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Meristematic endodermis and secretory structures in adventitious roots of *Richterago* Kuntze (Mutisieae-Asteraceae)

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ABSTRACT – (Meristematic endodermis and secretory structures in adventitious roots of *Richterago* Kuntze (Mutisieae-Asteraceae)). The meristematic endodermis in adventitious roots of *Richterago* species originates in one of the fundamental meristem cells, which undergo sucessive anticlinal and periclinal divisions to build the inner cortex. The meristematic endodermis or proendodermis remains as a meristematic layer until its differentiation into endodermis, with Casparian strip. When sieve elements differentiate, endodermic secretory canals of esquizogenous origin are present at the region adjacent to primary phloem. Articulated laticifers, with cells perforated at both terminal and transversal walls, also occur during initial phases of secondary development. Presence of inulin as reserve carbohydrate in the inner cortex and vascular tissue may be related to abiotic factors, as an adaptive strategy of these species.

Key words - Asteraceae, laticifers, meristematic endodermis, *Richterago*, secretory canals

RESUMO – (Endoderme meristemática e estruturas secretoras em raízes adventícias de *Richterago* Kuntze (Mutisieae-Asteraceae)). Nas raízes adventícias de espécies de *Richterago*, a endoderme meristemática origina-se a partir de uma das células do meristema fundamental, que irá sofrer sucessivas divisões anticlinais e periclinais para formar o córtex interno, permanecendo como uma camada meristemática até sua diferenciação em endoderme com as estrias de Caspary. Quando os elementos crivados já se encontram diferenciados, canais secretores endodérmicos, de origem esquizógena, podem ser visualizados nas regiões adjacentes ao floema primário. Laticíferos articulados ocorrem na fase inicial do desenvolvimento secundário, cujas células apresentam pontoações nas paredes terminais e transversais. A presença de inulina no córtex interno e no cilindro vascular, como carboidrato de reserva, pode estar relacionada com fatores abióticos, sendo uma estratégia adaptativa das espécies.

Palavras-chave - Asteraceae, canais secretores, endoderme meristemática, laticíferos, *Richterago*

Introduction

The occurrence of a meristematic phase of endodermis in Asteraceae was first demonstrated by Williams (1947). That author demonstrated that the cellular layer, which surrounds the plerome (pericycle), acts as a cambium generating the cortex, which later will differentiate into endodermis. Subsequent to Williams's paper, a considerable amount of work (Hurst 1956 *apud* Van Fleet 1961, Van Fleet 1961, Mueller 1991, Seago Júnior *et al.* 1999, Seago Júnior *et al.* 2000) recognised meristematic endodermis in the root´s of other vascular plants.

From the second half of the 19th century, many authors have studied secretory structures in Asteraceae (Tetley 1925). The intercellular canals and laticifers are features recognized in this family (Col 1899, 1901, 1903, 1904, Tetley 1925, Williams 1947, 1954, Metcalf & Chalk 1950, Esau 1960, Fahn 1974, Heywood 1978, Bremer 1994). In roots, secretory canals may occur in the inner cortex (Col 1899, Triebel 1885, Solereder 1908, Tetley 1925, Williams 1947, 1954, Lersten & Curtis 1986, Luque *et al.* 1997), pericycle (Grotta 1944, Hoehne *et al.* 1952) and phloem (Metcalf & Chalk 1950, Grotta 1944). Nevertheless, no studies so far have focused on root secretory canals species of the tribe Mutisieae.

The genus *Richterago* Kuntze belongs to the tribe Mutisieae and is endemic to Brazil. The present work focuses on morphoanatomic features of its adventitious roots, with emphasis on the occurrence of meristematic endodermis and secretory structures.

Material and methods

Eleven species of *Richterago* were studied: *R. stenophylla* Cabrera, *R. angustifolia* (Gardner) Cabrera,

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R. arenaria (Baker) Roque, *R. radiata* (Vell.) Cabrera, *R. polymorpha* (Less.) Cabrera, *R. conduplicata* Roque, *R. hatschbachii* Zardini, *R. polyphylla* (Baker) Roque, *R. riparia* Roque, *R. amplexifolia* and *R. lanata* Roque, all collected at Serra do Cipó, Santana do Riacho country (Minas Gerais-Brazil). Material is deposited in the herbarium of Universidade de São Paulo, SPF (*Roque et al. 347*, *Roque et al. 352*, *Melo et al. 19*, *Melo & Vitta 4*, *Melo et al. 15*, *Melo & Vitta 10*, *Roque et al. 345*, *Roque et al. 450*, *Roque & Hervêncio 493*, *Melo & Vitta 8* and *Melo et al. 12*).

The primary root apex and adventitious roots were obtained from wild-collected young plants fixed in FGAA (Lersten & Curtis 1988). After dehydration in graded ethanol series, the material was preserved in 70% ethanol and embedded in paraffin (Johansen 1940). The material was double-stained with Astra blue and basic fucsin, following Kraus *et al.* (1998). Dissociation technique with hydrogen peroxide and acetic acid (Franklin 1945) was used to analyze the laticifers.

The following stains were used for histochemical tests: Sudan IV (Sass 1951); 10% ferric chloride (Johansen 1940) and lugol (Berlyn & Mikche 1976), for lipidic substances, phenolic substances and starch, respectively. The technique described by Purvis *et al.* (1964) was utilized to crystallize inulin with 100% ethanol for 48 hours.

Results

The rootcap generated by calyptrogen was observed at the region of subapical meristem in adventitious roots (figures 1-2). Protoderm, ground meristem and procambium originated in the promeristem. Ground meristem generated the proendodermis or meristematic endodermis through longitudinal (tangential) divisions, creating many rows.

On transverse section of the meristematic region, the meristematic endodermis is distinguishable from the pericycle, due to morphoanatomical difference between cells (figures 3-5). A thickening on the contact walls between the meristematic endodermis and the pericycle cells was also observed (figure 6). Meristematic activity of the inner layer of the cortex shows cytoplasmic gradient characterized by the vacuole enlargement in the derivative cells, if compared to cells closer to the meristematic endodermis (figure 3). Over subsequent stages, cells resultanting from the meristematic endodermis will be arranged radially, forming the inner cortex (figures 3, 4).

At this stage, secretory canals are seen at innermost layers of the cortex, originated by an esquizogenous process, and restricted to regions adjacent to the phloem (figure 5). After meristematic activity of the proendodermis, the innermost layer of the cortex will differentiate in endodermis with deposition of Casparian strips in anticlinal walls. In innermost canals, endodermal cells with Casparian strips constitutes two of the four cells underlying the canal. The contents of secretory canals react positively to phenolic substances, carbohydrates and lipids.

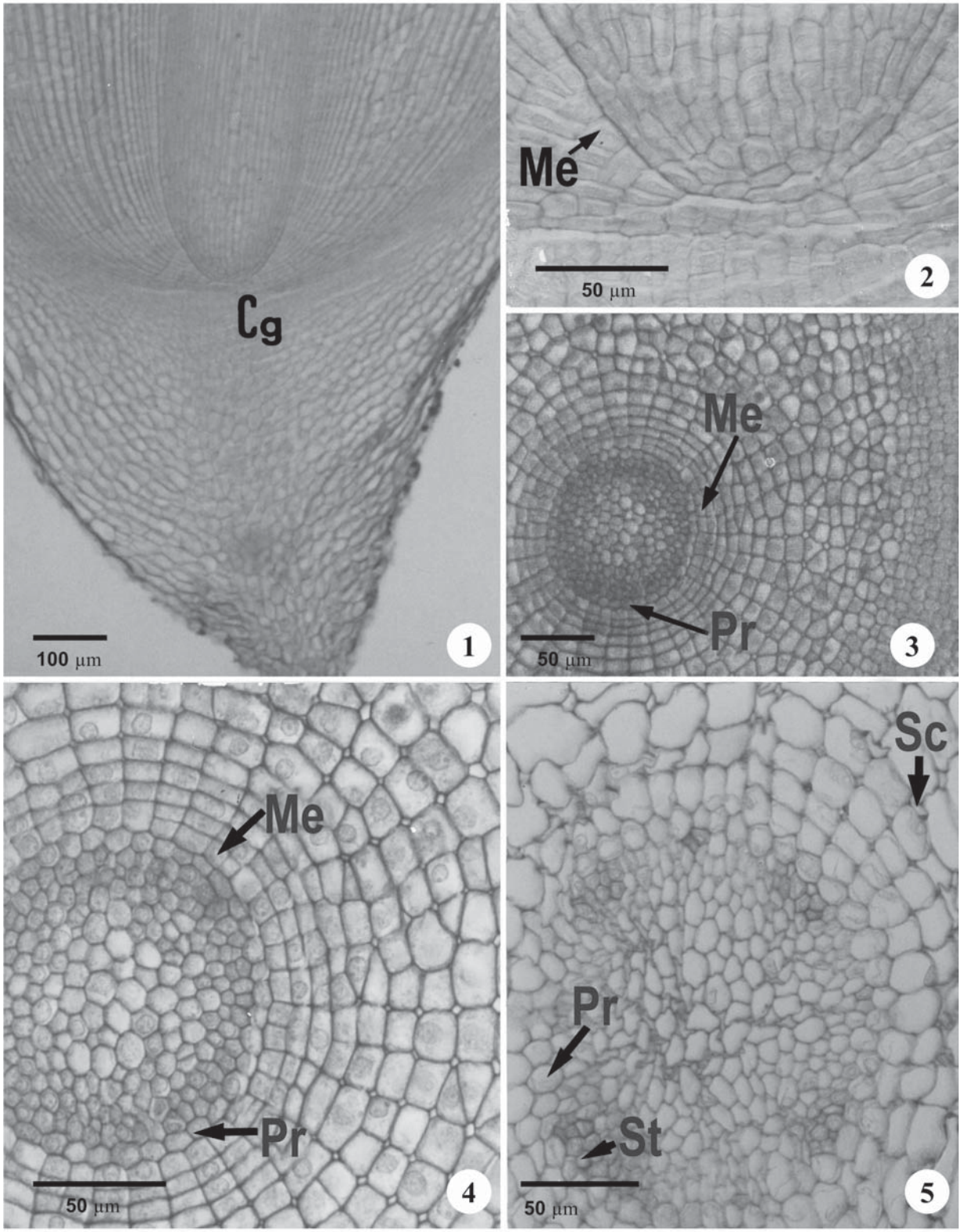
During initial phase of differentiation, sieve tube elements are clearly observed on transverse section (figure 5). At subsequent stages, protoxylem differentiation initiates.

The radial arrangement of the cells generated by meristematic endodermis is shown in figure 4. Intercellular spaces are present closer to the exodermis, forming cavities. In *Richterago arenaria* and *R. stenophylla*, sclereids were present within the entire cortical region (figure 7). At the outer cortical region, cells contaning lipidic droplets were observed (figure 8). The pericycle is located internally to the endodermis and it may be biseriated or triseriated inwardly (figure 9). The radial arrangement of innermost layers of the cortex becomes less evident at advanced stages of the secondary structure (figures 10, 11).

Articulated laticifers at the cortex with perforation fields on transverse and terminal walls were observed (figures 12-14). Inulin content is observed in the inner cortex cells, including endodermis (figure 15), in the pericycle and in xylem cells. Phloem parenchyma cells also contain inulin. Inulin crystals, when analyzed under polarized light, form Malta crosses (figures 16, 17).

Discussion

Williams (1947) discussed the occurrence of a cellular layer which surrounds the tissue he called plerome which later differentiates into endodermis. The author states this layer acts as a cambium, generating every tissue between endodermis and hypodermis in the primary body of the roots. This meristematic phase of the endodermis was called proendodermis by Hurst (1956 *apud* Van Fleet 1961), even though Van Fleet (*l.c.*) and Williams (1947) had previously refered to it as "meristematic endodermis". The term proendodermis has been used by several authors (Mueller 1991, Seago Júnior *et al.* 1999, Seago Jr. & Scholey 1999, Seago Júnior *et al.* 2000), who described it as a layer derived from an initial cell of the ground meristem, located near the procambium and which would differentiate into endodermis. These features have been found in species of *Richterago*, especially the meristematic role of the



Figures 1-5. Region of the sub-apical meristem in adventitious roots of *Richterago arenaria*. 1. Longitudinal section, showing the rootcap generated by the caliptrogen. 2. Detail of the meristematic region showing meristematic endodermis. 3. Transverse section, showing a radial row of cortical cells originated from the meristematic endodermis. 4. Close up of figure 3 showing cells of the meristematic endodermis in division. 5. Transverse section 200 µm proximal to figure 4, showing the secretory canals. (Cg = calyptrogen; Me = meristematic endodermis; Pr = pericycle; St = sieve tube element; Sc = secretory canals).

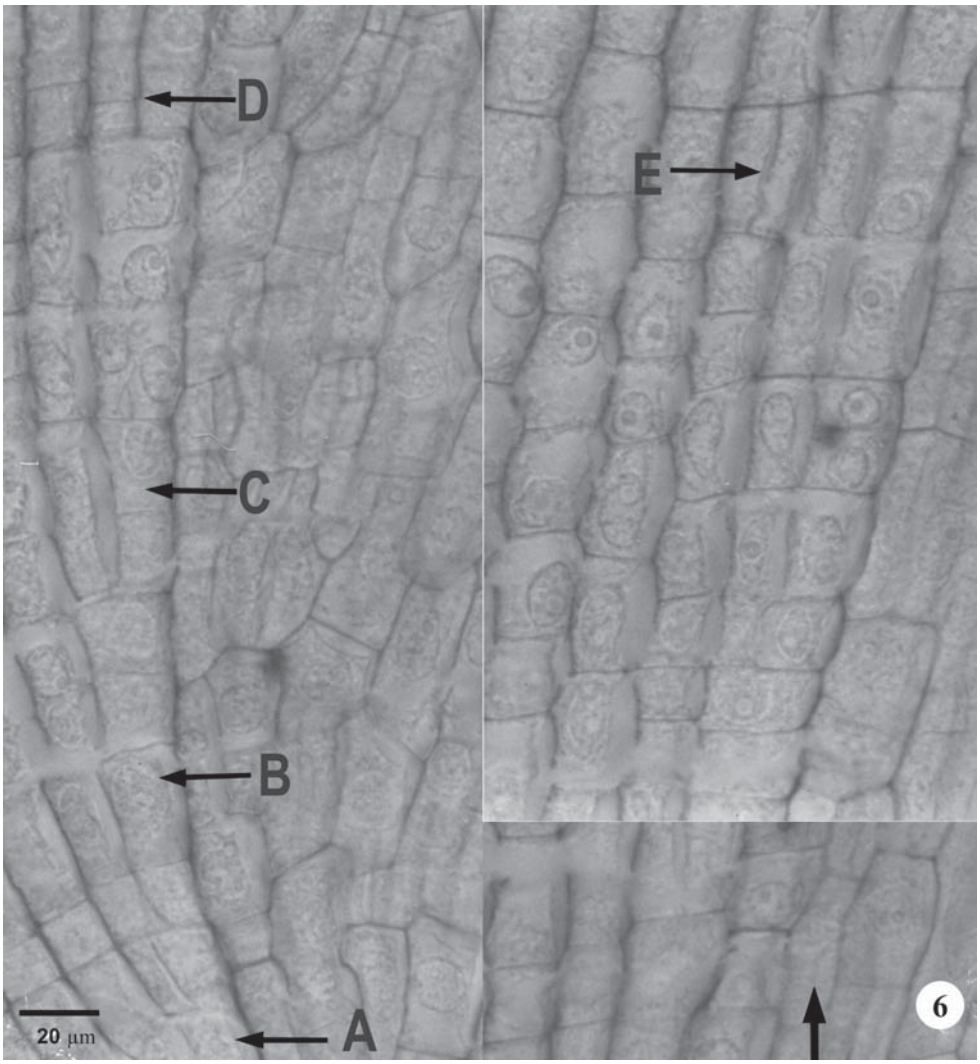


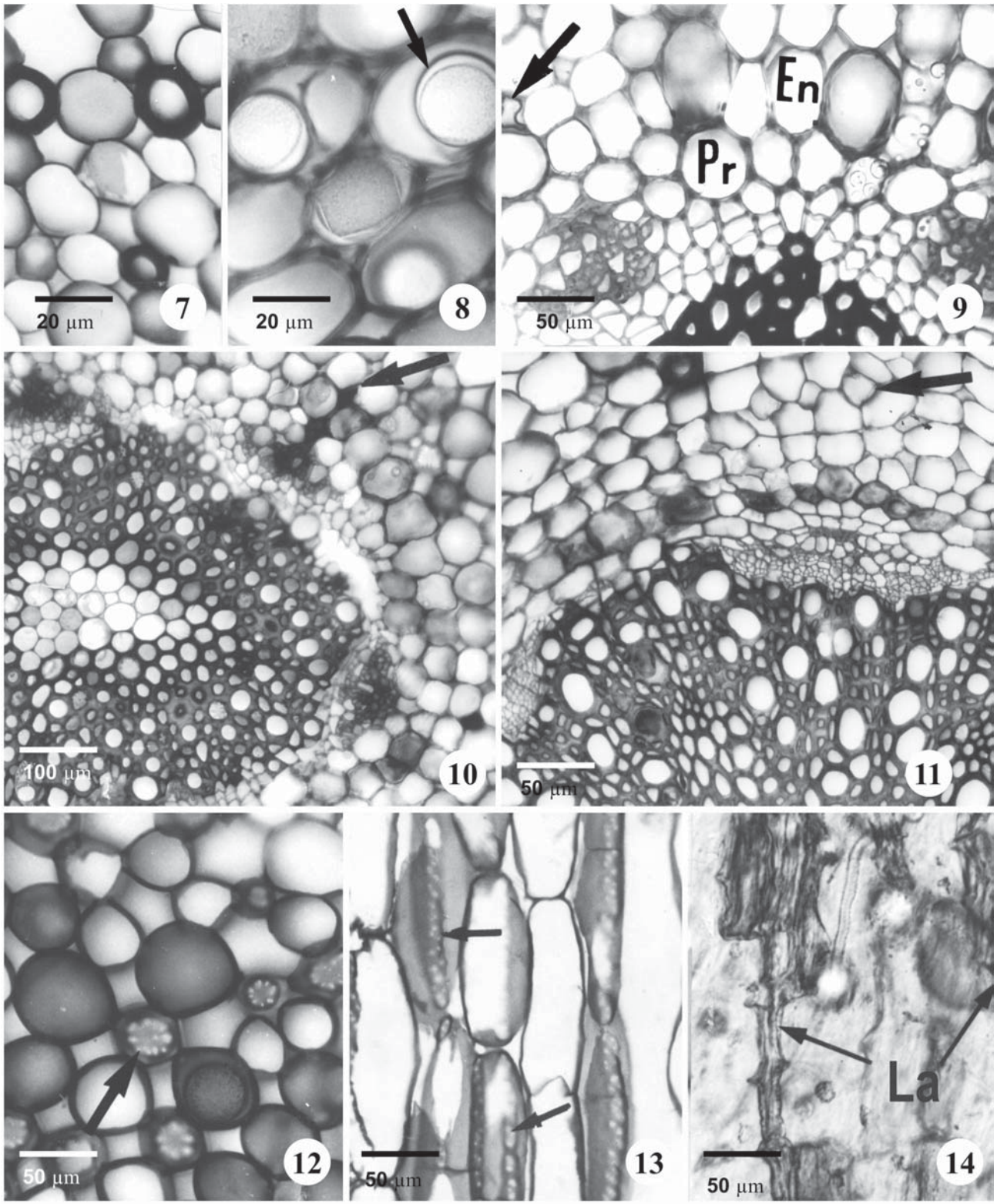
Figure 6. Longitudinal section of the subapical meristem region in adventitious root of *Richterago arenaria*. Arrows A-E, divisions from a single cell of the meristematic endodermis.

inner layer of the cortex, which differentiates into endodermis.

The organization of secretory structures in Asteraceae has been extensively studied by Col (1899, 1901, 1903, 1904). Three types of organization in secretory structures of Asteraceae have been recognized by that author: anastomosed laticifers, secretory canals and isolated cells, which secrete latex. Col also recognized two distinct types of secretory canals: the secretory canal itself, which is always formed near the endodermis, and secretory purses, which are wider and shorter than the canals, and have their cavity surrounded by secretory cells. These purses differ from the canals only in size.

Tetley (1925) described two types of secretory canals: endodermic and non-endodermic. According to him, endodermal secretory canals may be surrounded by four epithelial cells. Nevertheless, in most cases, these cells keep dividing originating 10 epithelial cells, as in the case of *Buphthalmum speciosum* (Tetley 1925). Endodermal secretory canals are present in the region of cells derived from meristematic endodermis in *Richterago* species, but the epithelial cells do not divide and the canal is limited by four cells only.

Papers that demonstrate the endodermis participation in the formation of secretory canals include Solereder (1908), Tetley (1925), Guttemberg (1968) and Luque *et al.* (1997). According to Solereder (*l.c.*), endodermic cells divide forming biseriated region and secretory canals through an esquizogenous process. Guttenberg (1968) describes the ontogeny of secretory



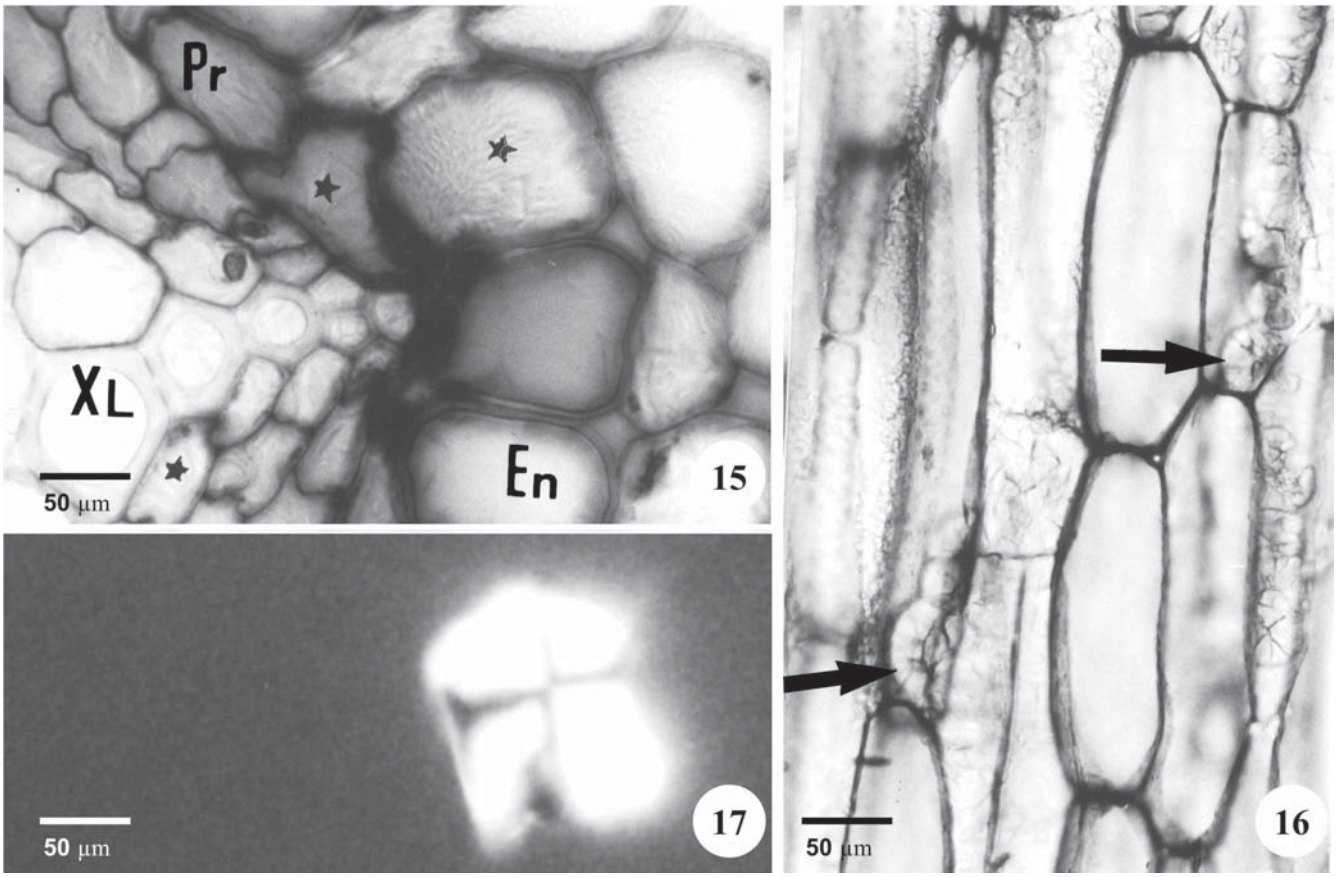
Figures 7-14. 7. Transverse section of *Richterago stenophylla*, showing intercellular spaces and the sclereids. 8. *Richterago riparia*, cortical cells containing lipidic drops (arrow). 9. *Richterago lanata*, endodermal cells making up two of those four cells of the secretory canal (arrow). 10-11. Transverse sections of the roots of *R. polyphylla*, showing endodermic scretory canals (arrows). 12-14. *Richterago lanata*. 12. Transverse section showing articulated laticifers at the cortex (arrow). 13. Longitudinal section of the cortical region, showing laticifer cells with perforation fields on transverse and terminal walls (arrows). 14. Articulated laticifers observed after dissociation technique. (En = endodermis; Pr = pericycle; La = laticifers).

canals in Asteraceae, from one endodermic mother cell, which undergoes divisions forming two cell layers. This fact was confirmed by Luque *et al*. (1997) on *Lychnophora* studied species.

A survey of works on species of the family Asteraceae (table 1) shows that the 42 studied species include good representation of the subfamilies Asteroideae and Cichorioideae, but no records of the subfamily Barnadesioideae. So far, the only reference to secretory canals in Mutisieae are for the genera *Richterago* (present paper) and *Ianthopappus* (Melo-de-Pinna 2000). Secretory canals occur on the inner cortex and phloem, but they may also occur internally to the endodermis, associated with the pericycle, and have been recorded in two species of the tribe Heliantheae (Grotta 1944, Hoehne *et al.* 1952). In *Spilanthes acmella*, Grotta (1944) observed that secretory canals appear in the parenchyma of secondary phloem as the root grows.

Some authors have suggested that secretory canals and primary phloem constitute a morphological unity in which the canals help the sieve tube elements on the conduction of metabolites (Solereder 1908, Guttenberg 1968, Williams 1947, 1954). Secretory canals in the primary phloem have not been observed in *Richterago*.

Tetley (1925) assumed that the contents of the canals come from the phloem, because they are formed when the first sieve elements are already distinguishable. That author also suggests that secretion is generated in the phloem and passes through the radial walls of the cell which subsequently differentiates in endodermis. The three species of *Lychnophora* studied by Luque *et al.* (1997) lack indication that secretory canals were aiding phloem on the conduction of metabolites. Nevertheless, histochemical tests revealed contents of the same nature in endodermal canals and phloem cells. Physiological studies must proceed in association with histochemical and ultrastructural



Figures 15-17. 15. *Richterago hatschbachii*, transverse section showing cortex, pericycle and xylem cells containing inulin (asterisk). 16. *Richterago conduplicata*, longitudinal section showing crystal of inulin (arrows). 17. Crystal of inulin when analyzed under polarized light, forming Malta crosses. (XL = xylem; En = endodermis; Pr = pericycle).

Table 1. Species of the Asteraceae studied listed the tribes and the position of the secretory canals in the roots.

Tribe Species	Position of the secretory canals	References
ANTHEMIDEAE		
Anacyclus spp.	Phloem	Metcalfe & Chalk (1950)
ASTEREAE		
Aster spp.	Inner córtex	Williams (1954)
Solidago spp.	Inner córtex	Williams (1954)
Erigeron spp.	Inner córtex	Williams (1954)
Erigeron canadensis L.	Inner cortex	Williams (1947)
CARDUEAE		
Cirsium spp.	Inner cortex	Williams (1954)
Carlina spp.	Phloem	Metcalfe & Chalk (1950)
Centaurea spp.	Phloem	Metcalfe & Chalk (1950)
Carthamus spp.	Phloem	Metcalfe & Chalk (1950)
EUPATORIEAE		
Eupatorium spp.	Inner cortex	Williams (1954)
Mikania spp.	Inner cortex	Williams (1954)
Eupatorium perfoliatum L.	Inner cortex	Williams (1947)
Eupatorium rugosum Spreng.	Inner cortex	Lersten & Curtis (1986)
HELENIEAE		
Helenium spp.	Inner cortex	Williams (1954)
Helenium spp.	Phloem	Tetley (1925)
Tagetes spp.	Inner cortex	Williams (1954)
Tagetes erecta L.	Inner cortex	Van Tieghem (1870/71, *apud* Guttemberg 1968)
HELIANTHEAE		
Coreopsis spp.	Inner cortex	Williams (1954)
Cosmos spp.	Inner cortex	Williams (1954)
Bidens spp.	Inner cortex	Williams (1954)
Silphium spp.	Inner cortex	Williams (1954)
Helianthus spp.	Inner cortex	Williams (1954)
Verbesina spp.	Inner cortex	Williams (1954)
Xanthium canadensis Mill.	Inner cortex	Williams (1947)
Rudbeckia lacinata L.	Inner cortex	Williams (1947)
Dahlia imperialis Roezl.	Inner córtex	Williams (1947)
Bidens pilosa L.	Inner córtex	Duarte (1997)
Galinsoga parviflora Cav.	Inner córtex	Duarte (1997)
Galinsoga ciliata (Raf.) Blake	Inner cortex	Duarte (1997)
Spilanthes acmella L.	Pericycle and secondary phloem	Grotta (1944)
Calea pinnatifida Banks	Pericycle	Hoehne *et al.* (1952)
Dahlia variabilis Benth. & Hook	Inner cortex	Mager (1932 *apud* Guttemberg 1968)
Dahlia spp.	Phloem	Metcalfe & Chalk (1950)
INULEAE		
Inula spp.	Phloem	Metcalfe & Chalk (1950)
Inula spp.	Phloem	Tetley (1925)
MUTISIEAE		
Richterago radiata (Vell.) Cabrera	Inner cortex	Present paper
Richterago arenaria (Baker) Roque	Inner cortex	Present paper
Richterago polymorpha (Less.) Cabrera	Inner cortex	Present paper
Richterago polyphylla (Baker) Roque	Inner cortex	Present paper
Richterago stenophylla Cabrera	Inner cortex	Present paper

(cont.)

Tribe Species	Position of the secretory canals	References
MUTISIEAE		
Richterago angustifolia (Gardner) Cabrera	Inner cortex	Present paper
Richterago lanata Roque	Inner cortex	Present paper
Richterago conduplicata Roque	Inner cortex	Present paper
Richterago riparia Roque	Inner cortex	Present paper
Richterago hatschbackii Zardini	Inner cortex	Present paper
Richterago amplexyfolia (Gardner) Roque	Inner cortex	Present paper
Ianthopappus corymbosus Roque & D.J.N. Hind	Inner cortex	Melo-de-Pinna (2000)
VERNONIEAE		
Lychnophora candelarium Sch. Bip.	Inner cortex	Luque *et al.* (1997)
Lychnophora cipoensis Semir & Leitão Filho	Inner cortex	Luque *et al.* (1997)
Lychnophora pohlii Sch. Bip.	Inner córtex	Luque *et al.* (1997)
Vernonia spp.	Inner cortex	Williams (1954)
Vernonia praealta Michx. DC.	Inner cortex	Col (1903, 1904)
Elephantopus spp.	Inner cortex	Williams (1954)
SENECIONEAE		
Senecio sibiricus L.	Inner cortex	Triebel (1885)

studies in order to elucidate a possible functional relationship between these canals and the phloem.

According to Solereder (1908), latex-secreting cells may be associated with phloem, endodermis or fibers and, when within the cortex, may be either isolated or in linear series. Datta & Iqbal (1994) suggested that articulated laticifers may be simply interconnected by plasmodesmata; either through perforations on terminal walls or by their complete absorption. For Asteraceae, Vertrees & Mahlberg (1975, 1978) described the presence of articulated laticifers with perforations on terminal walls in *Cichorium intybus*. *Richterago* species have articulated laticifers in linear series not associated with the endodermis. These laticifers have perforations on both terminal and transversal walls, in contrast to the condition described by Vertrees & Mahlberg (1975, 1978).

The carbohydrate reserve detected through histochemical tests in the roots of *Richterago* is only inulin. Starch grains and other polysaccharides have not been detected. Some works have emphasized the occurrence of inulin in species of the family Asteraceae (Figueiredo-Ribeiro *et al.* 1986, Blocklebank & Hendry 1989, Felipe & Dale 1990, Isejima & Figueiredo-Ribeiro 1991, Tertuliano & Figueiredo-Ribeiro 1993). According to Tertuliano & Figueiredo-Ribeiro (1993), in species of Asteraceae, crystals of inulin occur in cells from the parenchyma associated or not with vascular bundles. The authors do not report inulin in species of the tribe Mutisieae, although they have detected its presence in two species of *Gochnatia* (*G. barrosii* and *G. pulchra*).

Inulin is associated with the secondary xylem and, in minor amounts, with the medullary parenchyma of *Viguiera discolor* (Isejima & Figueiredo-Ribeiro 1991). In *Microseris lanceolata* (Incoll *et al.* 1989) and Helianthus tuberosus (Soja *et al.* 1989), inulin is associated with the secondary phloem. The *Richterago* species studied in this work have the same pattern of inulin distribution recorded in species of the tribes Heliantheae and Eupatorieae, *i.e.*, cortical parenchyma, pericycle and axial parenchyma of xylem and phloem.

According to some authors (Blocklebank & Hendry 1989, Felipe & Dale 1990, Isejima & Figueiredo-Ribeiro 1991), fructans have functions other than that of energy source or reserve carbohydrate, and are also related to environmental stress tolerance, especially in savannas, as an adaptive strategy to the dry season. *Richterago* species studied occur in the campos rupestres, where abiotic factors like fire, low water availability in the soil and high temperatures all may affect the metabolism of these plants, and so inulin reserve might represent an adaptive strategy.

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