BARK ANATOMY AND INTERCELLULAR CANALS IN THE STEM OF
DELARBREA PARADOXA (ARALIACEAE)

by

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SUMMARY

The anatomy of the primary tissues and secondary phloem in the stem of Delarbrea paradoxa Vieill. (Araliaceae) was examined with emphasis on structure and topography of secretory canals. Secretory canal systems of primary (axial canals in cortex and pith, radial canals in medullary rays) and secondary origin (axial canals in secondary phloem, radial canals in rays of secondary phloem and secondary xylem) were distinguished. Two distinct types of axial parenchyma (sheath parenchyma near axial secretory canals, and phloem parenchyma associated with conducting elements) occur in the secondary phloem. Distribution, size and number of cells per strand, occurrence of starch, and mode of transformation during phloem collapse serve to distinguish these two types. Three stages of secretory canal development (canal formation, active secretion, and senescence) were distinguished on the basis of TEM observations. The secretory canal lumina are formed simultaneously with the differentiation of meristematic cells into epithelial secretory cells. During the active secretion phase the epithelial cells contain leucoplasts aggregated into small groups, each accompanied by 2 to 3 mitochondria. These aggregations indicate terpene production in the cell. The secretion of terpenes is accompanied by swelling and loosening of the cell walls facing the canal lumina. Secretory processes were not indicated in the highly vacuolated senescent epithelial cells.

Key words: Intercellular canals, axial parenchyma, epithelial cells, ultrastructure, terpenes.

INTRODUCTION

The occurrence of secretory canals in vegetative organs of plants belonging to the family Araliaceae was reported by many plant anatomists. This information was summarized by Metcalfe & Chalk (1950) and Carlquist (1988). Although these structures are traditionally regarded as a character of great diagnostic importance for this family (Harms 1894–1897; Viguier 1906; Takhtajan 1987, among others), no information is yet

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available on development, structure and ultrastructure of the secretory canals in any genus of Araliaceae. Our ignorance of this subject seems especially evident in view of the progress made during the last two decades with reference to the secretory canals in other plant families, such as Pinaceae (Werker & Fahn 1969; Fahn & Benayoun 1976; Benayoun & Fahn 1979; LaPasha & Wheeler 1990), Burseraceae (Bhatt 1987; Nair & Subrahmanyam 1998), Anacardiaceae (Fahn & Evert 1974; Joel & Fahn 1980a, b, c; Nair et al. 1983; Venkaiah & Shah 1984; Bhatt & Mohan Ram 1992; Venkaiah 1992), Rutaceae (Gedalovich & Fahn 1985). The principal results of these studies were summarized by Fahn (1979), Denisova (1989), and Nair (1995).

The present study describes the structure of primary and secondary tissues (with the exception of the wood) in the stem of Delarbrea paradoxa Vieill. subsp. paradoxa, and examines the ultrastructure, mode of secretion, and the three-dimensional arrangement of the secretory canals. The wood anatomy of Delarbrea was described by Oskolski et al. (1997), but no information on bark and pith structure of this genus was available prior to our study.

The plants of D. paradoxa are monocaulous or sparsely branched treelets or trees ranging from c. 1.5 to 20 m in height with large pinnate leaves densely clustered at the stem top, and petiole bases. This species has the most extensive distribution among Araliaceae of the South Pacific region, i.e. from New Caledonia through Vanuatu and the Solomon Islands to the Moluccan and Lesser Sunda Islands. Besides D. paradoxa, the genus Delarbrea comprises four more species endemic to New Caledonia, and a single species restricted to Queensland, Australia (Lowry 1986).

Delarbrea is closely related to the genera Pseudosciadium and Myodocarpus, both endemic to New Caledonia. These three genera form a well delimited monophyletic group occupying a distinctly isolated position within Araliaceae. Probably, Delarbrea, Pseudosciadium, and Myodocarpus are relics of an ancient araliaceous lineage from which both members of the order Araliales (Araliaceae and Apiaceae) evolved. This hypothesis is supported by data on biogeography (Raven & Axelrod 1972, 1974; Raven 1980; Lowry 1998), flower and fruit morphology (Baumann 1946; Eyde & Tseng 1971; Lowry 1986), wood anatomy (Rodriguez 1957, 1971; Oskolski 1994, 1996; Oskolski et al. 1997), and molecular phylogenetics (Plunkett 1998; Plunkett et al. 1996, 1997; Lowry et al. 2001). In fact, the presence of secretory canals in vegetative organs of Delarbrea and its relatives is considered as one of few indicators responsible for attributing these peculiar genera to Araliaceae (Viguier 1906; Oskolski 1996; Oskolski et al. 1997). Therefore, a detailed study of these structures in Delarbrea is of importance for the taxonomy and phylogeny of the family.

MATERIAL AND METHODS

The material for anatomical studies was collected by P. P. Lowry II, A. A. Oskolski, and G.M. Plunkett during a field trip in New Caledonia (Prov. Nord, Ponandou River Valley) in December 1996 from a sparsely branched tree of Delarbrea paradoxa subsp. paradoxa, c. 5 m tall (P. P. Lowry II et al. 4766; vouchers deposited at LE, MO, NOU, P). Specimens 2–3 cm long were cut from a) the branch tip as well as from other stem
parts distinguished visually as the leaf-bearing zone (c. 10 cm from the tip), b) the zone of the leaf scars (c. 30 cm from the tip), and c) the zone of mature bark (at breast height, stem diameter 60 mm), and fixed in FAA (Johansen 1940). Transverse, radial, and tangential sections, 15–30 $\mu$m thick, were double stained with a 1% aqueous solution of safranin and astra blue. Maceration of secondary phloem was carried out in a mixture of equal volumes of acetic acid and hydrogen peroxide at 60 °C for 48 hours (Johansen 1940). Length of sieve-tube members and sclerified fibres was determined from the macerated material mounted in glycerin.

The descriptive terminology for bark structure follows Trockenbrodt (1990) and Junikka (1994). The parenchyma associated with the axial secretory canals is termed ‘sheath parenchyma’ after Roth (1981) whereas the term ‘axial phloem parenchyma’ is used for the parenchyma associated with the conductive elements (sieve tubes and companion cells). The term ‘fibre-like sclereids’ describes elongated sclerified cells which secondarily differentiated from the fusiform axial phloem parenchyma cells. Those cells neither fit the definitions of fibres nor sclereids according to Trockenbrodt (1990).

The specimens for ultrastructural studies were taken in June 1996 and July 1997 from an individual of Delarbrea paradoxa subsp. paradoxa cultivated in the greenhouses of the V.L. Komarov Botanical Institute, St. Petersburg. Small portions of the stem, the shoot apices, and the young leaves were fixed in a mixture of 2.5% glutaraldehyde and 2% paraformaldehyde in 0.1 M phosphate buffer (pH 7.3) at 20 °C for 2.5 hours. The material was postfixed with 1% OsO$_4$ in the same buffer for 18 hours, dehydrated in a graded series of ethanol and acetone and embedded in Epon-Araldyte resin. Ultrathin sections were cut with a Reichert-Jung ULTRACUT E ultramicrotome, stained with lead citrate for 10 min, and viewed with a Philips CM 12 transmission electron microscope at an accelerating voltage of 80 kV.

RESULTS

Stem anatomy of Delarbrea paradoxa

Three zones (stem tip, leaf-bearing zone, and leafless zone) can be distinguished on the unbranched stem of D. paradoxa. The leaf-bearing zone of the stem varies considerably in length ranging in different plants from 5 to 20 cm. A complete ring of secondary tissue is formed at 20–25 mm from the stem tip (stem diameter 9–12 mm). The periderm on the stem surface usually becomes distinct in the lower part of the leaf-bearing zone, i.e., at about 10 cm from the stem apex. The bark below the leaf-bearing zone is brownish-gray, smooth, with small rounded lenticels. The mature bark is gray, rough, and covered with irregular shallow fissures. The main components of the bark are described as follows:

Epidermis: formed by a single layer of isodiametric, rounded, thin-walled cells; subepidermal sclereids absent (Fig. 2).

Cortex (Fig. 2, 3): cortical collenchyma lamellar (occasionally angular-lamellar), in 2–8 layers formed by strands of 2–7 isodiametric or axially elongated cells of 60–100 $\mu$m in tangential diameter. Cortical parenchyma formed by 20–50 layers of isodiametric or somewhat axially elongated thin-walled parenchyma cells of 70–130 $\mu$m in tangential
diameter; with rather large intercellular spaces. Druses present in cortical parenchyma, and, rarely, in cortical collenchyma cells; axial secretory canals scattered throughout the cortex (mostly in cortical parenchyma), 25–35 \( \mu m \) in tangential diameter, lined by a single layer of 4–7 epithelial cells. Vascular bundles collateral, arranged in a ring in the branch tip region (Fig. 2), or persistent as leaf traces in the cortex of older branch portions; axial secretory canals associated with the bundles somewhat smaller than those in the cortex (20–30 \( \mu m \) in tangential diameter), lined by a single layer of 4–6 epithelial cells. Primary bark fibres thick-walled, aggregated into large cap-like clusters, 10–20 tangential layers deep. Dilatation of the cortical tissue is effected mostly by stretching of the cells in tangential direction, and also by anticlinal divisions of cortical collenchyma and parenchyma cells. Tangentially elongated and isodiametric sclereids of 60–140 \( \mu m \) in tangential direction with thin to thick walls commonly present in the outermost region of dilated cortical parenchyma.

Periderm: of subepidermal origin (Fig. 3); phellem composed of 5–15 layers of isodiametric to radially flattened thin-walled cells with thickened inner tangential walls; phelloderm composed of 4–6 layers of radially flattened cells with thin, lignified walls (Fig. 4, 6). Prismatic crystals present in some phelloderm cells.

Secondary phloem: composed of alternating tangential bands of different cell composition crossed by phloem rays (Fig. 5). Tangential zones 10–15 cell layers deep, made up of sieve elements, companion cells, axial phloem parenchyma cells and/or their derivatives, alternating with tangential zones 5–10 cell layers deep and composed by a network of secretory canals associated with axial sheath parenchyma. This pattern of alternating zones is obscured in the outermost region where the phloem parenchyma is heavily collapsed (Fig. 4, 6). The transition from non-collapsed to collapsed secondary phloem is gradual (Fig. 5). Sieve tube members are 20–30 \( \mu m \) wide and between 600–1000 \( \mu m \) long (average length 800 + 20 \( \mu m \)); sieve plates compound with (4–)6–10(–13) sieve areas, located on vertical or slightly oblique cross walls (Fig. 13). Axial phloem parenchyma cells (associated with conductive elements) mostly thin-walled and fusiform in the non-collapsed secondary phloem (Fig. 7); these cells are transformed into both thin-walled chambered crystaliferous cells containing numerous prismatic crystals (Fig. 9, 10), and into thick-walled fibre-like sclereids (20–35 \( \mu m \) in diameter, between 500–1000 \( \mu m \) in length, average 760 + 20 \( \mu m \)) or strands of 2–7 sclerified cells (Fig. 10–12). Both are few in the inner regions of the non-collapsed secondary phloem but their number increases considerably outwards.

Axial secretory canals (lumen diameter 20–35 \( \mu m \)) present throughout the secondary phloem (Fig. 5–7), lined by a single layer of 4–6 epithelial cells, and accompanied by 1–3-seriate axial parenchyma sheaths. The axial sheath parenchyma consists of strands of 5–12 thin-walled cells containing starch grains or, rarely, prismatic crystals; some of these cells have undergone anticlinal divisions. Solitary isodiametric crystals occur in the sheath parenchyma of the collapsed phloem.

Non-dilated phloem rays, mostly 2–4- (up to 5-)seriate, consist mainly of procumbent cells (occasionally with 1 or 2 marginal rows of square or nearly upright cells) (Fig. 7, 13). Phloem ray dilatation is restricted to small parts of the rays (Fig. 4, 5). The cells of dilated rays (Fig. 8) are enlarged by tangential expansion and, to a lesser
Fig. 1. Longitudinal section of stem near the apex: axial secretory canals (arrows). – Fig. 2. Primary structure of stem (TS of a branch c. 1 cm below the apex): epidermis, ring of conducting bundles accompanied by primary bark fibres (PF), numerous axial secretory canals scattered in cortex and pith. – Fig. 3. Young stem after formation of the narrow continuous ring of secondary xylem and secondary phloem (TS of a branch c. 3 cm below the apex): young periderm, conducting bundles of leaf traces in cortex, clusters of the primary bark fibres (PF) outside secondary phloem, radial secretory canal (RC) in medullary ray. – Fig. 4. Mature bark (transverse section): non-collapsed (NC) and collapsed secondary phloem, dilated rays (DR), heavily dilated secondary phloem (DP), periderm (P). — Scale bars = 0.5 mm.
Fig. 5. Alternating tangential bands of different cell composition in non-collapsed and collapsed secondary phloem (TS): zone with conducting elements associated with phloem axial parenchyma or its derivatives (crystalliferous and sclerified (SC) axial parenchyma cells), zone with axial secretory canals accompanied by sheath axial parenchyma, dilated ray (DR). – Fig. 6. Mature bark (LRS): interconnection (arrow) between axial (AC) and radial (RC) secretory canals in secondary phloem – Fig. 7. Secondary phloem in an early stage of dilatation (LTS): network of anastomosing axial secretory canals (AC), homogeneous rays with radial secretory canals, strands of sheath axial parenchyma, strands of crystalliferous axial parenchyma cells (CC). – Fig. 8. Dilated secondary phloem (LTS): dilated rays with radial secretory canals, prismatic crystals in ray cells (arrows). — Scale bars of Fig. 5 = 0.2 mm, of Fig. 6 = 0.3 mm, of Fig. 7 & 8 = 0.5 mm.
Fig. 9–12. Cells derived from phloem axial parenchyma (associated with conducting elements) in collapsed secondary phloem (maceration). – 9: Strand of thin-walled chambered crystaliferous cells. – 10: Thin-walled cells with and without prismatic crystals and sclerified cell forming part of the same strand. – 11: Strand of sclerified cells. – 12: Two fibre-like sclereids. — Fig. 13: Non-collapsed secondary phloem, cambial zone (C), and xylem (LRS): sieve tubes with compound sieve plates (S), axial secretory canals (AC), interconnection of radial secretory canal (RC) from phloem ray to xylem ray, vessel elements with simple perforation plates (P). — Scale bars = 100 µm.
Fig. 14–17. Secretory canals at different developmental stages (TEM): epithelial cells (EC) surround canal lumen (CL). – 14: The formation stage: secretory canal with narrow canal lumen surrounded by moderately vacuolated epithelial cells. – 15: Phase of active secretion: loosening of the epithelial cell wall at the secretory canal lumen. – 16: Senescence phase with strongly vacuolated epithelial cells surrounding a secretory canal lumen filled with osmiophylic substance. – 17: Electron-opaque droplets (OD) between cellulose fibrils of the cell wall (CW) of epithelial cells (EC) and in the canal. — Scale bars of Fig. 14 & 15 = 5 µm, of Fig. 16 = 10 µm, of Fig. 17 = 0.5 µm.
Fig. 18–21. Plastids (PL) with inclusions (PI) in epithelial cell (TEM). – 18: Typical leucoplast of an epithelial cell during an active secretion phase with two adjacent osmiophylic droplets (OD). – 19: Plastid adjacent to plasma membrane, cell wall (CW), invaginations of plasma membrane during the senescence phase of canal development. – 20: Cisternal endoplasmic reticulum (ER) with vacuole-like extensions (arrows) in epithelial cell during active secretion phase. – 21: Strongly vacuolated epithelial cell (EC) with spherical nucleus (N), at senescence stage. — Scale bars of Fig. 18 & 19 = 0.5 µm, of Fig. 20 = 0.2 µm, of Fig. 21 = 2 µm.
degree, by anticlinal divisions (ray width increases during dilatation up to 10-seriate). Radial secretory canals (Fig. 6, 7, 8, 13) present in many rays, lumen diameter 30–40 µm, lined by a single layer of 9–15 epithelial cells. Prismatic crystals common in the dilated ray tissue. Some ray cells in the outer part of the collapsed phloem develop into thick-walled sclereids.

_Pith:_ consists mostly of parenchymatous tissue (Fig. 2); medullary cells thin-walled, similar to the cells of cortical parenchyma in shape and size, with non-lignified walls in young parts of the stem, and with poorly lignified walls in the older parts. Druses and prismatic crystals present in some pith cells. Perimedullar zone marked by 1–5 layers of small (15–30 µm tangentially) axially elongated parenchyma cells with moderately thickened, lignified walls. Axial secretory canals present, 30–50 µm in diameter, lined by a single layer of 6–9 epithelial cells, and surrounded by 1 or 2 layers of parenchyma cells which are somewhat smaller (20–50 µm in diameter) and more elongate than those of the parenchymatous ground tissue (the walls of these cells remain non-lignified in older parts of the stem); canal lumen diameter 30–50 µm. No medullary bundles were observed.

For information on the wood anatomy of _Delarbrea paradoxa_, see Oskolski et al. (1997).

**Distribution of secretory canals**

Secretory canal systems of primary and secondary origin can be distinguished in the stem of _D. paradoxa_. The primary system consists of axial secretory canals of cortex and pith (Fig. 1) which interconnect through radial secretory canals in medullary rays (Fig. 3), and of axial secretory canals associated with vascular bundles. Axial secretory canals in cortex and pith are branched and anastomosed.

The secondary system formed by axial secretory canals of the secondary phloem (there are no axial secretory canals in the secondary xylem) interconnecting with radial secretory canals in phloem and xylem rays (Fig. 13). The axial secretory canals show numerous ramifications and anastomosis, and form a rather dense network in each tangential layer of the sheath parenchyma (Fig. 7, 8). The various networks of the axial secretory canals located in successive sheath parenchyma layers are communicating only through secretory canals in phloem rays (Fig. 6, 13).

No links between canals of the primary and secondary networks were observed; their communication (e.g. through medullary rays that become part of the secondary ray system during their ontogeny), however, cannot be excluded on the basis of our observations.

**Development and ultrastructure of secretory canals**

The formation of the primary secretory canals in the shoot apex can be subdivided into three sequential phases from the shoot apex on down.

1) _Canal formation_

The canal formation was first registered at a distance up to 3 mm from the shoot apex. Young secretory canals (Fig. 14) are small and have electron-transparent polygo-
nal canal lumina; they are surrounded by 4–7 cells of secretory epithelium containing electron-dense cytoplasm with few small or moderately large vacuoles, and relatively large nuclei with a significant amount of uncondensed chromatin. The epithelial cells are equal in size to the meristematic cells of the subapical region (see Fig. 14, 15); the latter, however, adjoin closely one to another and form no intercellular spaces as large as the intercellular canals.

The epithelial cells at the formation stage differ from meristematic cells of the sub-apical region by the presence of peculiar leucoplasts, which appear at the earliest stages of canal differentiation (Fig. 18). These plastids are irregular in shape and devoid of thylakoids, have a dense matrix, and contain one or sometimes two large membrane-coated inclusions of fibrillar structure. The well-developed tubular plastid reticulum contains a dense substance with small electron-opaque droplets. Usually these leucoplasts are accompanied by one or few large osmiophilic globules in the cytoplasm.

The endoplasmatic reticulum is abundantly represented by both cisternal and tubular forms. The tubular reticulum bears solitary or groups of 2–4 ribosomes. The cisternae of the granular reticulum form no extensions. Some leucoplasts are in contact with the granular or smooth reticulum, but the formation of expressively reticular plastid envelopes was not observed. Dictyosomes are not numerous (1 to 3 per cell transection), consisting of 5–7 cisternae usually accompanied by few small vesicles.

The cell wall portions facing the canal lumina differ from those between neighbouring cells in the distribution pattern (density) of cellulose fibrils. The fibrils are packed tightly adjacent to neighbouring cells and in the vicinity of the plasmalemma in the cell wall portion facing the canal lumen. They are more loosely arranged in the outer side of the cell wall facing the lumen, forming solitary fibrillar strands or a loose web. Electron-opaque droplets occur between the fibrils of the web and in the canal (Fig. 17). No plasmalemma invaginations were observed.

2) The active secretion phase

Active resin synthesis and secretion into the newly formed intercellular canals can first be observed at a distance of (2–)3–5(–7) mm from the shoot apex. During this stage the canals commonly fill with osmiophilic materials while the epithelial cells are moderately vacuolised, and contain numerous osmiophilic globules. The number of epithelial cells surrounding the canals increases slightly (5–8); their size remains more or less constant whereas the adjacent axial parenchyma cells undergo considerable enlargement (Fig. 15). The number and structure of the various organelles such as cell nuclei, mitochondria, and leucoplasts remains more or less constant. However, the leucoplasts tend to aggregate into small groups, each accompanied by 2 to 3 mitochondria, and one to few osmiophilic droplets with direct contact. Large diameter osmiophilic droplets also form in the cytoplasm. These droplets are surrounded by a membrane (as evident from the sections transecting the droplet center) and are accompanied by the dispersed tubuli or cisternae of the endoplasmatic reticulum. The granular reticulum cisternae are solitary or stacked into piles of 5 to 8. These cisternae form small vacuole-like extensions (Fig. 20) sometimes containing the osmiophilic droplets. The
number of dictyosomes reaches 3–5 per cell transection, their vesicles are somewhat enlarged in comparison with the earlier phase of canal formation.

The canal lumina are of irregular outline and filled with osmiophilic materials. In the corners formed between neighbouring epithelial cells, fibrillar cell wall material is deposited in a very loose fashion. Between those fibrils some electron-opaque droplets can be observed.

3) The senescence of the secretory canals

The first signs of senescence can be observed at a distance of 5–7 mm from the shoot apex. The intercellular canals have grown considerably in size and possess no electron-dense materials except for occasional large osmiophilic droplets and clusters of fibrillar material (Fig. 16). The surrounding epithelial cells contain several large vacuoles; the nuclei and few organelles have been pushed aside and are now located in a thin layer of electron-transparent cytoplasm along the cell wall facing the canal lumen (Fig. 21). The nuclei are more or less spherical and contain only condensed chromatin. Solitary plastids and a few mitochondria are enclosed in the clear peripheral layer of the cytoplasm. The endoplasmatic reticulum is scarce, dictyosomes occur rarely.

The leucoplasts are circular or somewhat elongate in shape and surrounded by few endoplasmatic reticulum tubuli bearing densely packed fibrillar material (Fig. 19). Each leucoplast contains one large membrane-coated inclusion of fibrillar structure. Some of the leucoplasts are accompanied by large osmiophilic droplets, some also contain starch grains.

The plasmalemma forms numerous invaginations of variable size. The cellulose fibrils are distributed regularly throughout the epithelial cell walls facing the canal lumen.

DISCUSSION

The axial secretory canals in *Delarbrea paradoxa* occur in primary parts of the stem body (primary phloem in vascular bundles, cortex, pith), and in the secondary phloem. Radial canals are formed in both primary (medullary) rays, and in the rays of secondary phloem and secondary xylem. The joint occurrence of secretory canals in both primary and secondary tissues is typical for many Araliaceae (Viguier 1906), and has been reported also for some Anacardiaceae (e.g. *Lannea* (Venkaiah & Shah 1984)), Burseraceae (e.g. *Boswellia* (Nair & Subrahmanyam 1998)), and other families (Metcalfe & Chalk 1950). The three-dimensional structure of the secretory canal network in the stem of *D. paradoxa* resembles that of *Lannea coromandelica* of Anacardiaceae (Venkaiah & Shah 1984). However, in the latter irregular ducts are also located in the phelloderm. Moreover, the primary secretory canals in *D. paradoxa* are associated with the vascular bundles (and, in particular, with clusters of the primary bark fibres), a characteristic feature of Anacardiaceae, Burseraceae, and some other taxa of Araliaceae (Viguier 1906; Metcalfe & Chalk 1950).

The axial secretory canals in the secondary phloem of *D. paradoxa* are surrounded by conspicuous sheaths of starch-containing axial parenchyma, forming strands of many (5–12) cells, some of which become sclerified during the phloem collars. On
the other hand, the axial phloem parenchyma cells associated with the conductive elements are mostly fusiform, free of starch grains, and are transformed into either chambered crystaliferous cells or sclerified fibres, or shorter strands of few (2–7) sclerified cells. Sheath parenchyma and associated secretory canals are arranged in the continuous tangential bands that alternate with the bands formed by conductive elements and axial phloem parenchyma cells. The presence of the sheath parenchyma, clearly distinguished from other types of axial parenchyma by its different distribution, size and number of cells per strand, occurrence of starch, and mode of transformation during phloem collapse, is apparently a characteristic feature for Araliaceae as well as for some species of other families (e.g. Anacardiaceae, Burseraceae, Clusiaceae, Flacourtiaceae) which also possess axial secretory canals in the secondary phloem (Zahur 1959; Roth 1981). As for the banded disposition of the sheath parenchyma in *D. paradoxa*, this feature is rather uncommon within Araliaceae. A similar pattern was reported by Zahur (1959) for *Cheirodendron trigynum* (Gaud.) A. Heller (cited as Ch. gaudichaudii), *Pseudopanax* (‘*Panax arborea’*), three species of *Tetraplasandra*, and also for *Schefflera* (syn.: *Didymopanax*) morototoni (Roth 1981). For the time being, however, the available data on the bark diversity in Araliaceae is too scarce for any comparative or systematic conclusions.

The secretory canal lumina in *D. paradoxa* are formed simultaneously with the differentiation of meristematic cells into secretory ones. Secretory activity as indicated by numerous mitochondria and abundant leucoplastids (Lüttge 1971; Fahn 1979) is already evident in the cells surrounding the smallest canal lumina in the earliest stages of their formation, while the neighbouring meristematic and young parenchyma cells do not contain any leucoplasts. Simultaneous differentiation of secretory cells and formation of the canal lumen or cavity is rather typical for a number of secretory structures, e.g., the leaf glands of Lamiaceae (e.g. *Origanum* (Bosabalidis & Tsekos 1982a), *Leonotis* (Ascensão et al. 1997), *Nepeta* (Kolalite 1998)), or the secretory cavities in fruits of *Citrus* (Bosabalidis & Tsekos 1982b) whose growth is completed by the start of their functional activity. On the other hand, this phenomenon is not common for the secretory canals or ducts whose lumen formation is completed before the secretory activity of epithelial cells starts, e.g., in *Mangifera indica* (Fahn & Joel 1976) and *Semecarpus anacardium* (Bhatt & Mohan Ram 1992) of Anacardiaceae, *Commiphora wightii* (Bhatt 1987) of Burseraceae, *Apium graviolens* (Bosabalidis 1996) of Apiaceae, etc.

Numerous leucoplasts observed in the epithelial cells of *D. paradoxa* (and their complexes with mitochondria and osmiophilic droplets as well) suggest that these cells produce secretions of a terpene nature. The presence of leucoplasts is characteristic for terpene-secreting cells of different secretory structures such as epidermal glands in *Mentha piperita* (Amelunxen 1964; Amelunxen et al. 1969), secretory cavities in *Citrus deliciosa* (Bosabolidis & Tsekos 1982b), and resin canals in *Pinus* (Carde 1976; Cheniclet & Carde 1985; Fahn & Benayoun 1976). The close correlation between the presence of leucoplasts in the secretory cells and of monoterpenes in essential oils was established by Cheniclet and Carde (1985) for 45 species of different families (including two Araliaceae – *Hedera helix* and *Eleutherococcus (= Acanthopanax) sessiliflorum*). Direct evidence of the leucoplasts participating in secretory activity was obtained by...
Gleizes et al. (1982) who observed the monoterpene synthesis in the leucoplast fraction isolated from the terpene-secretory cells of *Citrofortunella mitis*.

An accumulation of osmiophilic substances in the periplasmatic spaces of the epithelial cells was not observed in *D. paradoxa*. Apparently, the material secreted permeates quickly through the cell walls into the canal lumina. The secretion of osmiophilic substances is accompanied by swelling and loosening of the cell walls facing the canal lumina in a similar way as described by Nair et al. (1981) for secretory canals (resin ducts) in Anacardiaceae and Burseraceae, and, moreover, in other secretory structures (e.g. epidermal glands in *Leonotis* of Lamiales (Ascensão et al. 1997)). As Nair et al. (1981) suggest, material of the loosening cell walls is transformed into the polysaccharid component of the secreting substance. However, the presence of polysaccharides in the secretion as well as the tentative role of the cell wall substances in their formation in Araliaceae need to be studied further by histochemical and autoradiographic methods.

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