of the main stem [from young (3 mm) stem to the maximum thickness (22–40 mm) available; 40–60 mm in length] were collected from ten plants of I. hederifolia (Convolvulaceae) growing in Panch Mahal forest (north-eastern Gujarat), Saurashtra region (Rajkot, western Gujarat), and Dediapada forest (Gujarat State) (i.e. ten plants from all three areas). These samples were collected three times (October, December, and March), fixed immediately in formalin–acetic acid–ethanol solution, dehydrated with a tertiary butanol series, and processed by the routine paraffin embedding method (Johanson, 1940). Thick/woody stem samples were also sectioned on a sliding microtome. Transverse, radial, and tangential longitudinal sections, 12–15 μm thick, were obtained with a rotary and sliding microtome, and stained with a combination of safranin and fast green (Johanson, 1940).

To obtain the length and width of vessel elements, fibriiform vessel elements, and xylem fibres, small pieces of xylem adjacent to the cambium of each successive ring were macerated with Jefferey’s solution (Berlyn & Miksche, 1976) at 55–60 °C for 24–36 h and stained with safranin to study the general morphology and size of the vessel elements and fibres. One hundred objects were chosen randomly to obtain the mean and standard deviation. Important results were microphotographed with a Leica trinocular research microscope.

RESULTS

MORPHOLOGY OF THE STEM

Morphologically, the stem portion adjacent to ground level and not in contact with any supporting object remains circular in outline and shows distinct concentric rings of cambia. However, the portion away from the ground and in contact with the supporting object shows differential cambial activity, ultimately resulting in a lobed pattern. The number of lobes is not constant and may vary for a given plant. The stem is often deeply furrowed, flattened, broadly lobed, or cylindrical. The change in the shape of the stem may be correlated with cambial variants and an unequal production of secondary vascular tissues in the stem. It has been observed that a lobed pattern forms as a result of increased cambial activity on the opposite side of the stem to the support.

DEVELOPMENT OF VASCULAR CAMBIUM

A normal vascular cambium arises as a continuous cylinder between the external phloem and metaxylem. The cambium functions in a normal way, as for other dicots, for a short time and produces several layers of secondary phloem centrifugally and secondary xylem centripetally. The secondary phloem consists mainly of sieve tubes, companion cells, and phloem parenchyma cells, whereas the secondary xylem consists of vessels, fibriiform vessels, fibre tracheids, and xylem ray parenchyma cells. This cambium remains functional for a definite period of time, producing 5–6 mm of secondary xylem, which
later ceases to divide. Up to this stage, the protoxylem remains unchanged, but clusters of internal phloem increase slightly in size as a result of the differentiation of additional pith cells into sieve tube elements. The cortex consists of discontinuous bands of perivascular fibres, large thin-walled parenchyma cells, secretory structures, and druse-containing cells.

A second ring of cambium develops from the axial parenchyma cells at a distance of about three to six cell layers outside the phloem produced by the previous cambium. During the development of new cambium, one or two parenchyma layers undergo repeated divisions and result in the formation of five- to six-layered wide bands of meristematic cells. Initially, these cells are arranged irregularly, but further periclinal divisions lead to a radial arrangement (Figs 1, 2). Cells in the centre of this band differentiate into vascular cambium, whereas the remaining cells on either side of the newly formed cambium differentiate into conjunctive tissues centripetally, and the outer cells into secondary cortex. These conjunctive tissues form the site for the origin of reverse cambium (Figs 3, 4). The newly developed cambium from the axial parenchyma is functionally normal, producing secondary xylem towards the centre and secondary phloem towards the periphery (Figs 5, 6). Each functionally normal successive cambium follows a similar pattern of development. The first ring of cambium forms a continuous band of xylem. In the second ring onwards, the differentiation of conducting elements of both the xylem and phloem remains restricted to certain segments of the meristem, with the remainder forming thin-walled conjunctive tissue on both the outer and inner sides.

The mature stem is composed of five to six successive rings of xylem alternating with phloem (Fig. 7). In these rings of secondary xylem, functionally normal cambium is produced. In most of the rings, there remains another discontinuous ring of secondary xylem, which is produced by functionally reverse cambium and has a reverse orientation, i.e. secondary xylem arranged centrifugally and secondary phloem centripetally (Figs 7, 8). However, these cambia do not form a complete ring, but rather are in the form of small segments present only on the lateral side of the flat stem. In some of the stem segments, tangentially arranged bicollateral vascular bundles are also observed. The xylem is diffuse and porous with indistinct growth rings, and is composed of both wider vessel elements and narrow fribiform vessels, which are indistinguishable in transverse view. Vessels are mostly solitary with a simple perforation plate on their slightly oblique to transverse end walls (length, 237–476 μm; width, 134–260 μm). The alternate bordered pits on the lateral walls are oval to elliptic or oblong (diameter, 7–10 μm). Tyloses are common in the wider vessels in all successive rings and are mostly thin walled.

As in other members of Convolvulaceae, fribiform vessels are also recorded in I. hederifolia. Fribiform vessels are similar to imperforate tracheary elements, except for the occurrence of a small subterminal perforation plate near each end of the cell. It is difficult to distinguish fribiform vessels in transverse view, and their dimensional details are studied either in longitudinal sections or in macerated material. The length and width of fribiform vessel elements vary from 478 to 518 μm and 28 to 34 μm, respectively. Xylem rays are mostly uniseriate, but biseriate rays are also frequent. Ray cell walls are thick and lignified, measuring about 1.2–1.4 μm. Conjunctive tissues are mostly thin-walled, un lignified parenchyma, forming a band of six to ten cells in each radial file and providing a site for the origin of reverse cambium.

**Origin of functionally reverse cambia**

The second ring of cambium is functionally bidirectional, as in other dicotyledons that form successive rings of cambia. After the formation of 15–20 xylem elements by this cambium, the parenchyma (conjunctive tissue) adjacent to the inner side of xylem derivatives undergoes periclinal divisions and results in the
of the present study in the primary xylem of the stem. An unexpected finding phloem between the periphery of the pith and inside Intraxylary or internal phloem consists of strands of about 6–9 mm (xylem) and 3–5 mm (phloem). In comparison with normal secondary xylem and plate on their slightly oblique to transverse end walls. They are mostly solitary with a simple perforation ray parenchyma cells. Wide vessels are rare or absent. They are also observed in the secondary xylem of functionally reverse cambia. It is mostly composed of very narrow fibriform vessels, fibre tracheids, and axial and ray parenchyma cells. Wide vessels are rare or absent. They are mostly solitary with a simple perforation plate on their slightly oblique to transverse end walls. In comparison with normal secondary xylem and phloem, smaller amounts are produced, measuring about 6–9 mm (xylem) and 3–5 mm (phloem).

DEVELOPMENT OF INTRAXYLARY PHLOEM AND CORK
Intraxylary or internal phloem consists of strands of phloem between the periphery of the pith and inside the primary xylem of the stem. An unexpected finding of the present study in I. hederifolia is that cambial action occurs at the inner face of intraxylary phloem (Figs 11, 12). This meristem (referred to here as internal cambium) divides bidirectionally and forms conducting elements of xylem and phloem in the opposite direction, i.e. secondary xylem towards the periphery and secondary phloem towards the centre. The activity of this cambium is evident not just by the crushing of protophloem, but also by the repeated cell divisions in the meristem (internal cambium) and by the differentiation of secondary xylem and intraxylary phloem (Fig. 12). In mature stems, the amount of xylem and phloem produced by the internal cambium is relatively greater. Therefore, it exerts a pressure on the pith and results in its complete obliteration (Figs 11, 13). This cambium originates first on those sides of the stem that do not touch the support. Later, it develops on the other side of the stem; however, only two segments, which are formed at the beginning, produce significant amounts of secondary xylem and phloem; the remaining segments produce a limited amount of secondary xylem and phloem. The xylem produced from this cambium is composed of fibre tracheids, wider vessels, narrow (fibriform) vessels, and axial and ray parenchyma. Similarly, the phloem consists of sieve tube elements, companion cells, and axial parenchyma cells. The length and width of the vessel elements remain more or less similar to those of the vessel elements produced from functionally normal and reverse cambium.

At the end of the growing season (i.e. February–May), concomitant with the increase in the amount of intraxylary phloem and xylem, the pith cells collapse and undergo obliteration (Figs 11, 15), followed by formation of an empty cavity in the centre. Pith cells towards the cavity and adjacent to the internal phloem undergo periclinal division and differentiate into phellogen/cork cambium. Initially, the cork cambium develops opposite the internal cambial arcs that are functionally more active (Figs 15, 16). Thereafter, it originates opposite other small arcs of the internal phloem cambium, which are functionally less active. The formation of more and more internal phloem and cork pushes the pith cells towards the centre, crushing the pith cells. Some of the parenchyma cells adjacent to the cork cells also accumulate phenolic compounds and form a boundary around the cork cells (Figs 15, 16).

DEVELOPMENT OF INCLUDED PHLOEM
Concurrent with or slightly later than the development of the successive ring of cambium, small isolated islands of included phloem arise from the xylem parenchyma (Figs 13, 14). However, the parenchyma cells situated deep inside the secondary xylem undergo radial and tangential divisions, followed by differentiation into isolated islands of included phloem (Fig. 14). The cellular composition of these islands is similar to that of normal phloem, and consists of narrow sieve tubes, companion cells, phloem parenchyma, and, occasionally, druse-containing cells.

DISCUSSION
Convolvulaceae is currently regarded as containing 56 genera with 1625 species. Of these, Ipomoea is the
we report some additional features which have not been studied previously (Lowell & Lucansky, 1986), cambial stage (Lowell & Lucansky, 1986: 387).

anomalous cambial stage, and (5) the supernumerary in secondary growth: (3) normal cambial stage, (4) the and (2) the cambium-like meristem stage. Three are I. hederifolia secondary growth, the developmental anatomy of & Lucansky, 1990: 242). Based on the primary and woody species of I. hederifolia, Carlquist (1975) reported that stems of lianas are often asymmetric in cross-section because of the addition of vascular tissues in relation to twining support. A asymmetric in cross-section because of the addition of vascular tissues is correlated with the development of the stem. This unequal production of secondary vascular tissues is correlated with the development of the cambial variant (Lowell & Lucansky, 1986: 386). The location of increased cambial activity on opposing sides of the stem is associated externally with those sides of the stem that do not touch a support. Carlquist (1975) reported that stems of lianas are often asymmetric in cross-section because of the addition of vascular tissues in relation to twining support. A similar correlation between the position of the cambium and stem support has also been established in I. versicolor (Scott, 1891) and I. quamoclit (Lowell & Lucansky, 1990: 242). Based on the primary and secondary growth, the developmental anatomy of I. hederifolia can be classified into five stages. Two are in primary growth: (1) the bicollateral bundle stage, and (2) the cambium-like meristem stage. Three are in secondary growth: (3) normal cambial stage, (4) the anomalous cambial stage, and (5) the supernumerary cambial stage (Lowell & Lucansky, 1986: 387).

Successive supernumerary cambia are common in woody species of Ipomoea, regardless of their growth habit (Metcalf & Chalk, 1950: 961; McDonald, 1981; Lowell & Lucansky, 1986: 393, 1990: 243). In I. hederifolia, the first ring of cambium remains functional for a definite period, and later ceases to divide. A new ring of cambium is developed from the axial parenchyma cells at a distance of about three to six cell layers outside the phloem produced by the previous cambium. D’Almeida & Patil (1945, 1946) and Pant & Bhatnagar (1975) have reported similar observations in other species of Ipomoea and Argyreia. However, the development of successive cambia of many plant families generally arises external to the areas of specialized vascular growth of normally positioned cambium (Studholme & Philipson, 1966; Esau & Chreadle, 1969; Lowell & Lucansky, 1986, 1990; Rajput & Rao, 1999, 2000, 2002; Rajput, 2001, 2002). Prior to the formation of new cambium, parenchyma cells three to six cell layers away from the phloem produced by the previous cambium undergo repeated divisions and form a wide band of meristematic cells. From this band, central cells differentiate into a new cambium, whereas surrounding cells differentiate into conjunctive tissues to the inside and parenchyma cells to the outside of the newly developed cambium. However, the parenchyma cells developed from the wide band of meristematic cells outside the newly developed cambium act as a site for new cambium in the future (Rajput & Rao, 2000, 2002; Rajput, 2001, 2002: 226). All of the investigated species in which successive cambia have been reported always produce xylem towards the centre and phloem towards the periphery. An unexpected finding of the present study in I. hederifolia, however, is the development of cambium that is functionally abnormal. This cambium produces xylem centrifugally and phloem centripetally. To our knowledge, this type of cambial variant has not been reported previously in I. hederifolia. The information generated from this study can be added to our previous report on Dolichos (Rajput, Rao & Patil, 2006: 68).

An internal cambium arises in the mature stems of I. hederifolia from parenchyma cells between the primary xylem and internal phloem. It produces secondary phloem centripetally and secondary xylem.

Figures 11–16. Transverse view of mature stem showing internal phloem, included phloem, and cork cambium in the pith region. Fig. 11. Pith region of the mature stem showing secondary xylem and phloem differentiated from the internal phloem cambium (arrows). Note the vessel elements towards the protoxylem and phloem towards the centre of the pith. Fig. 12. Enlarged view of the pith in a relatively young stem showing distinct cambium (arrowhead) and vessel element. V, vessel. Fig. 13. Arrowhead showing included phloem islands in the secondary xylem. Fig. 14. Enlarged view of the secondary xylem showing included phloem islands (arrowhead). Fig. 15. Pith region of the mature stem showing secondary xylem and phloem differentiated from the internal phloem cambium. Dark black bands in the centre represent obliterated pith cells. Fig. 16. Enlarged view of the pith region showing the formation of cork. Arrowhead shows cork cambium with distinct nucleus and cambial cells arranged in radial files. Also note the heavy accumulation of phenolic compounds (PC) in crushed pith cells. Scale bars: Figs 11, 15, 75 μm; Figs 12–14, 16, 225 μm.

largest and most diverse genus of the family, comprising about 500 species (Angiosperm Phylogeny Group website, version 8, June 2007, http://www.mobot.org/MOBOT/research/APweb). Generally, it is characterized by a vine growth habit (McDonald, 1992: 262). The stem and wood anatomy of Convolvulaceae has been studied by different workers, with the most important contributions being those of D’Almeida & Patil (1945, 1946), Metcalfe & Chalk (1950), Mennega (1969), Pant & Bhatnagar (1975), McDonald (1981), Lowell & Lucansky (1986), Carlquist & Hanson (1991), and McDonald (1992). These studies have shown that most of the genera form successive cambia, and that intraxylary phloem is a characteristic feature of the family. Although I. hederifolia has been studied previously (Lowell & Lucansky, 1986), we report some additional features which have not been described before.

The stem shape in I. hederifolia is a result of the bidirectional activity of the original cambium and successive rings of cambia, with the production of increased vascular tissues on opposing sides of the stem. This unequal production of secondary vascular tissues is correlated with the development of the cambial variant (Lowell & Lucansky, 1986: 386). From this band, central cells differentiate into a new cambium, whereas surrounding cells differentiate into conjunctive tissues to the inside and parenchyma cells to the outside of the newly developed cambium. However, the parenchyma cells developed from the wide band of meristematic cells outside the newly developed cambium act as a site for new cambium in the future (Rajput & Rao, 2000, 2002; Rajput, 2001, 2002: 226). All of the investigated species in which successive cambia have been reported always produce xylem towards the centre and phloem towards the periphery. An unexpected finding of the present study in I. hederifolia, however, is the development of cambium that is functionally abnormal. This cambium produces xylem centrifugally and phloem centripetally. To our knowledge, this type of cambial variant has not been reported previously in I. hederifolia. The information generated from this study can be added to our previous report on Dolichos (Rajput, Rao & Patil, 2006: 68).

An internal cambium arises in the mature stems of I. hederifolia from parenchyma cells between the primary xylem and internal phloem. It produces secondary phloem centripetally and secondary xylem.
centrifugally. No mention is made of the development of secondary xylem having a reverse orientation and its differentiation from internal cambium in a previous study (Lowell & Lucansky, 1986). The development of internal phloem remains characteristic to some families of dicotyledons, with Convolvulaceae being one of them. This internal cambium is functionally bidirectional, producing secondary xylem centrifugally and secondary phloem centripetally. The formation of such internal cambium, similar in origin, position, and product, also arises in the pith region of *I. versicolor* (Scott, 1891), *Calystegia* (Philipson et al., 1971), *I. quamoclit* (Lowell & Lucansky, 1990: 244), and *Ericibe coccinea*, *Operculina palmerie*, and *Stictocardia benavensis*, members of the same family (Carlquist & Hanson, 1991: 60, 62). This cambium originates first on those sides of the stem that do not touch a support. Later, it develops on the other side of the stem, but only two segments of the cambium, which are produced at the beginning, give rise to more secondary xylem and phloem. The other segments are suppressed, with a limited amount of secondary xylem and phloem, giving an impression of vascular bundles embedded in the pith region. According to Carlquist & Hanson (1991: 89, 90), this type of cambial action has not been reported previously in any species of *Ipomoea*. Thus, one more genus can be added to the list of genera that produce an interxylary phloem cambium which divides bidirectionally, forming secondary xylem centrifugally and secondary phloem centripetally.

The occurrence of interxylary cork in the perennial organs of some angiosperms has been reported previously in *Epilobium* and in several species of *Artemisia* (Moss, 1934, 1936, 1940; Diettert, 1938; Moss & Gorham, 1953; Ginzburg, 1964). Most of the work performed up to 1940 was treated thoroughly by Moss & Gorham (1953). This article listed around 40 species with interxylary cork and splitting of the stem, and aimed to correlate various reports with the hope of stimulating further research in this area. In the present study in *I. hederifolia*, the development of intraxyllary cork is reported for the first time. To our knowledge, this is the first report for Indian plants. Previous workers have reported interxylary cork in the secondary xylem, but in *I. hederifolia* it is formed in the pith region and not as an interxylary cork.

Various physiological functions have been ascribed to the formation of interxylary cork. Moss (1940: 768) proposed that interxylary cork was formed as a protection mechanism against ‘damage from animals, pathogens and wind blown soil’, and helped plants to retard the loss of water and to restrict its upward movement through relatively narrow wound zones. Ginzburg (1964) added that, apart from its being a protection layer, interxylary cork also functions as a separating layer in extremely dry habitats, such as the Negev of Israel. In *I. hederifolia*, the formation of intraxyllary cork may be associated with a similar function, i.e. for protection, and requires further study.

Later, ontogenetically, a foraminate pattern of included phloem islands develops from the xylem parenchyma of mature stems. The formation of included phloem islands by the differentiation of xylem parenchyma, or centripetal differentiation of phloem elements directly from the cambium, has been reported in the stems of *I. versicolor* (Scott, 1891) and *I. quamoclit* (Lowell & Lucansky, 1990: 241). In *I. hederifolia*, parenchyma cells situated deep inside the secondary xylem undergo differentiation into included phloem islands; no direct differentiation of phloem from the cambium towards the xylem side is observed.

Structurally, the xylem produced from both functionally normal and reverse cambia shows considerable variation. The number of xylem elements produced by reverse cambium is relatively less than the elements produced by functionally normal cambium. Xylem produced from reverse cambium is mostly composed of fibriform vessels, fibre tracheids, and axial and ray parenchyma cells. Vessels with larger diameter are few or almost absent. Xylem produced from normal cambium is composed of vessels (both wide and fibriform vessels), xylem fibres, and ray and axial parenchyma cells. An interesting feature of *I. hederifolia* xylem is the presence of vessel dimorphism, which has been reported in several species of Convolvulaceae (Pant & Bhatnagar, 1975: 62; Carlquist & Hanson, 1991: 87). Vessel dimorphism is a term that can be applied to the presence of wide plus narrow vessel elements (Carlquist, 1981: 326; Carlquist & Hanson, 1991: 74). Fibriform vessel elements are considered to be at least as effective as tracheids in resisting the formation of air embolism in vessels, because air embolism forms far less commonly in narrow vessels than in wide ones (Ellmore & Ewers, 1985; Carlquist & Hanson, 1991: 74). Thus, fibriform vessel elements, which are common in Convolvulaceae and other lianas, can form a subsidiary conductive system with a degree of conductive safety virtually as high as that provided by tracheids (Ayensu & Stern, 1964; Carlquist, 1991: 151).

The occurrence of a thin-walled, un lignified band of parenchyma (also called conjunctive tissue) followed by every xylem ring in *I. hederifolia* may be associated with its scandent habit. One of the potential advantages claimed for such a conformation is the protection of vessels from damage during torsion in stems of lianas (Schenck, 1893; Carlquist, 1975). This explanation appears to be valid, because protection from injury is presumably a better option than recov-
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REFERENCES


Rao KS, Rajput KS. 1998. Rayless secondary xylem of
Schenck H. 1893. Beiträge zur biologie und Anatomie der
Lianen. II. In: Schimper AFW, ed. Botanische Mitteilungen
Scott DH. 1891. On some points on the anatomy of Ipomoea
Studholme WP, Philipson WR. 1966. A comparison of the
cambium in two woods with included phloem: Heimerlidendron
brunianum and Avicennia resinifera. New